

Reproductive success of planktivorous seabirds in the North Pacific is related to ocean climate on decadal scales

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ABSTRACT: Growing evidence indicates relationships between seabird demography and both large- and small-scale variation in climate and oceanography, yet few studies have examined multiple species and locations simultaneously. As secondary consumers, least, whiskered, and crested auklets (*Aethia pusilla*, *A. pygmaea*, and *A. cristatella*, respectively), congeneric planktivorous seabirds endemic to the Bering and Okhotsk seas, are expected to respond to changes in ocean climate due to their low trophic positioning. From 1990 to 2008, we measured reproductive success (productivity) and breeding phenology (mean hatching date) of auklets on Buldir, Kiska, and Kasatochi, 3 islands spanning 585 km across the Aleutian Islands, Alaska, USA. A model including Island, Species, and Winter Aleutian Low Pressure Index (ALPI) best explained productivity, with reproductive success decreasing among all species with increasing ALPI ($\beta = -0.273 \pm 0.0263$ [SE]), likely through control of water temperature and prey (zooplankton) availability. Auklet productivity also increased with increasing winter sea surface temperature (SST) in the western North Pacific and western Bering Sea (and correspondingly decreased with increasing SST in the Gulf of Alaska), and was correlated negatively with spring sea-level air pressure in the North Pacific. These responses are reflective of positive values of the Aleutian low pressure system. Though our datasets cover only 19 yr or less, we found similar correlations between climate and auklet productivity among all species and islands. Together, our results suggest that ocean climatic conditions and reproductive success of planktivorous auklets are significantly related.

KEY WORDS: Productivity · Oceanography · Demography · *Aethia* spp. · Least auklet · Crested auklet · Whiskered auklet · Aleutian Islands

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INTRODUCTION

Climate and oceanographic conditions in the North Pacific Ocean covary on decadal time scales or longer (Overland et al. 1999, Biondi et al. 2001), often characterized by 'regimes' of 20 to 30 yr duration (Hare &

Mantua 2000, Biondi et al. 2001, d'Orgeville & Peltier 2009). A well known regime shift occurred in 1976–1977, with warmer sea surface temperature (SST), lower sea-level pressure (SLP), and a more intense Aleutian low pressure system (Aleutian low) (Hare & Mantua 2000, Rodionov et al. 2005). In the North

Pacific and Bering Sea, this shift resulted in greater climatic variability (Bond et al. 2003, Hunt & Elliott 2004, Rodionov et al. 2005), greater stratification of the water column, and increased primary productivity (Trenberth & Hurrell 1994, Iida & Saitoh 2007). Other purported ecosystem shifts have occurred in 1989–1990 and 1998–1999, but these putative shifts in system state have not been well documented (Overland et al. 1999, Hare & Mantua 2000, Mueter et al. 2007).

Seabirds, as conspicuous, generally unexploited, secondary and tertiary consumers in marine systems, provide a unique opportunity to investigate coupled climate-ecosystem variation (Durant et al. 2009). Indeed, the relationship between ocean climate, ranging from direct measures of SST to multivariate climate indices, e.g. Pacific Decadal Oscillation (PDO) (Mantua & Hare 2002), and seabird breeding performance has been investigated frequently in the North Pacific (e.g. Gjerdrum et al. 2003, Abraham & Sydeman 2004, Byrd et al. 2008) and elsewhere (e.g. Harris et al. 2005, Durant et al. 2006, Møller et al. 2006, Lavers et al. 2008, Jenouvrier et al. 2009). Some authors found significant relationships between large-scale climate indices and seabird demographic rates (Kitaysky & Golubova 2000, Byrd et al. 2008, Sandvik et al. 2008), whilst others did not (Wanless et al. 2009). In the North Pacific, variation in seabird breeding performance is thought to result from 'bottom-up' climate forcing of seabird prey abundance (Lehodey 2004).

