

THE INFLUENCE OF DIET AND OCEAN CONDITIONS ON PRODUCTIVITY OF AUKLETS ON ST LAWRENCE ISLAND, ALASKA

LISA M. SHEFFIELD GUY^{1,2}, DANIEL D. ROBY¹, ADRIAN E. GALL^{1,3}, DAVID B. IRONS⁴ & IAN C. ROSE¹

¹USGS–Oregon Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, 97331, USA
(Sheffield.Lisa@gmail.com)

²Current address: 11539 Corliss Avenue N, Seattle, Washington, 98133, USA

³Current address: ABR, Inc., PO Box 80410, Fairbanks, Alaska, 99708, USA

⁴Migratory Bird Management, US Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska, 99503, USA

Received 2 October 2008, accepted 30 September 2009

SUMMARY

SHEFFIELD GUY, L.M., ROBY, D.D., GALL, A.E., IRONS, D.B. & ROSE, I.C. 2009. The influence of diet and ocean conditions on productivity of auklets on St. Lawrence Island, Alaska. *Marine Ornithology* 37: 227–236.

A warming trend since the early 1990s is changing the Bering Sea ecosystem, causing increased sea surface temperatures and reduced sea ice cover. Models suggest that these changes may alter the availability of prey to a diverse array of upper trophic level consumers, including seabirds. To better understand how seabird productivity would be affected by potential changes in prey availability and ocean conditions in the Bering Sea, we studied the two most abundant species of planktivorous seabirds in the region, Least Auklets *Aethia pusilla* and Crested Auklets *A. cristatella* nesting on St Lawrence Island. We investigated the relationships between chick survival, taxonomic composition of chick diets, timing of sea ice retreat, winter sea ice cover, and flow through the Bering Strait during 2000–2004. Interannual variation in diet explained the largest percentage of variation in chick survival. Our results are consistent with the hypothesis that Least Auklet chick survival is negatively related to consumption of the small neritic copepod *Calanus marshallae* and positively related to consumption of the oceanic copepod *Neocalanus flemingeri/plumchrus*. In Crested Auklets, diets rich in larger species of zooplankton (i.e. *N. cristatus* copepods and *Thysanoessa* euphausiids) were associated with higher chick survival. Timing of sea ice retreat, winter sea ice cover, and flow through the Bering Strait were weaker predictors of chick survival in both species of auklets than were the effects of diet, but the effects of these variables were in the predicted directions (i.e. higher chick survival associated with earlier sea ice retreat, greater winter sea ice cover and greater flow through the Bering Strait). Auklet diet composition could be developed as an indicator of foraging conditions available to these abundant planktivores.

Key words: Least Auklet, *Aethia pusilla*, Crested Auklet, *Aethia cristatella*, chick provisioning, nest survival, Bering Sea, Alaska, St Lawrence Island, Anadyr Current, *Calanus*, *Neocalanus*, *Thysanoessa*

INTRODUCTION

Recent evidence suggests that the Bering Sea is experiencing a warming trend that may be changing this highly productive marine ecosystem (Overland & Stabeno 2004, Grebmeier *et al.* 2006). The northward flowing Anadyr Current transports nutrient-rich water from the deep basin in northwestern Bering Sea far onto the northern Bering Sea shelf (Coachman *et al.* 1975). This transport creates productive shelf waters in the area north of St Lawrence Island and south of the Bering Strait known as the Chirikov Basin (Springer *et al.* 1987, Springer *et al.* 1989, Piatt & Springer 2003). Productivity in the Bering Shelf region is declining, however, placing seabirds and other apex predators in the Bering Sea, including Native subsistence communities, at risk (Grebmeier *et al.* 2006).

Least *Aethia pusilla* and Crested *A. cristatella* auklets are abundant planktivorous seabirds that aggregate in dense mixed colonies on St Lawrence Island to take advantage of the highly productive waters of the Anadyr Strait to the west and the Chirikov Basin to the north. Least Auklets weigh c. 85 g and feed primarily on calanoid copepods; the larger Crested Auklets weigh c. 260 g and

feed primarily on euphausiids (Bédard 1969, Hunt *et al.* 1990, Piatt *et al.* 1990, Gall *et al.* 2006).

The response of seabirds to variation in climate and ocean conditions can be monitored through studies of diet, productivity and populations, making those birds potentially valuable indicators of change in marine food webs (Cairns 1987, Ainley & Divoky 2001, Abraham & Sydeman 2004). Assuming that the taxonomic composition of the diet of these auklets reflects the relative abundance of prey types and overall prey abundance in foraging areas, then diet studies of Least and Crested auklets on St Lawrence Island may provide an efficient and relatively inexpensive means to monitor zooplankton standing stocks and their advection in the northern Bering Sea, where ship-based studies of zooplankton are costly and infrequent.

Variation in transport and stratification of the Anadyr Current, which flows northward to the west of St Lawrence Island, may be one of the most important factors affecting the reproductive success of planktivorous auklets nesting on the island (Russell *et al.* 1999). The Anadyr Current is composed of nutrient-rich slope and

basin waters, and varies in strength both annually and seasonally, reaching its greatest velocity during July [approximately 1.3 Sv (Roach *et al.* 1995)]. Consequently, primary production on the northern Bering Sea shelf during summer months varies with the strength of northward flow associated with the Anadyr Current (Springer *et al.* 1989). The current also transports large, lipid-rich *Neocalanus* copepods typical of deeper basin waters to the Chirikov Basin, where they are a preferred prey of Least Auklets (Springer & Roseneau 1985; Springer *et al.* 1987, 1989; Hunt *et al.* 1990; Obst *et al.* 1995). When the Anadyr Current is weaker, planktivorous seabirds presumably rely more on zooplankton associated with northern Bering Shelf waters, such as the euphausiid *Thysanoessa raschii*, the small copepod *Calanus marshallae* and the large amphipod *Themisto libellula* (Coyle *et al.* 1996, Russell *et al.* 1999). When preferred *Neocalanus* copepods are not available within foraging distance of the breeding colony, nesting auklets must switch to less profitable prey types.

