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ORIGINAL ARTICLE

Diet of auklet chicks in the Aleutian Islands, Alaska: similarity among islands, interspecies overlap, and relationships to ocean climate

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Abstract Seabirds are effective samplers of the marine environment, and can be used to measure resource partitioning among species and sites via food loads destined for chicks. We examined the composition, overlap, and relationships to changing climate and oceanography of 3,216 food loads from Least, Crested, and Whiskered Auklets (*Aethia pusilla*, *A. cristatella*, *A. pygmaea*) breeding in Alaska during 1994–2006. Meals comprised calanoid copepods (*Neocalanus* spp.) and euphausiids (*Thysanoessa* spp.) that reflect secondary marine productivity, with no difference among Buldir, Kiska, and Kasatochi islands across 585 km of the Aleutian Islands. Meals were very similar among species (mean Least–Crested Auklet overlap $C = 0.68$; Least–Whiskered Auklet overlap $C = 0.96$) and among sites, indicating limited partitioning of prey resources for auklets feeding chicks. The biomass of copepods and euphausiids in Least and Crested Auklet food loads was related negatively to the summer (June–July–August) North Pacific Gyre Oscillation, while in Whiskered Auklet food loads, this was negatively related to the winter (December–January–February) Pacific Decadal Oscillation, both of which track basin-wide sea-surface temperature (SST) anomalies. We found a significant quadratic relationship between the biomass of calanoid copepods in Least Auklet food loads at all three study sites and summer (June–July) SST, with maximal copepod biomass between 3–6°C ($r^2 = 0.71$). Outside this temperature range, zooplankton becomes less available to auklets through delayed development. Overall, our results suggest that auklets are able to buffer climate-mediated bottom-up forcing of demographic parameters like productivity, as the composition of chick meals has remained constant over the course of our study.

Keywords *Aethia* · Aleutian Islands · Auklet · Climate · Diet · Overlap

Zusammenfassung Seevögel „beproben" ihre marine Umwelt und können so verwendet werden, um mittels des für die Küken bestimmten Futters die Ressourcenaufteilung zwischen Arten und Orten abzuschätzen. Wir haben die Zusammensetzung, Überlappung und Beziehung zu Veränderungen in Klima und Ozeanographie von 3,216 Futterportionen von in Alaska zwischen 1994 und 2006 brütenden Zwerg-, Schopf- und Bartalken (*Aethia pusilla*, *A. cristatella*, *A. pygmaea*) untersucht. Die Futterportionen enthielten calanoide Ruderfußkrebse (*Neocalanus* spp.) und Leuchtkrebse (*Thysanoessa* spp.), die marine Sekundärproduktion widerspiegeln, und es gab diesbezüglich keine Unterschiede zwischen den Inseln Buldir, Kiska und Kasatochi, die sich innerhalb der Aleuten über 585 km erstrecken. Die Futterportionen waren für die verschiedenen Arten (mittlere Zwergalk-Schopfalk-Überlappung $C = 0.68$; Zwergalk-Bartalk-Überlappung $C = 0.96$) und an den verschiedenen Orten sehr ähnlich, was auf eine begrenzte Aufteilung der Beuteressourcen Küken fütternder Alken

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hindeutet. Die Biomasse von Ruderfuß- und Leuchtkrebsen in den Futterportionen von Zwerg- und Schopfalken stand in negativer Beziehung zur Nordpazifischen Oszillation im Sommer (Juni-August), während sie bei Bartalken in negativer Beziehung zur Pazifischen Dekaden-Oszillation im Winter (Dezember–Februar) stand. Beide Oszillationen beschreiben Anomalien der Oberflächentemperatur des Ozeans (SST) im gesamten Pazifikbecken. Wir fanden eine signifikante quadratische Beziehung zwischen der Biomasse calanoider Ruderfußkrebse in den Futterportionen von Zwergalken und der Sommer-SST (Juni–Juli) in allen drei Untersuchungsgebieten, mit einer maximalen Copepoden-Biomasse zwischen 3–6°C ($r^2 = 0.71$). Außerhalb dieses Temperaturbereichs ist Zooplankton für die Alken schlechter verfügbar, da es sich verzögert entwickelt. Insgesamt deuten unsere Ergebnisse darauf hin, dass Alken in der Lage sind, klimavermitteltes „Bottom-up Forcing" demographischer Parameter wie Produktivität abzupuffern, da die Zusammensetzung der Kükenmahlzeiten in unserer Studie konstant blieb.

Introduction

Seabirds are useful models for investigating dietary resource use and overlap in a community setting. In particular, seabird nestling diets reflect availability, desirability, and perhaps competition for prey in a changing marine environment (Cairns 1987; Piatt et al. 2007). During the breeding season, parents are tied to their breeding sites, as chicks cannot feed themselves for several weeks in most species (Hamer et al. 2002). Forced into becoming central-place foragers, adults must balance their own energetic investment with the need to obtain and deliver food to the chick in environments where food resources are potentially limiting, and where adults may experience bottom-up control (Furness and Birkhead 1984).

Ecologists have long been interested in how multiple similar species coexist in stable communities (Darwin 1859; Wallace 1876), leading to the development of the concepts of "niche" and "niche overlap" (Grinnell 1917; Geisel 1955; Hutchinson 1957; Pianka 1974). The idea that two or more species cannot occupy the same niche in space and time ("competitive exclusion principle;" Gause 1934) has led to innumerable studies of how species accommodate their ecological similarity (Hubbell 2001; Chase and Leibold 2003). This overlap can be reduced by exploiting different resources, or by exploiting the same resources but in different areas or at different times, especially during peak resource demand (Schwemmer et al. 2008). Decreasing competition would be expected to benefit individual survival and reproductive success (Hutchinson 1957), and is therefore central to studies of demography. The coexistence of five small planktivorous auklets (Alcidae, genera *Aethia* and *Ptychoramphus*) in the Aleutian Islands (Jones 1999; all five breeding at Buldir Island, Alaska) thus presents a potential test case for evaluating hypotheses about food resource competition.

Seabirds could act as sentinels of climate change over multiple spatial and temporal scales (Parsons et al. 2008; Durant et al. 2009), a possibility that has led to some studies relating demographic parameters (e.g., breeding success, adult survival) to large-scale multivariate climate indices such as the North Atlantic Oscillation, Pacific Decadal Oscillation, or El Niño Southern Oscillation (e.g., Jones et al. 2002; Sandvik et al. 2005). Some studies invoked a bottom-up control mechanism whereby oceanographic conditions limit prey availability (e.g., Durant et al. 2003; Irons et al. 2008; Mills et al. 2008) or cause a temporal mismatch between consumer requirements and prey availability (e.g., Hipfner 2008; Gaston et al. 2009). Auklet foraging may provide an ideal subject for testing the "sentinel" hypothesis, as foraging by these planktivores would be expected to relate closely to secondary ocean productivity.