While linkage between climatic and oceanographic variability has been found in many marine organisms (Beamish et al. 1997, Mantua et al. 1997, Chavez et al. 1999, Hunt et al. 2002, 2008, Durant et al. 2006, Byrd et al. 2008), most studies did not address spatial components in climatic and oceanographic variability. Integrating data over large areas can mask smaller-scale variation over space and time. More recently, there has been a focus on examining relationships between seabirds' demography and oceanographic variables in spatial terms, providing a better understanding of how geographic patterns of climate affect marine species (Byrd et al. 2008, Watanuki et al. 2009).

Auklets (Charadriiformes: Alcidae: *Aethia*) are a group of planktivorous seabirds occurring in the Bering and Okhotsk Seas. They consume and provision offspring with zooplankton, primarily euphausiid crustaceans and large copepods (Day & Byrd 1989, Flint & Golovkin 2002, Gall et al. 2006). Annual reproductive output is reflected by success in the hatching and rearing of offspring from a single egg (Byrd & Williams 1993, Jones 1993a,b). Here, we test the hypothesis that the productivity (and timing of breeding) of auklets covaries with ocean climate, and that this covariation is consistent among species and breeding colonies in the western Aleutian Islands. We con-

sidered the correlation between productivity, large-scale ocean climate indices (Aleutian Low Pressure Index [ALPI], PDO), and direct measures of SST and SLP based on satellite data for 3 auklet species: least, whiskered, and crested auklets (*Aethia pusilla*, *A. pygmaea*, and *A. cristatella*) breeding on Buldir, Kiska, and Kasatochi in the central and western Aleutian Islands, Alaska (Fig. 1). Our objectives were to: (1) quantify relationships between auklet reproductive success and indices and direct measures of ocean climate; (2) identify the oceanographic regions where productivity-climate correlations are strongest; (3) examine the covariance in productivity among different island-breeding colonies and among different auklet species; and (4) to better understand underlying mechanisms determining demographic variation in planktivorous seabird species in the North Pacific.

MATERIALS AND METHODS

Productivity (the proportion of eggs laid that produced independent young) and phenology (mean date of hatching of eggs) were measured over 19 yr (1990–2008) at Main Talus, Buldir (52° 22.45' N, 175° 54.33' E; least and crested auklets, 1990–2008; whiskered auklets, 1991–2008), Thundering Talus, Kasatochi (52° 10.77' N, 175° 31.48' W; least and crested auklets, 1996–2008), and at Sirius Point, Kiska (52° 08' N, 177° 36' E; least and crested auklets, 2001–2008), in the Aleutian Islands, Alaska. No data were collected from Buldir in 1999 or from Kiska in 2005 due to logistical constraints.

Auklet productivity. Each year, we checked a sample of auklet breeding nest sites (rock crevices) from late May until early August using established protocols (for details see Fraser et al. 1999, Hunter et al. 2002, Major et al. 2006), encompassing the entire breeding season for all 3 species. To account for potential vari-

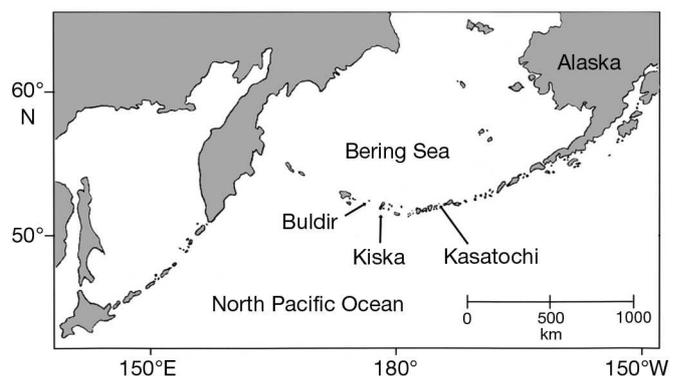


Fig. 1. North Pacific Ocean with productivity measurement study sites on the islands Buldir, Kiska, and Kasatochi, Aleutian Islands, Alaska, indicated