A three-year study by Gall *et al.* (2006) found that prevalence of the large oceanic copepod *Neocalanus cristatus* in chick diets of both Least and Crested auklets on St Lawrence Island explained much of the among-year variation in chick survival. Additionally, chick survival was lowest in a year when Least Auklets consumed more of the small neritic copepod *C. marshallae* and Crested Auklets consumed more of the mid-sized copepod *N. flemingeri*. Further investigation is needed to understand how auklet chick survival is affected by prey species composition and also by abiotic factors such as sea ice conditions and strength of the Anadyr Current.

Our objective was to understand how interannual variation in chick survival during the nestling period and in diet composition of Least and Crested auklets are related to ocean conditions in the northern Bering Sea. We investigated diet composition and reproductive success of Least and Crested auklets nesting on St Lawrence Island, Alaska, during the 2003 and 2004 breeding seasons. We also combined chick survival from our study with a comparable data set from 2000–2002 (Gall *et al.* 2006) to

- determine the relationships of interannual variation in chick survival of Least and Crested auklets breeding in the northern Bering Sea with diet composition, timing of sea ice retreat, winter sea ice cover, and flow through the Bering Strait, and
- test the predictions of Gall *et al.* (2006) that Least and Crested auklets will experience higher rates of chick survival in years when *N. cristatus* is more prevalent in chick diets and lower rates of chick survival when *C. marshallae* is prevalent in Least Auklet diets and *N. flemingeri*/*plumchrus* is prevalent in Crested Auklet diets.

MATERIALS AND METHODS

Study area

St Lawrence Island, Alaska (c. 63°30'N, 170°30'W) is located in the northern Bering Sea (Fig. 1). Auklets nest in talus slopes along the western and north-central coasts. Our research was conducted on the north-central coast of St Lawrence Island, east of the village of Savoonga, from 16 June to 5 September 2003 and from 17 June to 4 September 2004. The two auklet colonies studied, Kitnik and Myaughee, are approximately three kilometers and 10 km east of Savoonga respectively.

Auklet diet composition

Auklet chick meals were collected at both the Kitnik and Myaughee colonies. Chick meals, which are transported by adults in a throat pouch that is separate from the digestive tract, were collected away from productivity plots to minimize disturbance of auklets whose reproductive success was being monitored. Adult auklets carrying chick meals were captured using noose-mats placed on large display rocks. Chick meals were collected in separate plastic Whirl-Pak bags (Nasco, Fort Atkinson, WI, U.S.A.) by placing the auklet's head in the opening and stroking the gular region gently to encourage ejection of the contents of the throat pouch. Chick meals were also collected from rock surfaces beneath noose-mats if the adult ejected contents of the throat pouch outside the bag.

Contents of chick meal bags were transferred immediately to glass vials in the field and preserved in 70% isopropyl alcohol. Whole and partial meals were both used for identification of prey taxa and calculation of the taxonomic composition of diets. Sorting of zooplankton prey to the lowest taxonomic level possible was conducted in the lab by K.R. Turco (Alaska's Spirit Speaks: Sound and Science, Fairbanks, AK). Zooplankton identifications were verified by K. Coyle (Institute of Marine Science, University of Alaska, Fairbanks, AK).

Zooplankton were grouped into six prey types (Tables 1 and 2; Gall *et al.* 2006):

- Euphausiids, primarily *T. raschii* (30.5–97.9 mg ww)
- The mid-sized copepod *N. flemingeri* [c. 3.8 mg ww (may also include the very similar *N. plumchrus*; *N. flemingeri* and *N. plumchrus* were not separated in this study and are jointly referred to as *N. flemingeri*)]
- The large copepod *N. cristatus* (c. 17.6 mg ww)
- The small copepod *C. marshallae* (c. 1.8 mg ww)
- Hyperiid amphipods, primarily *Them. libellula* (32.3–167.0 mg ww)
- "Other prey types," a group that included less common prey types such as larval shrimp and pteropods

Biomass estimates for each taxon in each chick meal were based on the number of individuals of each prey taxon in the sample and the average mass of that prey type based on fresh samples collected in the Bering Sea as part of a separate study (K. Coyle unpubl. data).

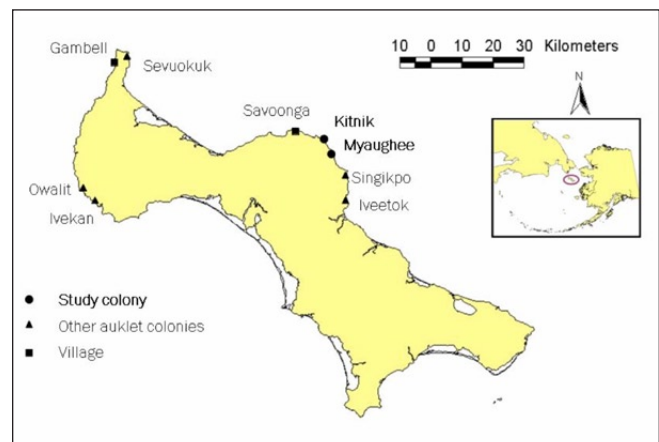


Fig. 1. Map of St Lawrence Island, Alaska, showing the location of the Kitnik and Myaughee study colonies (Gall *et al.* 2006).

The average mass of each prey type encountered in auklet diet samples follows that of Table 1 in Gall *et al.* (2006).

We described auklet diet composition by calculating aggregate percent biomass (APB) to give equal weight to each sampled chick meal (Swanson *et al.* 1974, Gall *et al.* 2006). A single meal was used as a sampling unit for diet analysis. ANOVAs with Tukey–Kramer procedures for multiple comparisons of means were used to determine if the composition of prey fed to chicks of each auklet species differed between years. Diet composition data were logit transformed to normalize the distribution of proportions.