In the North Pacific Ocean, changes in climate and oceanography have been well documented (Overland et al. 1999; Hare and Mantua 2000; Biondi et al. 2001). Following a marked change in climate and oceanography in 1976–1977, climatic variability increased (Bond et al. 2003), sea surface temperature (SST) increased, and sea-level pressure decreased (Hare and Mantua 2000; Rodionov et al. 2005). These changes had demographic consequences for several seabird species (e.g., Gjerdrum et al. 2003; Abraham and Sydeman 2004; Jones et al. 2007; Byrd et al. 2008; Bond et al. 2011).

Least (*Aethia pusilla*, mean adult mass 85 g), Crested (*A. cristatella*, 260 g) and Whiskered (*A. pygmaea*, 108 g) auklets are planktivorous alcids endemic to the Bering and Okhotsk seas of the North Pacific. They breed sympatrically in dense colonies on remote islands, are socially monogamous, and share incubation and chick rearing (Byrd and Williams 1993; Jones 1993a, b). Auklets' chick diet consists mainly of calanoid copepods (*Neocalanus* spp.) and euphausiids (*Thysanoessa* spp.), with some amphipods, decapods, and other invertebrates (Day and Byrd 1989; Harrison 1990; Gall et al. 2006). The quality of the chick diet (e.g., the amount of lipid-rich zooplankton; Roby et al. 1986) is related to chick survival in auklets (Gall et al. 2006; Sheffield Guy et al. 2009), and other seabirds (e.g., Durant et al. 2003). The reproductive success of auklets in the Aleutian Islands may be linked to foraging success through climate- and oceanographic-mediated processes (Bond et al. 2011). To explore this possibility further, we quantified auklets' chick diet over the same period as Bond et al. (2011), and investigated the relationship of the auklet chick diet to indices of North Pacific climate and oceanography. Sometimes it is assumed that auklet adult and chick diets are the same, but Crested Auklet adults may feed heavily on cephalopods, which were never fed to chicks (Hunt et al. 1998); our study therefore focuses on food loads captured by adults and destined for their nest-bound chick. Previous work suggested that breeding *Aethia* auklets reduce interspecific competition through dietary differences (e.g., Hunt et al. 1998) or spatial separation (Russell et al. 1999), ideas that have not been tested at multiple colony sites over time.

Our objectives were to: (1) quantify the diets of Least, Crested, and Whiskered Auklet chicks sampled across a 585 km span of the Aleutian Islands from 1994 to 2006; (2) determine diet variation among species, islands, and stage of the breeding season; (3) examine the relationships of diet to key indices of annual oceanographic and climatic variability; and (4) investigate correlations between chick diet and productivity as measured by Bond et al. (2011).

Methods

Study sites and field collection

We performed this study at three colonies: Main Talus, Buldir Island (52°23′N, 175°55′E; 1994–2006, Crested, Least, and Whiskered Auklets); Sirius Point, Kiska Island (52°08′N, 177°36′E; 2001–2006, Crested and Least Auklets); and Tundering Talus, Kasatochi Island (52°11′N, 175°31′W; 1996–2006, Crested and Least Auklets). The auklet colonies at Buldir and Kasatochi consisted of about 10^5 birds, with Crested Auklets predominating, while at Kiska about 10^6 birds were present, mostly Least Auklets (authors' unpublished data). These colonies span 585 km of the Aleutian chain (Fig. 1), and because auklets forage within 50 km of their breeding colony (Hunt and Harrison 1990; Obst et al. 1995; Flint and Golovkin 2002), we assume that there is little spatial overlap of foraging birds from different sites. There was no significant difference in SST around auklet colonies (data not shown; see "Climatic and oceanographic indices" below), so we assumed that auklets from all colonies experienced similar oceanographic conditions in a given year.

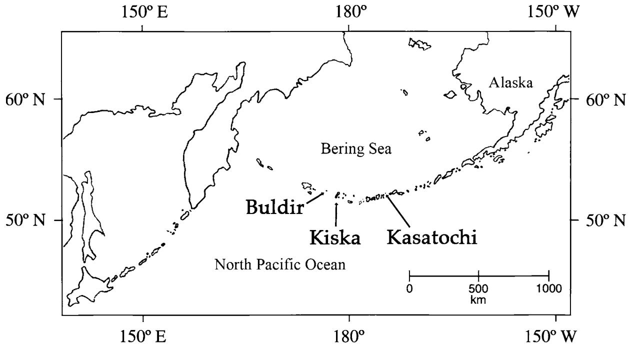

Fig. 1 We studied auklet food loads at Buldir, Kiska, and Kasatochi islands, Aleutian Islands, Alaska, from 1994 to 2006

Adults carry food for the chick in a throat pouch (Portenko 1934), and regurgitate this food when captured in a noose carpet or mist net (Jones et al. 2002, 2004, 2007). We sampled food regurgitated by adults throughout the chick-rearing period (late June–early August) in each year. Each year, we collected food samples in the same 24-h period over two calendar days during early, mid, and late chick rearing on each island, weather permitting. *Early* was defined as roughly when 50% of the chicks had hatched (late June or early July); *mid* was defined as the period when all of the chicks had hatched (mid-July, about 10 days following the first collection period); and *late* was defined as 10 days after the second collection (just before the start of fledging). For a subset of samples where regurgitated food was clearly delineated (e.g., not overlapping with another regurgitated food load, or where portions were regurgitated down rock crevices), we estimated the percentage of food recovered from regurgitated contents to the nearest 5%, and stored samples in 75% ethanol. We identified prey to the lowest taxonomic level possible, and counts of individuals were converted into wet biomass (hereafter "biomass") using our own measurements and published data (Appendix 1 of the Electronic supplementary material, ESM), and we use biomass (or % biomass) throughout. The mass of some food loads was estimated based on the proportion (±5%, as noted above) of each food load collected. To compare food load mass to adult body mass, we used published data on adult body mass from auklets in the Aleutian Islands (Byrd and Williams 1993; Jones 1993a, b).

Prey availability

As a measure of prey availability, we used data from a continuous plankton recorder (CPR) during the period of chick rearing (late June to early August) 2000–2006 between 173°W–173°E and 52–54°N. Data on prey availability were unavailable south of this area, so while some auklets may forage outside the "CPR area," we believe the data are sufficient to capture inter-annual variability in mesozooplankton abundance. The Pacific CPR program of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) provided the data. Nets were towed for 18 km at a depth of <15 m; further details are given in Richardson et al. (2006). Maximum estimated diving depths for all three species are <25 m, and most dives are likely shallower (Haney 1991).