ability among islands, years, and observers, one trained observer was stationed on each island in each year to ensure consistency. Within each year, the same individual would check the same nest sites, and all observers used the same methods and criteria for determining nest success (Fraser et al. 1999, Major et al. 2006). We visited breeding sites every 4 to 7 d and determined their status (empty, egg, chick, adult, unknown). New sites were located and included in the sample each year, to account for previously monitored sites that were no longer in use, but the majority of crevice nests in most years consisted of sites that had been monitored in previous years. We assumed that our annual sample of breeding sites monitored at each colony was representative and reflective of productivity at each colony site. We considered sites active when we found an adult on 2 consecutive visits, or when we saw an egg. We scored sites as successful in fledging a chick if the chick disappeared after 25 d for least auklets (Roby & Brink 1986a), 26 d for crested auklets (Fraser et al. 1999) or 32 d for whiskered auklets (Hunter et al. 2002).

Timing of breeding. We estimated date of hatching for a sub-sample of crevice breeding sites monitored. We included only crevices that we scored as an egg on one visit, and as a chick on the very next visit (4 to 7 d later), and we assumed hatching date to have occurred at the midpoint between the 2 visits. We then used the mean hatching date for each species-island combination in each year as a measure of timing of breeding.

Climate and oceanographic data. We used multiple large-scale atmospheric and oceanographic climate indices, and evaluated their relationship to auklet reproductive success. While metrics of climate are interrelated, as might be expected, we chose a variety of indicators since no one index reflects the variability of the North Pacific adequately (Bond et al. 2003). The ALPI (Beamish & Bouillon 1993, Beamish et al. 1997) is the anomaly from the 1950 to 1997 mean of the area with pressure ≤ 100.5 kPa over the area 20 to 70° N, 120° E to 120° W; positive ALPI values indicate a relatively strong Aleutian low-pressure system. ALPI is centered on our study area (approximately 51 to 53° N, 175° E to 175° W). The related North Pacific Index (NPI) is the area-weighted sea-level pressure over the region bounded by 30 to 65° N and 160° E to 140° W (Trenberth & Hurrell 1994). The PDO is a temporally long (20 to 30 yr) El Niño Southern Oscillation (ENSO)-like oscillation based on the leading principle component of SST north of 20° N (Mantua et al. 1997). Finally, the North Pacific Gyre Oscillation (NPGO) is derived output from a model; it represents the second principal component of sea surface height anomalies measured over the same areas as the PDO (Di Lorenzo et al. 2008). Several of these indices (ALPI, NPI, and PDO)

have been related to auklet demography (Jones et al. 2002)

For SST, we used the 4 km AVHRR (advanced very high resolution radiometer) Pathfinder Version 5 dataset (available at www.nodc.noaa.gov/SatelliteData/pathfinder4km/available.html). We measured SST in a 50 km² radius around each colony, reflecting the likely foraging range of auklets (Obst et al. 1995, Thayer et al. 2008, Wolf et al. 2009). We assessed SST during June and July, when auklets are present at the breeding colonies. For our geospatial approach (see 'Statistical procedures' below), large-scale climate data (SST and SLP) over the North Pacific were taken from the National Centers for Environmental Protection/National Center for Atmospheric Research (NCEP-NCAR) reanalysis (Kalnay et al. 1996).

Statistical procedures. All statistical tests were performed in SPSS 16.0.2, and were weighted by the sample size of nest sites studied each year for each species at each island. To investigate whether there were linear trends in productivity or timing of breeding over time, we used a linear regression for each species-island combination. We used nonparametric correlations (Spearman's ρ) to look for covariance among and between species and islands (Byrd et al. 2008). To control for multiple comparison error inflation, we used the False Discovery Rate (Benjamini & Hochberg 1995), which is less restrictive and more powerful than a Bonferroni-type family-wise correction (García 2004, Grosbois et al. 2008). We use $p < 0.10$ to determine significance. Setting a higher α level is desired when the sample size (in this case, number of years) is low, to increase the power to detect a relationship when one is present (Lebreton et al. 1992, Field et al. 2004, Grosbois et al. 2008). This approach has been used regularly in other studies of seabirds in the North Pacific (e.g. Abraham & Sydeman 2004, Byrd et al. 2008).