Reproductive success

Reproductive success of Least and Crested auklets was measured at both the Kitnik and Myaughee colonies during 2003 and 2004. Active nests were located and marked during the mid-incubation

period. Contents were checked at four-day intervals at the Kitnik colony and eight-day intervals at the Myaughee colony, following the methods of Williams *et al.* (2000) and Gall *et al.* (2006).

Egg and chick survival of Least and Crested auklets in 2003 and 2004 were estimated using nest survival models in program MARK (White & Burnham 1999, Dinsmore *et al.* 2002, Jehle *et al.* 2004). We estimated daily survival rate (DSR) separately for eggs and chicks, following the methods of Gall *et al.* (2006), because egg survival was often unknown until the egg failed to hatch and because we could infer relationships between chick diets and reproductive success only during the chick-rearing period. Egg survival was modeled as a function of Year and breeding Site following the methods of Gall *et al.* (2006).

We modeled chick survival as a function of Year, Site, and a temporal variable (Stage) for stage of the chick-rearing period

TABLE 1
Taxonomic composition (% biomass) of meals delivered to Least Auklet *Aethia pusilla* chicks on St Lawrence Island, Alaska^a

Prey type	2000 ^b	2001 ^b	2002 ^b	2003	2004
Samples (n)	77	71	45	70	58
Amphipods ^c	28.5 (±5.9)	4.5 (±2.7)	1.9 (±1.6)	4.7 (±2.8)	4.6 (±3.9)
Euphausiids ^d	1.5 (±1.8)	13.3 (±5.2)	5.9 (±4.3)	29.0 (±8.8)	16.4 (±7.5)
<i>Neocalanus cristatus</i>	9.8 (±4.1)	7.9 (±2.6)	21.3 (±9.1)	2.5 (±2.1)	18.1 (±6.7)
<i>Neocalanus flemingeri</i> ^e	41.0 (±5.5)	37.6 (±6.9)	61.8 (±8.9)	52.8 (±8.2)	56.1 (±8.9)
<i>Calanus marshallae</i>	4.5 (±2.8)	20.1 (±6.1)	0.0 (±0.0)	5.1 (±1.8)	0.9 (±1.3)
Other prey types ^f	14.7 (±3.8)	16.7 (±5.3)	8.8 (±3.4)	5.9 (±3.3)	4.0 (±2.5)

^a Values in parentheses indicate the 95% confidence limits.

^b Data from years 2000–2002 are from Gall *et al.* (2006).

^c Primarily *Themisto libellula*, with some *Parathemisto pacifica*.

^d Primarily *Thysanoessa raschii*, with some *Euphausia pacifica* in 2003.

^e May also include *N. plumchrus*.

^f Includes *Diastylis bidentata*, *Calliopius laevisculus*, *Anisogammarus pugetensis*, *Icherocerus* spp., *Pontogeneza* spp., *Erichthonius hunteri*, pandalid shrimp, crangonid megalopa, brachyuran zoea, pagurid crab, crangonid crab, larval fish and pteropods.

TABLE 2
Taxonomic composition (% biomass) of meals delivered to Crested Auklet *Aethia cristatella* chicks on St Lawrence Island, Alaska^a

Prey type	2000 ^b	2001 ^b	2002 ^b	2003	2004
Samples (n)	29	42	44	37	42
Amphipods ^c	9.9 (±8.7)	16.2 (±8.6)	7.2 (±6.0)	5.6 (±7.6)	0.4 (±0.5)
Euphausiids ^d	73.5 (±11.9)	59.5 (±11.9)	59.4 (±12.0)	88.3 (±9.7)	51.4 (±15.0)
<i>Neocalanus cristatus</i>	7.0 (±2.7)	8.2 (±4.5)	26.3 (±9.4)	2.9 (±3.6)	39.3 (±14.2)
<i>Neocalanus flemingeri</i> ^e	8.6 (±4.6)	16.0 (±7.0)	4.7 (±3.8)	0.4 (±0.5)	2.2 (±1.3)
<i>Calanus marshallae</i>	0.2 (±0.2)	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	0.1 (±0.2)
Other prey types ^f	0.7 (±1.3)	0.2 (±0.2)	2.4 (±1.9)	2.9 (±5.5)	6.6 (±7.2)

^a Values in parentheses indicate the 95% confidence limits.

^b Values from years 2000–2002 are from Gall *et al.* (2006).

^c Primarily *Themisto libellula*.

^d Primarily *Thysanoessa raschii*.

^e May also include *N. plumchrus*.

^f Includes *Diastylis bidentata*, *Calliopius laevisculus*, *Anisogammarus pugetensis*, pandalid shrimp, *Theragra chalcogramma* and unknown larval fish.

(Gall *et al.* 2006). The chick-rearing stage was divided into early (days 1–10 post-hatch), and late (days 11–25 and days 11–26 post-hatch for Least and Crested auklets respectively) because most chick mortality probably occurs during the first 10 days post hatching (Fraser *et al.* 2002) when chicks are most vulnerable if left unattended.

We fit a total of seven models to estimate chick survival for each species. We considered models that included Year and Site individually and the additive effects of Year and Site. We included effects of Stage of the chick-rearing period in an additive model with Year and Site, and in a global model with effects of Year, Site, and a Year*Site interaction. Additionally, we considered an intercept-only (Constant) model in which a single daily nest survival rate was estimated across the two breeding sites, both years, and both stages to determine if our *a priori* candidate models explained important variation in chick survival (Shaffer 2004, Gall *et al.* 2006). We used Akaike's Information Criterion corrected for small sample size (AIC_c) to determine the best approximating model or models from the set of candidate models (Burnham & Anderson 2002) in program MARK. Only models within 2 AIC_c units of the top model were considered well-supported by the data for drawing inference (Burnham & Anderson 2002). Model-averaged estimates based on AIC_c model weights for chick survival were reported to account for model selection uncertainty (Burnham & Anderson 2002). Inference about the relative importance of explanatory variables was based on the strength of evidence provided by

- the sum of Akaike weights for each variable,

- model-averaged estimates of parameter effect, and
- associated confidence intervals (Burnham & Anderson 2002).