Climatic and oceanographic indices

We used multiple large-scale atmospheric and oceanographic climate indices, as no single index reflects the entire variability of climate or oceanography in the North Pacific Ocean (Bond et al. 2003). The Aleutian Low Pressure Index (ALPI, Beamish and Bouillon 1993; Beamish et al. 1997) is the anomaly from the 1950–1997 mean of the area with pressure ≤100.5 kPa over the area 20–70°N, 120°E–120°W; positive ALPI values indicate a relatively strong Aleutian low-pressure system. ALPI is centered on our study area (approximately 51–53°N, 175°E–175°W). The related North Pacific Index (NPI) is the area-weighted sea-level pressure over the region bounded by 30–65°N and 160°E–140°W (Trenberth and Hurrell 1994). The Pacific Decadal Oscillation (PDO) is a long (20–30 years) oscillation based on the leading principal component of sea-surface temperature (SST) north of 20°N (Mantua et al. 1997). Finally, the North Pacific Gyre Oscillation (NPGO) is the second principal component of sea surface height anomalies measured over the same areas as the PDO, but it also closely matches the second empirical orthogonal function (EOF; a spatial statistic similar to a principal component score) of SST anomalies (Di Lorenzo et al. 2008). Several of these indices have been related to auklet demography in previous studies (Jones et al. 2002, 2007; Bond et al. 2011). These metrics of climate are interrelated, but each is based on slightly different primary components (Trenberth and Hurrell 1994; Bond et al. 2003; Di Lorenzo et al. 2008). We used seasonal averages of three monthly means (e.g., winter: December–January–February, or DJF) for all indices except ALPI, which is an annual value.

For sea-surface temperature (SST), we used the 4 km AVHRR Pathfinder Version 5 dataset (available at http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/available.html). We extracted SST in a 50 km radius around each colony site, which is the likely foraging range of auklets during June and July (Hunt and Harrison 1990; Obst et al. 1995; Thayer et al. 2008; Wolf et al. 2009).

Statistical analyses

All statistical tests were conducted in SPSS 16.0.2 (SPSS Inc., Chicago, IL, USA). For food load mass, we fitted a generalized linear mixed model for each species, using island and food-sampling period (early, middle, or late chick rearing) as predictors of load size for each species, and year as a random factor. We used the estimated marginal means and 95% confidence intervals from the parameter estimates to determine significant pairwise differences; pairs with nonoverlapping confidence limits were considered to differ statistically.

To measure pairwise dietary overlap between species within islands and within species among islands in a given year, we used Horn's (1966) modification of Morisita's index (1959), as recommended by Diamond (1983). This provides an annual index $0 \leq C \leq 1$, where identical diets have $C = 1$ and completely dissimilar diets have $C = 0$.

We used nonparametric correlations (Spearman's ρ) to look for covariance between overlap indices, load composition, prey availability and oceanographic or climatic variables. The same approach was used to examine changes in load composition over time. To control for multiple comparisons, we used the False Discovery Rate and $P < 0.10$ (Benjamini and Hochberg 1995; García 2004; Grosbois et al. 2008). Setting a higher α level is desirable when the sample size (in this case, number of years) is low, as this increases the power to detect a genuine relationship between climate and ecological variables (Lebreton et al. 1992; Field et al. 2004; Grosbois et al. 2008).

After significant diet–climate relationships were identified, we included those climate variables in a series of generalized linear models with a gamma function error structure and identity link, and used the quasi Akaike's information criterion adjusted for small sample sizes and extra-binomial variation ($\mathrm{QAIC_c}$) for model selection. Using only a subset of covariates decreases the number of candidate models, and reduces the risk of multicollinearity (Grosbois et al. 2008). We considered the model with the lowest $\mathrm{QAIC_c}$ value to be the best-fitting model to the data (Burnham and Anderson 2002). We constructed a null model (intercept only) and models that included additive terms and their interactions for sampling periods (early, middle, or late chick rearing), and islands (the global model). Once the best-fitting model was identified, the climate and oceanographic covariates of interest as well as biologically significant interaction terms were added to subsequent models to examine the effect of climate (a procedure similar to modeling recapture rate and then survival rate in mark–recapture studies; Lebreton et al. 1992; Grosbois et al. 2008). Models with $\Delta\mathrm{QAIC_c} > 2$ were considered to have substantially less support, and overall model support was assessed using Akaike weights (denoted w_i, Burnham and Anderson 2002). This was done on both the full dataset and on data from Buldir and Kasatochi islands because the dataset from Kiska Island is briefer (5 years), and because Kiska is anomalous because it has introduced predators that might affect provisioning behavior (Major et al. 2006).

Results

We identified 40 prey taxa categories in Least Auklet food loads ($n = 810$), 29 in Crested Auklet food loads

($n = 1{,}110$), and 32 in Whiskered Auklet food loads ($n = 486$; Appendices 2–4 of the ESM). Food loads were composed mainly of *Neocalanus* copepods and *Thysanoessa* euphausiids (Appendices 2–4 of of the ESM). Fine taxonomic resolution was not possible in all years, so items were grouped for subsequent analysis into higher-level taxa as "*Neocalanus*" or "euphausiids;" other taxa (e.g., amphipods, decapods, *Calanus marshallae*) were not included in analyses because they often comprised <5% biomass in any given year. Notable exceptions were for Least Auklet on Kasatochi in 1997, 1999, and 2006 (18.9, 38.5, and 13.1% decapods, respectively), Crested Auklets on Buldir in 2003 (12.9% *Themisto* amphipods), and on Kasatochi in 2004 (20.5% *Themisto* amphipods; Figs. 2, 3, 4).

After correcting for the false discovery rate, we found no significant annual trends in the proportions of *Neocalanus* or euphausiids in loads of Least, Crested, or Whiskered Auklets (all $P > 0.12$).

Food load mass

Food load masses were estimated for 683 Least, 1,071 Crested, and 316 Whiskered Auklet food loads (64% of the total). Meal size differed significantly among sampling periods (all $P < 0.01$), but not among islands (all $P > 0.32$). The random effect of year explained less than 5% of the variance in all three species. Based on 95% confidence intervals of marginal means, load sizes increased significantly throughout the chick-rearing period for Crested and Least Auklets. In Whiskered Auklets, load size was smaller in the early than in the mid period, and load size in the late period did not differ from that in other periods (Table 1). As