We used a 3-step process to investigate relationships among ocean climate and auklet productivity. First, we used Spearman rank correlations to search for potential parameters to include in a statistical model. Second, as this analysis does not account for spatial variability in variables (e.g. SST and SLP), we examined spatial correlations to provide inference regarding spatial variability (Szép & Møller 2005, Schroeder et al. 2009, Watanuki et al. 2009); we limited this analysis to the Buldir and Kasatochi time series, which were >10 yr in duration. Spearman correlation coefficients between reproductive success and SLP or SST were mapped over the North Pacific and Bering Sea, and areas of significant correlations ($p < 0.10$) were delineated. We used generalized linear models with a binomial logit-link function (a logistic regression approach), to select the most important climate variables. Variable selection was based upon quasi-

Akaike's Information Criteria adjusted for small sample sizes (QAIC_c) and extra-binomial variation by including an estimate of model deviance (\hat{c} = model deviance ÷ df for the global model). We chose this information-theoretic approach rather than a null-hypothesis testing because the variation in the dependent variable (productivity) was generally small (9 to 16 % among all species and all islands) (Grosbois et al. 2008). We considered the model with the lowest QAIC_c value to be the best-fitting model for the data (Burnham & Anderson 2002). We constructed 12 *a priori* models composed of biologically plausible combinations of 5 variables of interest, including a Null Model (intercept only) and a Global Model that included all additive terms, and their interactions with species and islands. Once the best-fitting model was identified, the climate and oceanographic covariates of interest and biologically important interaction terms were added to subsequent models to examine the effect of climate, a similar procedure to the modeling of recapture rate and then survival rate in mark-recapture studies (Lebreton et al. 1992, Grosbois et al. 2008). We only included potential climate covariates that were correlated significantly with auklet reproductive performance in our preliminary assessment. This decreases the number of candidate models and reduces the risk of multi-collinearity in covariates (Grosbois et al. 2008). Models with QAIC_c > 2 were considered to have substantially less support, and overall model support was assessed using Akaike weights (w_i) (Burnham & Anderson 2002). This was done on both the full dataset and again using data from Buldir and Kasatochi only, as in the geospatial analysis. In the latter case, Kiska is excluded because its observation period was shorter (7 yr), and because Kiska is anomalous in that it also has introduced predators that affect auklet reproductive performance. Finally, we used the estimated marginal means (EMMs) from the top-ranked generalized linear model to examine differences among species and islands, and differences were considered significant if 95% confidence intervals did not overlap.

RESULTS

We studied between 23 and 215 breeding pairs of each species on each island in each year (total = 7733 breed-

ing sites over all years and all species) (Table S1 in the supplement at www.int-res.com/articles/suppl/m424p205_supp.pdf). Auklet productivity ranged from 0.10 to 0.85 chicks per nest for most species for most years, with 2001 and 2002 being unusually low on Kiska, and 2003 being unusually low on Buldir (Fig. 2; Table S2 in the supplement at www.int-res.com/articles/suppl/m424p205_supp.pdf).

Linear regression identified only one significant trend in reproductive success or phenology. Since that trend was an increase in reproductive success over time for least auklets on Kiska, our smallest dataset ($p = 0.012$, all other sites $p > 0.11$), we used raw data, not detrended values, for further comparisons (Tables S2 & S3 in the supplement at www.int-res.com/articles/suppl/m424p205_supp.pdf). There was a general pattern of correlation among species within islands, and using our shortest time series (Kiska), 9 of 10 correlations were positive despite the small sample size ($n = 7$ yr), providing reasonably strong evidence of covariation (Table 1). Timing of breeding was rarely correlated among species or islands; crested auklet timing of breeding on Buldir and Kiska was correlated positively (Table 2).