Relationships between chick survival, diet composition, and conditions in the Bering Sea

To explore the relationships between chick survival, diet composition, timing of sea ice retreat, winter sea ice cover, and flow through the Bering Strait, we combined the data sets from 2000–2002 (Tables 1 and 2 in Gall *et al.* 2006; Appendix 1) with our data from 2003–2004. We considered a total of 31 models each for Least and Crested auklets to examine the questions of interest. First, we included all models from the 99% confidence interval set reported in Gall *et al.* (2006) to test the predictions that variation in chick survival can be explained by proportions of *N. cristatus* and *C. marshallae* in Least Auklet chick diets and by proportions of *N. cristatus* and *N. flemingeri* in Crested Auklet chick diets.

In addition to covariates for the prevalence of *N. cristatus*, *C. marshallae* and *N. flemingeri* in diets, we included two other covariates to account for the possibility of prey switching between the two primary prey items for both auklet species. Least Auklets are highly associated with the Anadyr front, where oceanic copepods are more abundant (Russell *et al.* 1999), and so we included a variable ($2^{Neocalanus}$) for the combined prevalence of *N. cristatus* and *N. flemingeri*. We expected that the combined proportions of these two oceanic copepods would have a positive effect on chick survival. Crested Auklets are not as strongly associated with the

TABLE 3
Nesting chronology and reproductive success of Least *Aethia pusilla* and Crested *A. cristatella* Auklets at two breeding colonies on St Lawrence Island, Alaska, during 2003 and 2004^a

Parameter	2003		2004	
	Kitnik	Myaughee	Kitnik	Myaughee
Least Auklets				
Nests (n)	69	41	70	53
Median hatch date	27 July	27 July	23 July	26 July
Egg survival	0.857 (0.749 to 0.911)	0.803 (0.634 to 0.887)	0.913 (0.793 to 0.946)	0.857 (0.709 to 0.927)
Chick survival	0.847 (0.779 to 0.920)	0.860 (0.784 to 0.944)	0.855 (0.788 to 0.926)	0.852 (0.782 to 0.928)
Nest survival	0.726	0.691	0.781	0.730
Crested Auklets				
Nests (n)	65	58	65	64
Median hatch date	27 July	27 July	1 Aug	3 Aug
Egg survival	0.863 (0.751 to 0.909)	0.798 (0.678 to 0.841)	0.866 (0.757 to 0.910)	0.726 (0.642 to 0.760)
Chick survival	0.930 (0.883 to 0.979)	0.934 (0.887 to 0.984)	0.916 (0.862 to 0.973)	0.919 (0.865 to 0.977)
Nest survival	0.803	0.745	0.793	0.667

^a Egg and chick survival rates estimated using nest survival models in program MARK; numbers in parentheses are 95% confidence intervals.

Anadyr front; they depend more upon euphausiids for food (Russell *et al.* 1999). We therefore included a variable (Euph&Cris) for the two most prevalent prey types in Crested Auklet diets, euphausiids and *N. cristatus*. We expected the combined proportions of these two primary prey types to have a positive effect on chick survival. Effects of year and diet on chick survival were highly correlated for Least and Crested auklets and were not included together in our models (Gall *et al.* 2006).

Finally, we considered three abiotic covariates to examine the influence of ocean conditions on chick survival. We included the maximum extent of sea ice cover during the previous winter and the date of sea ice retreat, because the extent and timing of sea ice has been associated with both timing and magnitude of primary production (Hunt *et al.* 2002). The extent of sea ice (Cover) is an index derived from six sources of ice-related variables (NOAA 2006). The ice retreat index (Retreat) represents the number of days with at least 10% ice cover after March 15 and is measured at Mooring 2 (56.8°N, 164°W) in the southeast Bering Sea (NOAA 2006). No indices of ice retreat were available for the northern Bering Sea. We also included a continuous variable for Flow through the Bering Strait during August, when the majority of auklet diet samples were collected, to determine if auklet chick survival was affected by strength of currents passing by St Lawrence Island. We expected that greater flow through the Bering Strait would advect more oceanic copepods to auklet foraging areas near St Lawrence Island and have a positive association with chick survival. Northward flow was measured at a mooring in the Bering Strait from January 2000 through August 2004 (data provided by R. Woodgate, University of Washington). This variable was used as a proxy for flow rate through the Anadyr Strait (R. Woodgate pers. comm.). Effects of abiotic factors and Year were modeled separately to evaluate the

relative ability of Year and ocean conditions to explain variation in chick survival. All estimates of coefficients and confidence intervals are presented on a logit scale.

RESULTS

Diet composition

Chick meals were collected from Least and Crested auklets at both the Kitnik and Myaughee breeding colonies during 2003 and 2004. There were no differences in APB of prey types delivered at the Kitnik and Myaughee colonies by either Least or Crested auklets ($P > 0.05$ for each prey type, for both species and in either year), with one exception: In 2004, Least Auklets delivered more *N. flemingeri* at the Myaughee colony (63.5%) than at the Kitnik colony (46.6%, $F_{1,54} = 4.55$, $P = 0.04$). Nevertheless, we combined diet composition data from the two colonies for analysis because

- the between-colony difference was for only one prey type out of six and in only one year of the study, and
- no significant differences in diet composition between the two colonies were detected by Gall (2004) during 2000–2002.