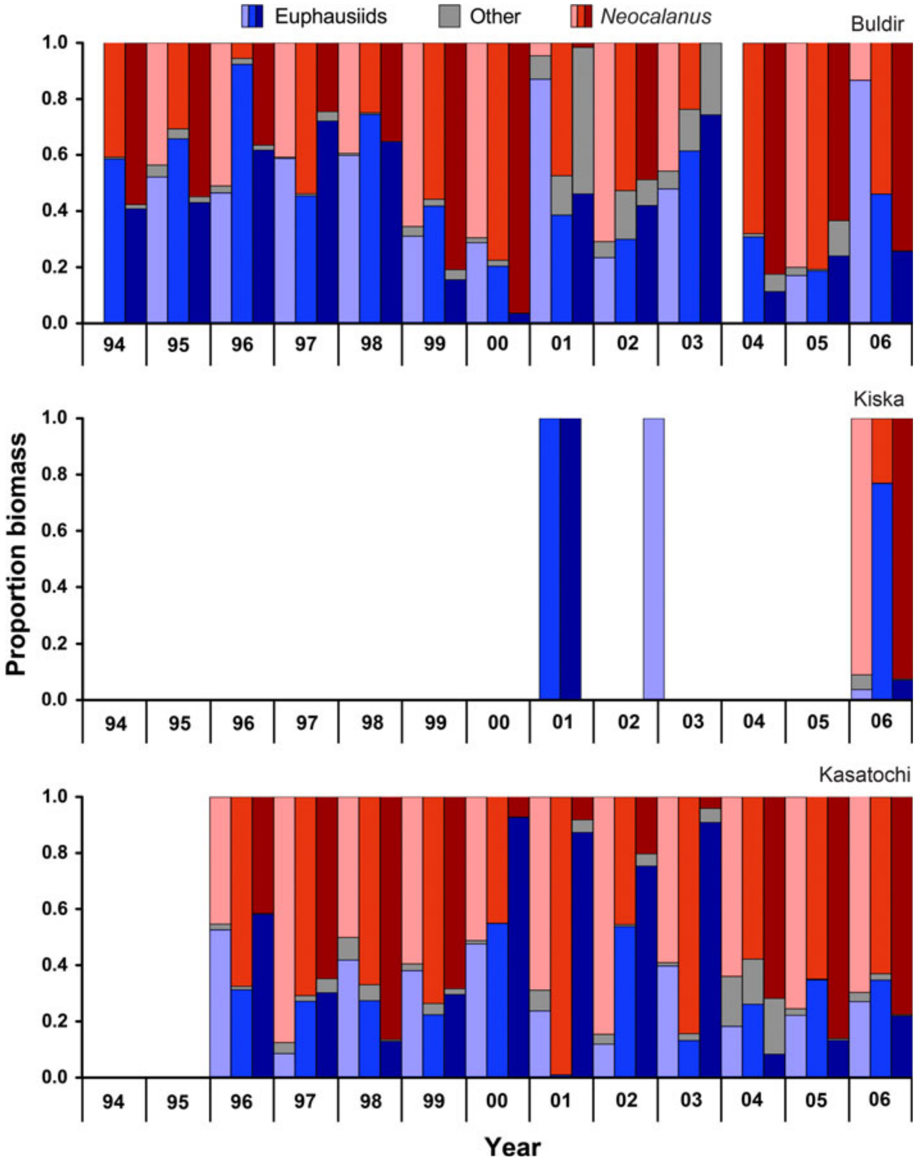

Fig. 2 Crested Auklet chick diet (as inferred from adult food loads) had greater proportions of euphausiids than those of Least or Whiskered Auklets. Data are presented as the proportional biomass of *Neocalanus* copepods, euphausiids, and other prey types. *Color shades* represent samples from early (*light*) mid (*medium*) and late (*dark*) chick rearing. Data are presented for Buldir (*top* 1994–2006), Kiska (*middle* 2001–2006), and Kasatochi (*bottom* 1996–2006)

Fig. 3 Least Auklet chick diet (as inferred from adult food loads) was almost entirely *Neocalanus* copepods. Data are presented as the proportional biomass of *Neocalanus* copepods, euphausiids, and other prey types. *Color shades* represent samples from early (*light*) mid (*medium*) and late (*dark*) chick rearing. Data are presented for Buldir (*top* 1994–2006), Kiska (*middle* 2001–2006), and Kasatochi (*bottom* 1996–2006)

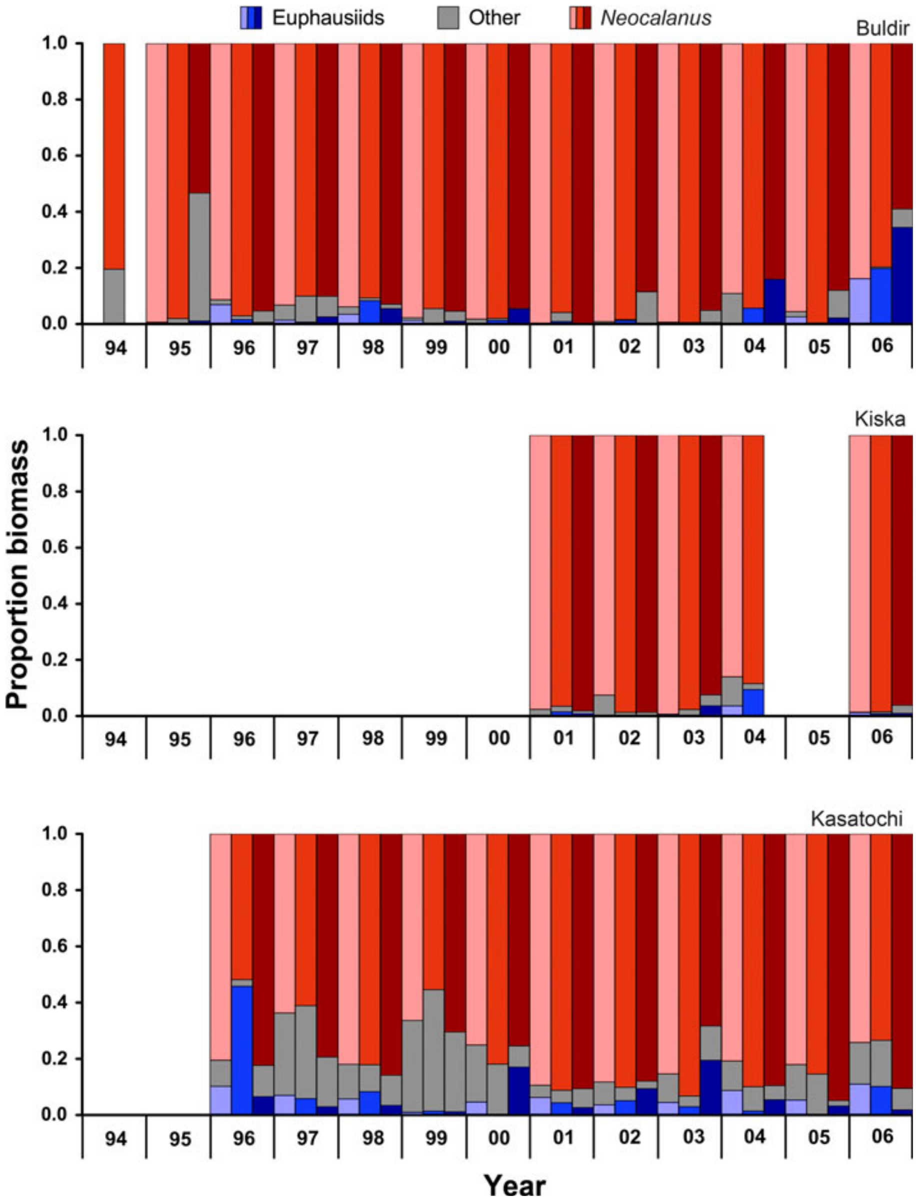

Fig. 4 Whiskered Auklet chick diet (as inferred from adult food loads) at Buldir (1995–2006) was very similar to that of Least Auklets, with large proportions of copepods. Data are presented as the proportional biomass of *Neocalanus* copepods, euphausiids, and other prey types. *Color shades* represent samples from early (*light*) mid (*medium*) and late (*dark*) chick rearing