Productivity was related to ocean climate indices significantly in 2 cases. Of the relationships examined,

Table 1. Spearman's ρ correlation matrix for breeding phenology (mean hatch date) of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) on Buldir, Kiska, and Kasatochi in the Aleutian Islands from 1990 to 2008. Significant correlations after correcting for False Discovery Rate (see 'Statistical procedures') are indicated with *

	Buldir LEAU	Kiska LEAU	Kasatochi LEAU	Buldir CRAU	Kiska CRAU	Kasatochi CRAU
Kiska LEAU	-0.239					
Kasatochi LEAU	0.458	-0.373				
Buldir CRAU	0.581	-0.108	0.378			
Kiska CRAU	0.667	0.200	0.616	0.900*		
Kasatochi CRAU	0.388	-0.248	0.519	0.208	0.051	
Buldir WHAU	0.452	0.673	-0.196	0.445	0.821	0.092

Table 2. Spearman's ρ correlation matrix for productivity of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) on Buldir, Kiska, and Kasatochi in the Aleutian Islands from 1990 to 2008. Significant correlations after correcting for False Discovery Rate (see 'Statistical procedures') are indicated with *

	Buldir LEAU	Kiska LEAU	Kasatochi LEAU	Buldir CRAU	Kiska CRAU	Kasatochi CRAU
Kiska LEAU	0.206					
Kasatochi LEAU	-0.260	0.216				
Buldir CRAU	0.569	0.090	-0.249			
Kiska CRAU	0.581	0.643	-0.601	0.219		
Kasatochi CRAU	0.162	0.865*	0.373	0.127	0.543	
Buldir WHAU	0.375	0.793	0.018	0.469	0.402	0.565

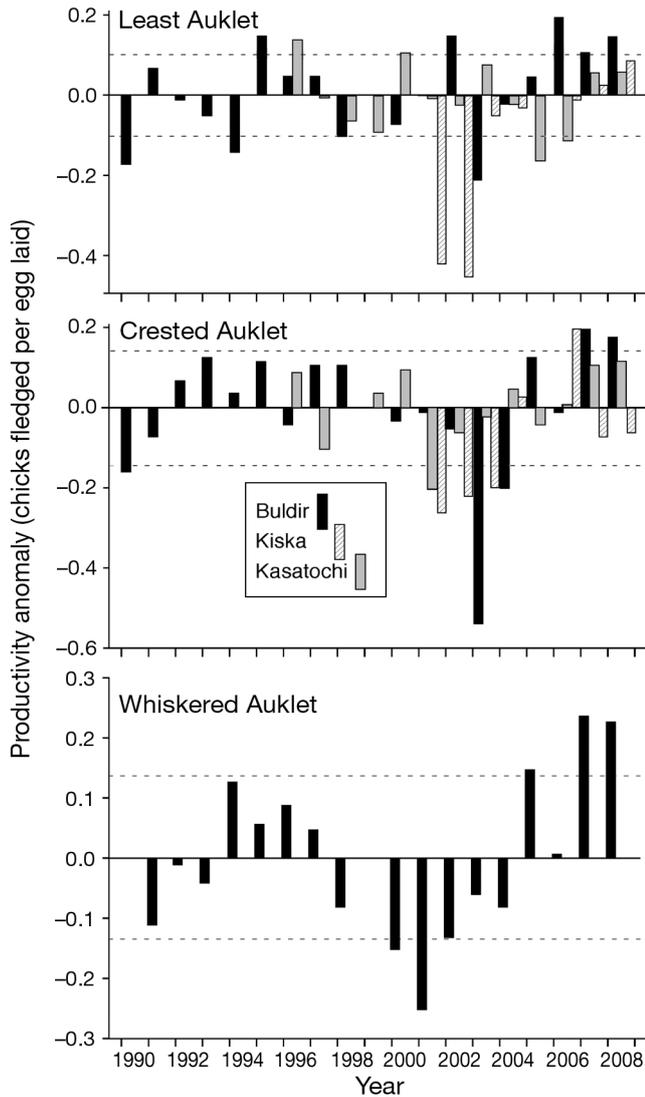


Fig. 2. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. Productivity anomalies (differences from the overall mean) of least, crested and whiskered auklets on Buldir, Kiska and Kasatochi, Aleutian Islands, Alaska, from 1990 to 2008. Dashed lines indicate ± 1 SD from the mean

crested auklet productivity was related to the NPGO (Table 3). Of the climate covariates we considered, ALPI and the winter and spring NPGO were most often related to auklet productivity.