During both years of our study, Least Auklets provisioned their chicks primarily with *Neocalanus* copepods; Crested Auklets provisioned their young mostly with euphausiids (primarily *T. raschii*—Tables 1 and 2). There were differences between years, however, in the proportions of the primary prey types for each auklet species.

Least Auklets fed their chicks significantly more euphausiids and less of the copepod *N. cristatus* in 2003 than in 2004 ($F_{1,126} = 5.93$, $P = 0.016$; Table 1). Least Auklets also fed their chicks significantly more *C. marshallae* in 2003 than in 2004 ($F_{1,126} = 60.12$, $P < 0.001$), but this relatively small neritic copepod was a minor part of the diet in both years. There were no significant differences between years in the APB of amphipods ($F_{1,126} = 0.004$, $P = 0.95$), the copepod *N. flemingeri* ($F_{1,126} = 3.14$, $P = 0.08$), or “other prey types” ($F_{1,126} = 0.05$, $P = 0.82$) fed to Least Auklet chicks. Amphipods (primarily *Them. libellula*) were a minor component of Least Auklet diets during both years. *N. cristatus* was the prey type in Least Auklet diets that differed most in APB between years (2.5% vs. 18.1%). *N. flemingeri* was the most prevalent prey type in both years, constituting 52.8% and 56.1% of the diet in 2003 and 2004 respectively (Table 1).

Crested Auklets fed their chicks significantly more euphausiids ($F_{1,77} = 19.20$, $P < 0.001$) and less *N. cristatus* ($F_{1,77} = 21.61$, $P < 0.001$) in 2003 than in 2004, differences that were also observed in Least Auklet diets. There was also significantly more *N. flemingeri* in the diet of Crested Auklet chicks in 2004 than in 2003 ($F_{1,77} = 25.40$, $P < 0.001$; Table 2), but this prey type was a minor component of Crested Auklet diets in both years. We found no significant between-year differences in the APB of *C. marshallae* ($F_{1,77} = 0.43$, $P = 0.52$), amphipods ($F_{1,77} = 1.50$, $P = 0.22$) or “other prey types” ($F_{1,77} = 1.02$, $P = 0.32$) for Crested Auklet diets. Euphausiids were the most prevalent prey type in Crested Auklet diets in both years, constituting 88.3% and 51.4% of the diet in 2003 and 2004 respectively. As in Least Auklet diets, *N. cristatus* was the prey type that differed most in APB between years, constituting 2.9% and 39.3% of Crested Auklet diets in 2003 and 2004 respectively (Table 2).

TABLE 4

Strength of evidence for effects on chick survival of parameters in competing models ($\Delta AIC_c \leq 2$) for Least *Aethia pusilla* and Crested *A. cristatella* Auklets during 2000–2004 on St Lawrence Island, Alaska

Parameter	Sum of Akaike weights	Model-averaged estimate	95% CI
Least Auklets			
<i>N. flemingeri</i>	0.21	6.37	(1.74 to 11.00)
<i>C. marshallae</i>	0.24	−6.96	(−11.73 to −2.20)
Site	0.89	0.59	(−2.00 to 3.17)
Retreat	0.45	−0.07	(−0.26 to 0.12)
Flow	0.45	0.08	(−0.10 to 0.26)
Cover	0.11	0.05	(−1.77 to 1.86)
Crested Auklets			
<i>N. flemingeri</i>	0.46	−6.63	(−7.32 to −5.94)
Euph&Cris	0.42	4.13	(−0.94 to 9.20)
Site	0.59	0.52	(−0.16 to 1.21)
Stage	0.23	0.40	(−2.97 to 3.76)

AIC = Akaike information criterion; CI = confidence interval.

Reproductive success

We monitored a total of 110 Least Auklet nests and 123 Crested Auklet nests in 2003, and a total of 123 Least Auklet nests and 131 Crested Auklet nests in 2004 (Table 3). Median hatch date for Least Auklets was similar in both years at both colonies (Table 3).

However, median hatch date for Crested Auklets was approximately one week later in 2004 than in 2003 (Table 3). Also, the timing of hatching for Least and Crested auklets was very similar in 2003; but in 2004, the median hatch date for Crested Auklets was about eight days later than that for Least Auklets. Egg survival for Least Auklets was similar between years and colonies (Table 3). Crested Auklet egg

TABLE 5
Model selection results for Least Auklet *Aethia pusilla* chick survival during 2000–2004 on St Lawrence Island, Alaska^a

Chick survival models ^b	Deviance	Parameters (n)	AIC _c	ΔAIC _c	AIC _c weight	Adjusted R ²
Site + Flow + Retreat	577.66	4	585.66	0.00	0.29	0.05
Site + <i>N. flemingeri</i>	580.92	3	586.92	1.25	0.15	0.04
Site + <i>C. marshallae</i>	581.05	3	587.05	1.39	0.15	0.04
Site + Flow + Retreat + Cover	577.66	5	587.66	2.00	0.11	0.05
Site + Year	576.53	6	588.54	2.88	0.07	0.05
Site + Stage + <i>N. flemingeri</i>	580.73	4	588.73	3.07	0.06	0.04
Site + Stage + <i>C. marshallae</i>	580.92	4	588.92	3.27	0.06	0.04
Flow + Retreat	583.12	3	589.13	3.46	0.05	0.04
Site + 2 _{<i>Neocalanus</i>}	583.93	3	589.93	4.27	0.03	0.04
<i>C. marshallae</i>	586.07	2	590.08	4.41	0.03	0.03
Constant	606.67	1	608.67	23.0	0.00	n/a

^a Top ten models presented, together with a model of constant chick survival. Models within two AIC_c units of the top model are considered well-supported by the data for drawing inference.