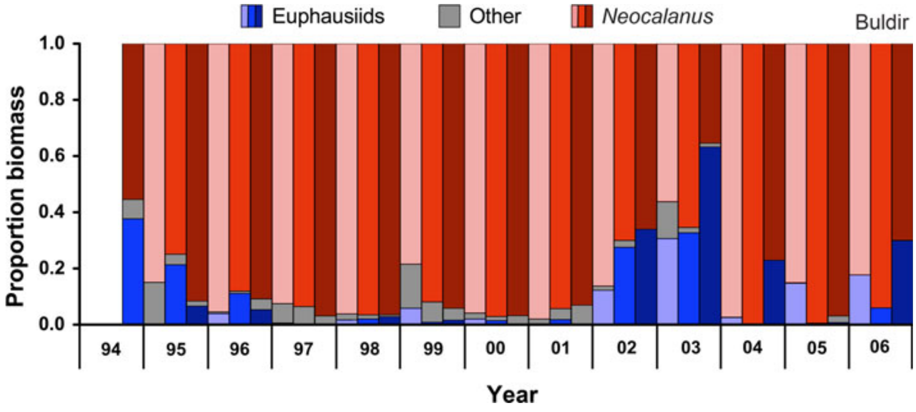

Table 1 The food load masses for Least, Crested, and Whiskered Auklets increases as the breeding season progresses (early, mid, and late) at three breeding sites in the Aleutian Islands, Alaska, in 1994–2006

Species	Early	Mid	Late
Crested Auklet	8.27 ± 0.83 (282)[a]	11.77 ± 0.74 (342)[b]	14.78 ± 0.73 (447)[b]
Least Auklet	2.94 ± 0.24 (234)[a]	4.23 ± 0.24 (249)[b]	5.20 ± 0.24 (200)[b]
Whiskered Auklet	8.02 ± 0.66 (113)[a]	10.90 ± 0.67 (108)[b]	9.29 ± 0.70 (95)[ab]

Samples were pooled among breeding sites and years. Values are estimated marginal means ± SE (*n*) in grams (wet weight). Values sharing the same letter are not significantly different based on overlapping 95% confidence intervals

a percentage of adult body mass, Least Auklet loads averaged 3.5–6.1% (adult mass: 85 g), Crested Auklets chick meals 3.2–5.7% (adult mass: 260 g), and Whiskered Auklet chick meals 7.4–10.1% (adult mass: 118 g).

Dietary overlap and similarity among species and islands

Within-island dietary overlap between species was considerable. At Buldir, overlap was highest between Least and Whiskered Auklets, followed by Crested and Whiskered Auklets, and in many years, overlap between species was >0.90 (Table 2). At Kasatochi, overlap between Least and Crested Auklets was higher than that on Buldir, and it was >0.90 in 5 of 11 years (Table 2). At Kiska, overlap between Least and Crested Auklets was low, but based on only 3 years' data, and small sample sizes (Table 2; Appendix 1 of the ESM). Based on the 95% confidence intervals given above, we conclude that at Buldir there was more dietary overlap between Least and Whiskered Auklets than between other species, and that overlap between Least and Crested Auklets differed among three sites (Kasatochi > Buldir > Kiska). Overlap between Least and Crested Auklets on Buldir was positively correlated with overlap between Least and Whiskered Auklets on Buldir after correcting for the false discovery rate ($P < 0.001$).

We also used the overlap index *C* as a measure of dietary similarity within species among islands. Load composition was consistent among islands for all species. Least Auklets' chick diet was identical on all islands (range of mean *C* for pairwise island comparisons = 0.97–0.99; Table 3). Similarity among Crested Auklet loads was lower than that for Least Auklets, but it was still high (range of mean *C* for pairwise island comparisons = 0.72–0.90). We conclude that the load compositions of Least and Crested Auklets did not differ among islands (Table 3).

Prey availability: CPR data

After correcting for multiple comparisons using the false discovery rate, we found no significant relationships between prey availability (*Neocalanus* stage V biomass, and euphausiid biomass) and oceanographic or climatic indices. We also found no relationship between auklet load composition (proportion of the *Neocalanus* or euphausiid biomass in chick meals) and total zooplankton biomass, *Neocalanus* (stage V copepodite) biomass, or euphausiid biomass in plankton tows during chick rearing in 2000–2006.

Relation to climate/oceanographic indices

After correcting for the false discovery rate, we identified only two significant correlations between load composition and climate indices. The proportion of euphausiids in Least Auklet loads was positively correlated with winter (December-January–February) NPGO on Buldir ($\rho = 0.72$, $P = 0.006$), and with spring (March–April–May) NPI on Kiska ($\rho = 0.98$, $P = 0.005$). Given the paucity of significant monotonic correlations, and the potential for more complex relationships (e.g., parabolic; Gjerdrum et al. 2003), we included all climate and oceanographic variables as covariates in subsequent analyses.

A model that included differences among islands, sampling periods, island × period interaction, and a negative relationship to the summer (June–July–August) NPGO best predicted the biomass of *Neocalanus* in Crested Auklet loads. An identical model, but with a negative relationship to winter NPGO, also received considerable support. The same model (covariation with summer NPGO) best predicted euphausiid biomass in Crested Auklet loads (Table 4). Both *Neocalanus* and euphausiid biomass in Least Auklet loads was best predicted by a model that included differences among islands, periods, period × island interaction, and a negative relationship with summer (June–July–August) PDO (Table 5). A model that included only a negative relationship with winter (DJF) PDO best predicted the biomass of *Neocalanus* and euphausiids in Whiskered Auklet loads on Buldir (Table 6).

Both NPGO and PDO track basin-wide SST anomalies, and as local SST was not among the highly-ranked models, we investigated other possible relationships between food load composition and SST using *Neocalanus* in Least Auklet diet. *Neocalanus* accounted for most biomass in most years, and sample sizes were large on all three

Table 2 The overlap among Least, Crested, and Whiskered Auklet food loads at Buldir, Kiska, and Kasatochi islands in 1994–2006 is variable, but consistently high

Year	Buldir			Kasatochi	Kiska
	Crested–Least	Crested–Whiskered	Least–Whiskered	Crested–Least	Crested–Least
1994	0.697	0.981	0.803		
1995	0.634	0.746	0.985		
1996	0.412	0.460	0.998	0.813	
1997	0.513	0.496	0.999	0.949	
1998	0.499	0.469	0.999	0.952	
1999	0.873	0.897	0.995	0.836	
2000	0.977	0.976	1.000	0.553	
2001	0.324	0.328	0.998	0.822	0.010
2002	0.836	0.971	0.932	0.703	
2003	0.170	0.684	0.765	0.740	0.015
2004	0.993	0.990	0.999	0.927	
2005	0.949	0.962	0.999	0.958	
2006	0.915	0.879	0.995	0.953	0.839
Mean	0.676	0.757	0.959	0.837	0.288
95% CI	0.149	0.132	0.044	0.077	0.540