Geospatial mapping of climate and reproductive success correlations

In 4 cases, geospatial correlation analysis found that reproductive success was correlated with winter (December to February) SST (Fig. 3) but in different areas of the North Pacific. Productivity of least and crested auklets on Buldir was negatively correlated with SST in the Gulf of Alaska region, while that of whiskered auklets on Buldir was positively related to SST in the western Bering Sea. The spatial correlation pattern for least auklets on Buldir is characterized by a negative correlation along the American west coast and a positive correlation in the central North Pacific, reminiscent of the SST pattern of a negative PDO (Mantua et al. 1997). Reproductive success of crested auklets on Kasatochi was positively related to SST in the northwestern Pacific Ocean between 40 and 50° N (Fig. 3). The only relationship between reproductive success and spring (March to May) SST was for whiskered auklets breeding on Buldir, and the pattern was identical to that for winter SST. This pattern is similar to the second mode of SST variations (Bond et al. 2003), which is closely related to the NPGO (Di Lorenzo et al. 2009). This is consistent with the relatively high correlation between productivity and climate indices (Table 3). No significant relationships were found between reproductive success and winter SLP, and only 2 for spring SLP. Whiskered auklet reproductive success on Buldir was negatively related to SLP in the eastern Pacific, while that of least auklets on Kasatochi was negatively related to the spring SLP in the western Pacific (Fig. 4).

Table 3. Spearman's ρ correlations for productivity and climate indices for least (LEAU), crested (CRAU), and whiskered auklets (WHAU) on Buldir, Kiska, and Kasatochi in the Aleutian Islands from 1990 to 2008. *: Significant correlations after correcting for False Discovery Rate (see 'Statistical procedures'). ALPI: Aleutian Low Pressure Index, NPGO: North Pacific Gyre Oscillation, PDO: Pacific Decadal Oscillation, SST: sea surface temperature

	ALPI	NPGO Dec–Feb	NPGO Mar–May	NPI Dec–Mar	NPI Aug–Apr	PDO Dec–Mar	PDO Aug–Apr	SST
Buldir LEAU	-0.161	-0.127	-0.148	0.258	0.350	-0.532	-0.411	-0.436
Kiska LEAU	-0.707	-0.729	-0.528	0.021	0.029	0.281	0.054	0.406
Kasatochi LEAU	-0.103	0.283	0.271	-0.133	-0.278	-0.128	-0.142	0.368
Buldir CRAU	-0.313	-0.387	-0.297	0.227	0.264	-0.192	-0.295	-0.027
Kiska CRAU	-0.469	-0.945*	-0.835*	0.287	0.436	0.029	-0.086	0.091
Kasatochi CRAU	-0.373	-0.169	-0.038	0.191	0.128	-0.122	-0.324	0.198
Buldir WHAU	-0.529	-0.474	-0.415	0.307	0.231	0.114	0.033	0.053