^b Models ranked by descending ΔAIC_c. Factors in models included effects of breeding Site, Year, Stage of the nesting cycle; proportions of *C. marshallae*, *N. flemingeri*, *N. cristatus*; and the combined proportions of *N. cristatus* and *N. flemingeri* (2_{*Neocalanus*}). Abiotic covariates included Flow through the Bering Strait, winter sea ice cover index (Cover), and date of ice retreat (Retreat).

AIC = Akaike information criterion; CI = confidence interval.

TABLE 6
Model selection results for Crested Auklet *Aethia cristatella* chick survival during 2000–2004 on St Lawrence Island, Alaska^a

Chick survival models ^b	Deviance (n)	Parameters	AIC _c	ΔAIC _c	AIC _c weight	Adjusted R ²
Site + <i>N. flemingeri</i>	373.33	3	379.33	0.00	0.19	0.02
Site + Euph&Cris	373.56	3	379.56	0.24	0.17	0.02
<i>N. flemingeri</i>	375.84	2	379.84	0.52	0.15	0.01
Euph&Cris	376.05	2	380.05	0.72	0.14	0.01
Site + Stage + <i>N. flemingeri</i>	372.34	1	380.35	1.02	0.12	0.02
Site + Stage + Euph&Cris	372.55	1	380.56	1.23	0.11	0.02
Cover	378.82	2	382.82	3.49	0.03	0.01
Constant	380.83	1	382.83	3.51	0.03	n/a
Site + Cover	377.08	3	383.08	3.75	0.03	0.01
Flow	379.14	2	383.14	3.81	0.03	0.00

^a Top ten models presented. Models within two AIC_c units of the top model are considered well-supported by the data for drawing inference.

^b Models ranked by descending ΔAIC_c. Factors in models included effects of breeding Site, Year; Stage of the nesting cycle; proportions of *N. flemingeri*, *N. cristatus*, euphausiids; and the combined proportions of euphausiids and *N. cristatus* (Euph&Cris). Abiotic covariates included Flow through the Bering Strait, winter sea ice cover index (Cover), and date of ice retreat (Retreat).

AIC = Akaike information criterion; CI = confidence interval.

survival was 6.5% and 14.0% lower at the Myaughee colony than at the Kitnik colony in 2003 and 2004 respectively (Table 3). Chick survival of Least Auklets was similar in 2003 and 2004, and at the two colonies within each year (84.7%–86.0%; Table 3). Similarly, chick survival did not vary between years or between colonies within each year for Crested Auklets (91.6%–93.4%; Table 3).

Relationships between chick survival, diet composition, and conditions in the Bering Sea

Among the explanatory variables considered, interannual variation in diet explained the largest percentage of variation in Least Auklet chick survival during 2000–2004 (Table 4). The proportion of *C. marshallae* in the diet was negatively associated with Least Auklet chick survival when averaged across models, and the proportion of *N. flemingeri* had a positive effect on Least Auklet chick survival (Table 4). The best approximating model for Least Auklet chick survival included effects of breeding site [β_{Site} : 0.59; 95% confidence interval (CI): 0.08 to 1.10], flow through the Bering Strait (β_{Flow} : 0.08; 95% CI: 0.05 to 0.11), and date of winter sea ice retreat (β_{Retreat} : -0.07; 95% CI: -0.12 to -0.03; Table 5). However, confidence intervals of the model-averaged effects of these three variables overlapped zero (Table 4). The three competing models (ΔAIC_c values ≤ 2.0) for explaining interannual variation in Least Auklet chick survival also included effects of breeding site and were considered well supported by the data (Table 5). Effects of site were positive in the three models, suggesting a trend toward higher chick survival at the Myaughee colony; however, model-averaged effects of site were small and the 95% confidence interval overlapped zero (Table 4). The weak effects of Site may be explained by more intensive nest monitoring at the Kitnik colony than at the Myaughee colony, with more frequently disturbed nests potentially experiencing lower nest success (Piatt *et al.* 1990). Stronger flow through the Bering Strait also had a positive effect on chick survival in the competing model that included that variable (β_{Flow} : 0.08; 95% CI: 0.03 to 0.13), and the extent of winter sea ice cover had a weak positive effect on chick survival in the single competing model that included that variable (β_{Cover} : 0.004; 95% CI: -0.34 to 0.35). The competing model including effects of later date of sea ice retreat had a negative effect on chick survival identical to that in the best approximating model (β_{Retreat} : -0.07; 95% CI: -0.12 to -0.03). The variables for the prevalence of *N. cristatus* in the diet and the combined proportions of *Neocalanus* copepods in the diet were not among the competing models explaining Least Auklet chick survival (Table 5).

Among the explanatory variables considered, variation in diet explained the largest percentage of variation in Crested Auklet chick survival as it did with Least Auklets. The proportion of *N. flemingeri* in the diet had a negative effect on chick survival when averaged across models (Table 4). Six models for explaining interannual variation in Crested Auklet chick survival had ΔAIC_c values of 2 or less during the five-year study (Table 4). The best approximating model included effects of proportion of *N. flemingeri* in the diet ($\beta_{N. flemingeri}$: -6.87; 95% CI: -12.17 to -1.56) and effects of breeding site (β_{Site} : 0.53; 95% CI: -0.14 to 1.21; Table 4). The model-averaged parameter estimate suggested a trend toward higher chick survival at the Myaughee colony (Table 4); however, this effect was small, and the 95% confidence interval overlapped zero. A competing model including effects of Euph&Cris ($\beta_{\text{Euph\&Cris}}$: 4.28; 95% CI: 0.92 to 7.64) and site (β_{Site} : 0.53; 95% CI: -0.14 to 1.21; Table 4) was close in model weight ($\Delta\text{AIC}_c = 0.24$), with some support for the positive

effect of prevalence of Euph&Cris on chick survival when averaged across models (Table 4). Two of the six competing models included effects of stage of the chick-rearing period (β_{Stage} : 0.39; 95% CI: -0.38 to 1.17; and β_{Stage} : 0.40; 95% CI: -0.38 to 1.17; Table 4), but the model-averaged effect of stage was not supported by the data (Table 4). Timing of ice retreat, winter sea ice cover, flow through the Bering Strait, proportion of *N. cristatus* and proportion of euphausiids in the diet were not included in the top six competing models explaining variation in Crested Auklet chick survival (Table 6).