Values are presented as Horn's (1966) modification of Morisita's (1959) overlap index (C), where $C = 0$ indicates completely dissimilar diets with no overlap, and $C = 1$ indicates identical diets (i.e., complete overlap)

Table 3 The compositions of food loads of Least and Crested Auklets at Buldir, Kiska, and Kasatochi islands in 1994–2006 are very similar

Year	Crested auklet			Least auklet		
	Buldir–Kasatochi	Buldir–Kiska	Kasatochi–Kiska	Buldir–Kasatochi	Buldir–Kiska	Kasatochi–Kiska
1996	0.944			0.959		
1997	0.702			0.929		
1998	0.743			0.992		
1999	1.000			0.877		
2000	0.626			0.969		
2001	0.806	0.815	0.527	0.995	1.000	0.996
2002	0.937			0.995	0.999	0.993
2003	0.785	0.897	0.652	0.988	1.000	0.991
2004	0.968			0.995	0.999	0.997
2005	0.998			0.993		
2006	0.945	0.981	0.990	0.973	0.934	0.964
Mean	0.859	0.898	0.723	0.969	0.986	0.988
95% CI	0.076	0.094	0.271	0.022	0.026	0.012

Values are presented as Horn's (1966) modification of Morisita's (1959) overlap index (C), where $C = 0$ indicates completely dissimilar diets with no overlap, and $C = 1$ indicates identical diets (i.e., complete overlap)

islands. We found a parabolic relationship of *Neocalanus* biomass to local summer SST ($r^2 = 0.25$). Major et al. (2006) hypothesized that introduced Norway rats (*Rattus norvegicus*) could affect the provisioning behaviour of auklets at Kiska; when data from Kiska were excluded, the parabolic relationship of *Neocalanus* biomass to SST increased ($r^2 = 0.71$). Maximal *Neocalanus* biomass occurred when summer (June–July) SST was ~4.5°C, was relatively constant between 3 and 6°C, and declined sharply outside this range (Fig. 5a, b).

Correcting for false discovery rate, the dietary overlap of Least Auklets among all three islands was correlated with winter (DJF) NPGO, and the overlap between Kiska and Kasatochi was related to the NPGO in spring (March–April–May, MAM) and summer (June–July–August, JJA). Within islands, overlap between Least and Crested Auklets was not related to any climate variable at Kiska or Kasatochi. At Buldir, Least and Whiskered Auklet overlap was related to spring (MAM) NPI.

Discussion

Overall, our results confirm previous studies of auklet chick diet (using adult food loads as a proxy) in the Aleutian Islands (Day and Byrd 1989) which indicated that

Table 4 Summary of the model set for predicting the proportion of Crested Auklet chick food load biomass represented by *Neocalanus* copepods and euphausiids at Buldir, Kiska, and Kasatochi, Aleutian Islands, Alaska from 1994 to 2006

	Number of parameters	$QAIC_c$	$\Delta QAIC_c$	w_i
Neocalanus				
I+P+IP+NPGO/JJA	11	2,536.183	0.000	0.57
I+P+IP+NPGO/DJF	11	2,537.723	1.541	0.26
I+P+IP+NPGO/MAM	11	2,540.412	4.230	0.07
I+P+IP+NPI/DJF	11	2,542.858	6.675	0.02
I+P+IP+ALPI	11	2,543.471	7.288	0.01
I+P+IP+SST/JJ	11	2,543.980	7.797	0.01
I+P+IP+NPI/MAM	11	2,544.054	7.871	0.01
I+P+IP+PDO/DJF	11	2,544.230	8.048	0.01
I+P+IP+PDO/MAM	11	2,544.470	8.287	0.01
I+P+IP	10	4,700.352	8.419	0.01
Euphausiids				
I+P+IP+NPGO/JJA	11	2,585.000	0.000	0.58
I+P+IP+NPGO/DJF	11	2,586.570	1.570	0.26
I+P+IP+NPGO/MAM	11	2,589.311	4.311	0.07
I+P+IP+NPI/DJF	11	2,591.804	6.804	0.02
I+P+IP+ALPI	11	2,592.429	7.429	0.01
I+P+IP+SST/JJ	11	2,592.948	7.948	0.01
I+P+IP+NPI/MAM	11	2,593.023	8.023	0.01
I+P+IP+PDO/DJF	11	2,593.203	8.203	0.01
I+P+IP+PDO/MAM	11	2,593.447	8.447	0.01
I+P+IP	10	2,593.602	8.602	0.01

Models are sorted by increasing $QAIC_c$ (quasi Akaike information criterion corrected for small sample size) value, with the most parsimonious model at the top. Akaike weight (w_i) is the likelihood that a given model of the model set is the best approximation of the data. Model parameters: *I* island, *P* sampling period, *ALPI* Aleutian Low Pressure Index, *NPGO* North Pacific Gyre Oscillation (*DJF* December to February; *MAM* March to May), *SST* sea surface temperature. Model corrected for $\hat{c} = 1.846$ (*Neocalanus*) and 1.811 (euphausiids). $\Delta QAIC_c$ is the difference from the top-ranked model. Only the top 10 ranked models are shown

Least and Whiskered Auklets rely heavily on large-bodied oceanic copepods, whereas Crested Auklet adults also deliver a significant amount of euphausiids to their chicks. Unlike studies from St. Paul Island in the Pribilof Islands, and on the continental shelf and shelf break, we found very few *Calanus marshallae* in chick meals of the three species. The amount of *C. marshallae*, a neritic copepod, in chick meals was negatively related to auklet chick survival at colonies on the continental shelf (St. Lawrence Island, Gall et al. 2006). Unlike the larger oceanic copepods *Neocalanus* spp., *C. marshallae* has a lower lipid content, and Least Auklets are thought to seek out *Neocalanus* spp. preferentially over less profitable prey resources (Hunt and Harrison 1990; Hunt 1997; Russell et al. 1999). Oceanic *Neocalanus* spp. copepods (*N. plumchrus*, *N. flemingeri*, and *N. cristatus*) are rich in lipids and wax esters required by auklets (Roby et al. 1986). At St. Lawrence Island, oceanic copepods are advected by the Anadyr Current (Springer et al. 1989), and contribute to higher chick survival (Gall et al. 2006; Sheffield Guy et al. 2009). Such oceanographic fronts concentrate zooplankton, including *Neocalanus* spp. (Hunt and Harrison 1990; Hunt 1997; Russell et al. 1999).

Around St. Lawrence Island, Crested Auklets were often associated with epibenthic advected euphausiid swarms (Russell et al. 1999), and their chicks' diet consisted largely of *Thysanoessa* spp. euphausiids (Bédard 1969; Piatt et al. 1990; Sheffield Guy et al. 2009). In addition to euphausiids, Crested Auklets in the Aleutians appear to also rely heavily on calanoid copepods to provision their chicks in most years (Appendix 2 of the ESM; Day and Byrd 1989), unlike their counterparts in the Bering Sea (Bédard 1969; Hunt et al. 1981; Sheffield Guy et al. 2009). Crested Auklets provisioning chicks exploit large-bodied oceanic copepods when they are available (Searing 1977), in some years delivering meals consisting wholly of these, consistent with the copepods' availability generally being greater in the oceanic domain of the western Aleutian Islands (Hunt 1997).

Much less is known about Whiskered Auklet chicks' diet. Our results agree with previous studies of chick meals

Table 5 Summary of the model set for predicting the proportion of Crested Auklet chick food load biomass represented by *Neocalanus* copepods and euphausiids at Buldir, Kiska, and Kasatochi, Aleutian Islands, Alaska from 1994 to 2006

	Number of parameters	AIC_c	ΔAIC_c	w_i
Neocalanus				
I+P+IP+PDO/JJA	11	1,805.820	0.000	1.00
I+P+IP+NPI/DJF	11	1,817.946	12.126	0.00
I+P+IP+NPGO/DJF	11	1,819.558	13.738	0.00
I+P+IP+NPGO/MAM	11	1,820.426	14.606	0.00
I+P+IP+PDO/MAM	11	1,822.822	17.002	0.00
I+P+IP	10	1,822.864	16.989	0.00
I+P+IP+NPI/MAM	11	1,824.606	18.786	0.00
I+P+IP+ALPI	11	1,824.862	19.042	0.00
P	4	1,829.568	23.467	0.00
I	4	1,856.368	50.267	0.00
Euphausiids				
I+P+IP+PDO/JJA	11	1,805.820	0.000	1.00
I+P+IP+NPI/DJF	11	1,817.946	12.126	0.00
I+P+IP+NPGO/DJF	11	1,819.558	13.738	0.00
I+P+IP+NPGO/MAM	11	1,820.426	14.606	0.00
I+P+IP+PDO/MAM	11	1,822.822	17.002	0.00
I+P+IP	10	1,822.864	16.989	0.00
I+P+IP+NPI/MAM	11	1,824.606	18.786	0.00
I+P+IP+ALPI	11	1,824.862	19.042	0.00
P	4	1,829.568	23.467	0.00
I	4	1,856.368	50.267	0.00

Abbreviations are identical to those in Table 4. Models are not corrected because $\hat{c} = 1.0$. Only the top 10 ranked models are shown

Table 6 Summary of the model set for predicting the proportion of Whiskered Auklet chick food load biomass represented by *Neocalanus* copepods and euphausiids at Buldir, Kiska, and Kasatochi, Aleutian Islands, Alaska from 1994 to 2006

	Number of parameters	$QAIC_c$	$\Delta QAIC_c$	w_i
Neocalanus				
PDO/DJF	2	1,127.850	0.000	0.98
PDO/JJA	2	1,136.976	9.126	0.01
NPGO/DJF	2	1,139.201	11.351	0.00
PDO/MAM	2	1,139.438	11.589	0.00
NPI/MAM	2	1,140.505	12.655	0.00
NPGO/JJA	2	1,141.627	13.778	0.00
NPI/DJF	2	1,142.397	14.548	0.00
SST/JJ	2	1,142.469	14.619	0.00
NPGO/MAM	2	1,142.880	15.030	0.00
NPI/JJA	2	1,142.923	15.074	0.00
Euphausiids				
P+PDO/DJF	5	1,133.402	0.000	0.98
P+PDO/JJA	5	1,143.130	9.728	0.01
P+NPGO/DJF	5	1,144.466	11.064	0.00
P+PDO/MAM	5	1,145.647	12.245	0.00
P+NPI/MAM	5	1,146.756	13.354	0.00
P+NPGO/JJA	5	1,147.303	13.900	0.00
P+NPGO/MAM	5	1,148.358	14.956	0.00
P+NPI/DJF	5	1,148.435	15.032	0.00
Intercept only	2	1,148.683	15.281	0.00
P+SST/JJ	5	1,148.759	15.357	0.00

Abbreviations are identical to those in Table 4. Model corrected for $\hat{c} = 1.673$ (*Neocalanus*) and 1.668 (euphausiids). Only the top 10 ranked models are shown

on Buldir (Day and Byrd 1989; Hunter et al. 2002), but contrast with studies of adult stomach contents in the eastern Aleutians, where euphausiids dominated the diet (Troy and Bradstreet 1991), pointing to differences in the provisioning behavior of adults depending on whether they are self-feeding or providing meals to chicks, or perhaps geography.

Dietary overlap and similarity among species

In the northern Bering Sea and eastern Aleutians, previous work has suggested that distributional differences among species are related to dietary differences (Hunt et al. 1998; Russell et al. 1999). We found considerable dietary overlap between species and among years that could be the result of two non-exclusive hypotheses: adult auklets acquire similar prey from different locations, or, because *Neocalanus* copepods are so abundant (Mackas et al. 1998), competition for them is insignificant. Different species of auklet may also exploit prey patches at different depths (Haney 1991); further study of individual diving depths is required.

Chick diet of auklets in the Aleutian Islands exhibits high interspecific overlap compared with other seabirds. Assuming significant overlap when $C \geq 0.6$ (Catry et al. 2009), we found that nearly 80% of all C-estimates were significant. Dietary overlap among Aleutian auklets was similar to that in other subarctic and temperate seabird communities (Pearson 1968; Baltz and Morejohn 1977; Barrett et al. 1997; González-Solís et al. 1997; Minich 2007), and generally higher than that in tropical communities (Ashmole and Ashmole 1967; Diamond 1983; Catry et al. 2009). Overlap among auklets was also higher than among seabirds at the more diverse subantarctic Crozet Island (Ridoux 1994). While this high degree of overlap is noteworthy, it agrees with the prediction that overlap is greater in temperate and subpolar communities, where small numbers of exploited prey taxa are very abundant (Diamond 1983). Dietary overlap was greater in the Aleutians than among auklets breeding at St. Matthew Island in the northern Bering Sea, where overlap between

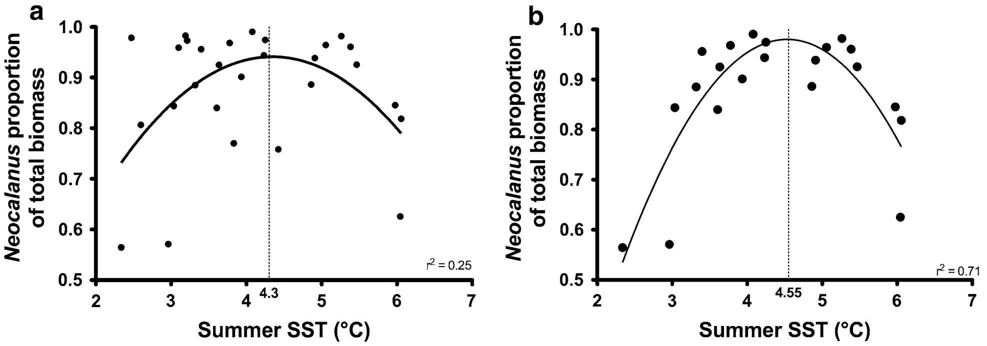

Fig. 5 The proportion of *Neocalanus* copepods in Least Auklet food loads was related quadratically to summer SST around all three breeding colonies (**a** $r^2 = 0.25$), and at Buldir and Kasatochi only (**b** $r^2 = 0.71$)

Least and Crested Auklets of $C = 0.52$ was at the lower end of the values we recorded (Harrison 1990).