DISCUSSION

Our data support the hypothesis that between-year variation in auklet chick survival is related to differences in diet composition (Gall *et al.* 2006). Specifically, prevalence of the small copepod *C. marshallae* in Least Auklet diets and of *N. flemingeri* in Crested Auklet diets was negatively associated with chick survival. We also found that prevalence of the large oceanic copepod *N. cristatus* was positively associated with chick survival for Crested Auklets. However, in contrast to the earlier study, we found that consumption of the oceanic copepod *N. flemingeri* had a stronger positive relationship with the survival of Least Auklet chicks than did the combination of *N. flemingeri* and *N. cristatus*, suggesting that the smaller copepod *N. flemingeri* may be more influential than the larger copepod *N. cristatus* in determining Least Auklet chick survival.

It is likely that the taxonomic composition of auklet chick diets reflects both relative and overall availability of prey types at sea (Adams *et al.* 2004), because certain prey types are more energetically profitable than others (Springer *et al.* 2007). The diets of Least and Crested auklets nesting on St Lawrence Island are probably good indicators of the relative abundances of their preferred prey types, but may include less profitable prey types only when preferred prey are less available (Springer *et al.* 2007). Our data suggest that presence of less profitable prey types in auklet chick diets (i.e. *C. marshallae* in Least Auklet diets and *N. flemingeri* in Crested Auklet diets) may be a predictor of poor nesting success during a season. Unfortunately, we lack the independent data on zooplankton abundance at sea to determine the extent to which auklet chick diets reflect zooplankton standing stocks.

The present extended analysis of dietary factors influencing chick survival over a five-year span (2000–2004) supports some, but not all, of the conclusions in Gall *et al.* (2006). The negative relationship between the prevalence of *C. marshallae* in the diet and Least Auklet chick survival was clear and consistent, as was the negative relationship between the prevalence of *N. flemingeri* in the diet and Crested Auklet chick survival. Although *N. flemingeri* was the dominant prey type for Least Auklets in all years and is about twice the mass of *C. marshallae*, it is nevertheless at the low end of the prey size spectrum for Crested Auklets and is usually only a minor component of the diet. All else being equal, small prey have less energy per item and are probably less efficiently exploited than are large prey. The prevalence of *N. cristatus* in the diet, however, was not positively related to Least or Crested auklet chick survival, as reported by Gall *et al.* (2006). The prevalence of *N. cristatus* in the diets of both Least and Crested auklets during 2003 was the lowest during the five years of our study, yet chick survival for both species was high. Euphausiids were also more prevalent in the diets of both Least and Crested auklet chicks (29.0 APB and 88.3 APB respectively) during 2003 than in the other four years of the study. The high proportion of *Thysanoessa* euphausiids in chick

diets during 2003 apparently compensated for the relative scarcity of *N. cristatus*. The apparent capacity of euphausiids to substitute for the large oceanic copepod *N. cristatus* in the diet of Crested Auklets is supported by the competing models from AIC model selection that included the explanatory variable Euph&Cris. There was also a strong positive association between Least Auklet chick survival and prevalence of *N. flemingeri* in chick diets. Consequently, in years when both species of *Neocalanus* copepods are less prevalent in Least Auklet diets, and *N. cristatus* and euphausiids are less prevalent in Crested Auklet diets (i.e. 2001—Gall *et al.* 2006), chick survival and overall reproductive success are likely to be lower.

Nest initiation of Crested Auklets was delayed in 2000 (Appendix 1; Gall *et al.* 2006) and in 2004, the only years in which this species provisioned the small shelf copepod *C. marshallae* to chicks. Snow cover, which is hypothesized to influence timing of nest initiation in Least and Crested auklets (Sealy 1975), had melted from productivity plots on the colonies before the median egg-laying date in both those years, suggesting that late snow cover was not a factor in delayed nest initiation. Nest initiation of Least Auklets was latest in 2000 when amphipods were prevalent in the diet (28.5%) and in 2001 when *C. marshallae* was prevalent in the diet (20.1%). Nest initiation of Least Auklets was earliest during 2002 and 2004 when the two *Neocalanus* copepods were most prevalent and chick survival was highest.

The preferred foraging areas of most Least and Crested auklets nesting on St Lawrence Island are thought to be more than 50 km from the large breeding colonies near Savoonga (Obst *et al.* 1995). Consequently, both auklet species may be more sensitive to changes in the availability of large, energy-rich prey types than are auklets nesting at colonies where foraging ranges are much smaller. Auklets are likely to experience lower net energetic efficiency while foraging on small prey items (i.e. *C. marshallae*), even if the small prey are abundant. It would require approximately 10 *C. marshallae* or five *N. flemingeri* to equal the mass of a single larger prey item such as *N. cristatus*. Higher lipid content and, consequently, higher energy density of prey types such as *N. flemingeri* and *N. cristatus*, relative to *C. marshallae*, may further contribute to the foraging efficiency of auklets that select those prey (Obst *et al.* 1995, Hunt & Harrison 1990). If warming of the Bering Sea leads to a shift in abundance from large to smaller taxa of zooplankton, as predicted by Coyle *et al.* (2008), auklets nesting on St Lawrence Island where foraging ranges are relatively large may be especially vulnerable.