To our knowledge, ours is the first study of dietary overlap over a large range of years, and we have shown that there is considerable variation from year to year and among sites, highlighting the need for long-term investigations to elucidate the ecological relationships among closely-related members of the same foraging guild in the context of coexistence. Dietary overlap at multiple sites has received little attention. We found that Least Auklet chick diets across the Aleutian Islands were nearly identical in all years and exhibited high overlaps between islands. These trends, combined with lack of interannual differences in the proportion of *Neocalanus* or euphausiids in the chick diet, suggest that auklets were able to locate suitable prey for their chicks in most conditions. The overlap was less between islands for Crested Auklets, but it was significant, further supporting the interpretation that chick diet is similar among all three sites. Previous research at Kiska quantified the near failure of Least Auklet breeding in 2001 and 2002, with productivity in those years being far lower than those recorded at any Least Auklet colony in any year anywhere in Alaska (Major et al. 2006; Bond et al. 2011). Most breeding sites failed during the chick rearing stage, with rat activity and nutritional stress being explanatory hypotheses. Our results here are relevant to this issue because we found no difference in Least Auklet chick diet ($C = 0.99$) between Buldir (where auklets had high productivity; Bond et al. 2011) and Kiska. Food load composition did not correlate with breeding failure at Kiska; nor was it aberrant in any way in the years of failure. This adds to the evidence that introduced Norway rats were responsible for auklet breeding failure in 2001 and 2002 at Kiska.

Food load mass

Food load mass varied across sampling periods within the breeding season in all three species. In Least and Crested Auklets (and to a certain extent in Whiskered Auklets), food load mass increased as the breeding season progressed, paralleling the increased energy demands of the chicks. Food load mass in the Least Auklet was smaller in our study than the load size recorded on the Pribilof Islands (5.28 g, Roby and Brink 1986, cf. Table 1). If energy requirements of Least Auklet chicks are the same in the Pribilof and Aleutian islands, then adults in the latter location must deliver food to the chicks more frequently (Roby and Brink 1986; Roby 1991). To our knowledge, there are no data from Crested or Whiskered Auklets to make similar comparisons. The Dovekie (*Alle alle*), which is similar to auklets ecologically, adapts to changes in zooplankton abundance by increasing the rate of food load deliveries to chicks (Jakubas et al. 2007).

Load size was larger relative to adult body mass in the Whiskered Auklet than in Least or Crested Auklets. Whiskered Auklet parents provision their chicks only once or twice per night (Konyukhov et al. 2000), much less than the other species (Roby and Brink 1986; Fraser et al. 2002). Whiskered Auklets forage in tide rips closer to shore than other auklet species (Byrd and Williams 1993), which may allow them to carry a heavier load over a shorter distance. In addition, because most provisioning of chicks is nocturnal, adults may be under pressure to deliver larger loads to meet their chicks' energy and growth demands (Ydenberg 1989; Hunter et al. 2002).

Relationship of food loads to prey availability, and indices of ocean climate

We found no relationship between prey availability, as assessed by CPR data from near breeding colonies, and food load composition. Auklets generally forage in areas of oceanic fronts and upwelling zones, which have high concentrations of zooplankton (Kinder et al. 1983; Hunt et al. 1998; Russell et al. 1999); CPR data are averaged over an entire tow, and would not indicate the presence of upwelling areas. The biomass of *Neocalanus* spp. copepods in CPR tows was also unrelated to indices of climate or oceanography. CPR data were not available further south, in areas completely surrounding our three study colonies, and auklets may have foraged outside this region, which may partially explain why we found no relationship between prey abundance and abundance in food loads in a given year.

The summer North Pacific Gyre Oscillation (NPGO) predicted food load composition of Crested Auklets, with a higher NPGO value corresponding to a decrease in the biomass of *Neocalanus* copepods and euphausiids. Least Auklet food load composition was related to the summer Pacific Decadal Oscillation (PDO), where a higher PDO value corresponded with a smaller biomass of both *Neocalanus* copepods and euphausiids. The NPGO is an index of sea-surface height and temperature anomalies over 110–180°W and 25–62°N (Di Lorenzo et al. 2008), and tends to explain more of the SST anomaly than the PDO (Bond et al. 2003). Our examination of the relationship between local summer SST and *Neocalanus* biomass in Least Auklet food loads showed a parabolic relationship, with copepod biomass peaking between 3 and 6°C and declining significantly outside this range. Such a parabolic relationship is found when an optimum exists, such as the relationship between Tufted Puffin (*Fratercula cirrhata*) breeding success and summer SST (Gjerdrum et al. 2003). *Neocalanus* copepods require cooler temperatures to develop (ideally less than 10°C; Ikeda et al. 1990), but when temperatures are cooler than 3°C, development may be delayed significantly as the copepods take longer to acquire the necessary lipids to grow and moult (Batten et al. 2003).

Interestingly, we found a decrease in *Neocalanus* copepods in Least Auklet chick meals at temperatures above 6°C. Such temperatures should be favorable for copepod growth and development (Ikeda et al. 1990; Batten et al. 2003), meaning that copepod abundance would likely remain high. Warmer temperatures correspond with an earlier start of the peak abundance of *Neocalanus*, and a difference of 4°C in SST between southern and northern sampling stations along the west coast of North American is reflected in a difference of 3–4 weeks in the timing of the *Neocalanus* bloom (Batten et al. 2003). Despite this, the variation in local SST measured around auklet breeding islands in June and July each year remained within the thermal limits of *Neocalanus* development (<10°C; Ikeda et al. 1990).

Implications of climate-influenced diet on demography

Many studies of relationships between climate and oceanographic indices and demographic parameters in seabirds suggest bottom-up control mechanisms, although seldom are these tested explicitly (e.g., Durant et al. 2004; Votier et al. 2005; Bond et al. 2011). In the Aleutian Islands, both adult survival and reproductive success are related to large-scale climate indices (Bond et al. 2011; authors' unpubl. data). A more detailed analysis of the relationship between auklet demography and diet is warranted, but the similarity in food load composition from year to year suggests that other factors (e.g., direct predation, density dependence, competition, changes in adult behavior) are regulating auklet populations in the Aleutian Islands.

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