As stated earlier, the Anadyr Current transports not only auklet prey, such as *Neocalanus* copepods, but also nutrients vital to production of resident shelf zooplankton such as *C. marshallae* and *T. raschii*. We observed a small, but important, positive effect on Least Auklet chick survival of greater flow through the Bering Strait in two competing models for this species. However, the effect of flow through the Bering Strait on chick survival for Least and Crested auklets was weak when averaged across models. Measurement of flow at a mooring site within the Anadyr Strait, rather than within the Bering Strait, may reveal a stronger relationship between auklet chick survival and northward flow.

The progressively earlier spring transition in the Bering Sea, and the resulting changes in primary and secondary productivity, may have large impacts on upper trophic-level consumers such as seabirds (Stabeno & Overland 2001, Grebmeier *et al.* 2006). Chick survival of Least and Crested auklets was consistently high in all years of this

study and most strongly influenced by interannual variation in diet in our models. However, most of the interannual variation in chick survival remains unexplained by our models. Least Auklet chick survival was more sensitive to variation in ice conditions and flow through the Bering Strait, suggesting that Least Auklets may be more sensitive than Crested Auklets to climate variability and ecosystem shifts in the northern Bering Sea. Crested Auklets feed primarily upon euphausiids, and the availability of this shelf-associated prey type may be less sensitive to variation in flow and climate than are the *Neocalanus* copepods associated with the Anadyr Current. Least and Crested auklets, as well as other planktivores, may experience higher food availability in years of earlier ice retreat, but climate-driven oceanographic changes that decrease the prevalence of *N. flemingeri* in Least Auklet diets and euphausiids in Crested Auklet diets without increasing the prevalence of suitable alternative prey such as *N. cristatus* will result in lower nesting success for these two seabird species. The strength of the Anadyr Current and the timing of sea ice retreat the previous spring appear to be related to the prevalence of preferred prey types in the diets of auklets nesting on St Lawrence Island. Future studies that capture more interannual variation in chick survival are warranted to gain a better understanding of how chick diet and other physical factors affect chick survival.

Planktivorous auklets, because of their direct dependence on secondary productivity and ocean physics, are indicators of effects of climate change on upper trophic-level predators in the northern Bering Sea. Long-term auklet monitoring at breeding sites will be vital to understanding how these abundant planktivores respond to changing ocean conditions in the northern Bering Sea and will also provide information on changes in secondary productivity that is otherwise difficult to obtain. Further study is also needed to assess the potential for increased top-down effects on zooplankton communities that may affect prey availability for nesting auklets on the northern Bering Sea shelf.

ACKNOWLEDGEMENTS

We thank the Native villages of Savoonga and Gambell for allowing us to conduct this research on St Lawrence Island. Funding was provided by the US Fish and Wildlife Service office of Migratory Bird Management and the US Geological Survey—Oregon Cooperative Fish and Wildlife Research Unit at Oregon State University. Statistical advice was provided by R. Anthony, K. Dugger and F. Ramsay. Assistance in the field was provided by V.A. Zubakin of the Russian Academy of Sciences, with additional help from C. Akeya, R. Alowa, F. Kingeekuk, H. Kingeekuk, T. Kiyuklook, T. Guy, L. Miller, S.K. Nelson, S.G. Sealy, J. Snyder, B. Waghiyi and T. Wahl. Zooplankton samples were identified by K. Turco of Alaska's Spirit Speaks: Sound and Science, and verified by K. Coyle. We are grateful to many people at both Oregon State University and USFWS for logistical support. We thank H. Batchelder, K. Dugger, S. Hatch, G. Hunt, J. Piatt, D. Rizzolo, W. Sydeman and two anonymous reviewers for comments and suggestions that improved earlier drafts of this manuscript.

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APPENDIX 1

Nesting chronology and reproductive success from Gall *et al.* (2006) of Least *Aethia pusilla* and Crested *A. cristatella* Auklets at two breeding colonies on St Lawrence Island, Alaska during 2000–2002^a

Parameter	2000		2001		2002	
	Kitnik	Myaughee	Kitnik	Myaughee	Kitnik	Myaughee
Least Auklets						
Nests (n)	30	33	63	41	62	27
Median hatch date	2 Aug	2 Aug	29 July	2 Aug	23 July	23 July
Egg survival	0.967	0.813	0.636	0.887	0.968	0.926
	(0.964 to 0.968)	(0.611 to 0.908)	(0.516 to 0.706)	(0.686 to 0.923)	(0.967 to 0.969)	(0.921 to 0.931)
Chick survival	0.741	0.885	0.551	0.802	0.926	0.972
	(0.598 to 0.884)	(0.796 to 0.975)	(0.407 to 0.696)	(0.687 to 0.918)	(0.857 to 0.994)	(0.940 to 1.000)
Nest survival	0.72	0.72	0.35	0.71	0.90	0.90
	(0.50 to 0.86)	(0.46 to 0.87)	(0.46 to 0.87)	(0.40 to 0.83)	(0.78 to 0.94)	(0.84 to 0.92)
Crested Auklets						
Nests (n)	33	54	49	50	65	40
Median hatch date	6 Aug	7 Aug	30 July	2 Aug	23 July	23 July
Egg survival	0.837	0.710	0.687	0.826	0.921	0.775
	(0.663 to 0.829)	(0.605 to 0.765)	(0.598 to 0.727)	(0.680 to 0.893)	(0.834 to 0.953)	(0.643 to 0.825)
Chick survival	0.865	0.934	0.787	0.885	0.908	0.954
	(0.725 to 0.999)	(0.854 to 1.000)	(0.620 to 0.954)	(0.787 to 0.982)	(0.828 to 0.989)	(0.900 to 1.000)
Nest survival	0.72	0.66	0.54	0.73	0.84	0.74
	(0.41 to 0.78)	(0.48 to 0.75)	(0.34 to 0.63)	(0.51 to 0.84)	(0.51 to 0.84)	(0.57 to 0.81)

^a Egg and chick survival rates estimated using nest survival models in program MARK; numbers in parentheses are 95% confidence intervals.