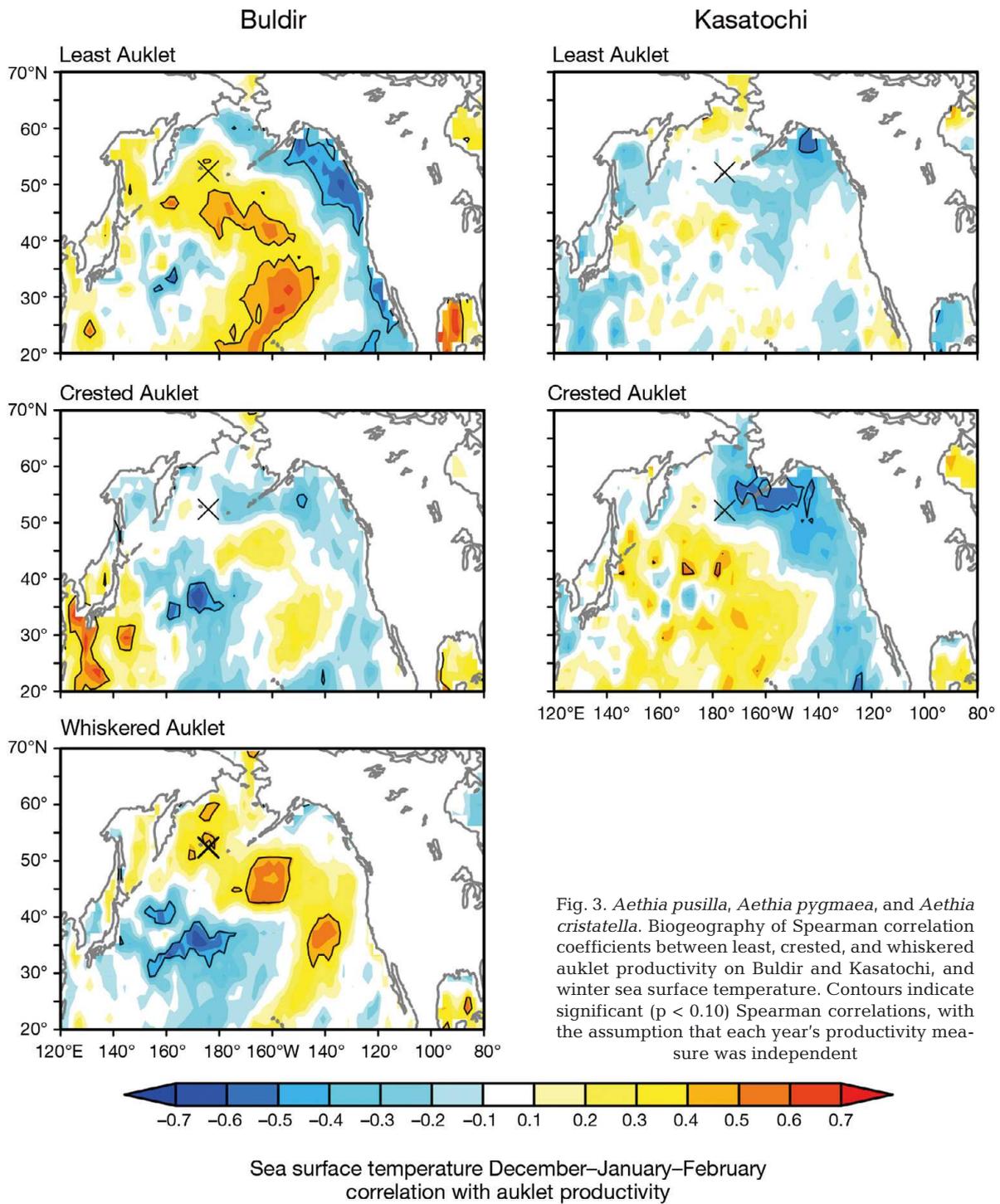


Fig. 3. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. Biogeography of Spearman correlation coefficients between least, crested, and whiskered auklet productivity on Buldir and Kasatochi, and winter sea surface temperature. Contours indicate significant ($p < 0.10$) Spearman correlations, with the assumption that each year's productivity measure was independent

Factors affecting auklet productivity

Based on the results from our examination of correlation coefficients and spatial correlation analysis, we included only ALPI and NPGO (winter and spring) along with local breeding-season SST as covariates in

the generalized linear models. The best-fitting model for productivity of all auklets from 1990 to 2008 included differences among species and islands, ALPI, and the Island \times ALPI interaction term. No other model had $\Delta QAIC_c < 2$, and the top model received 72% support, 3 times more than the second-best model after adjust-

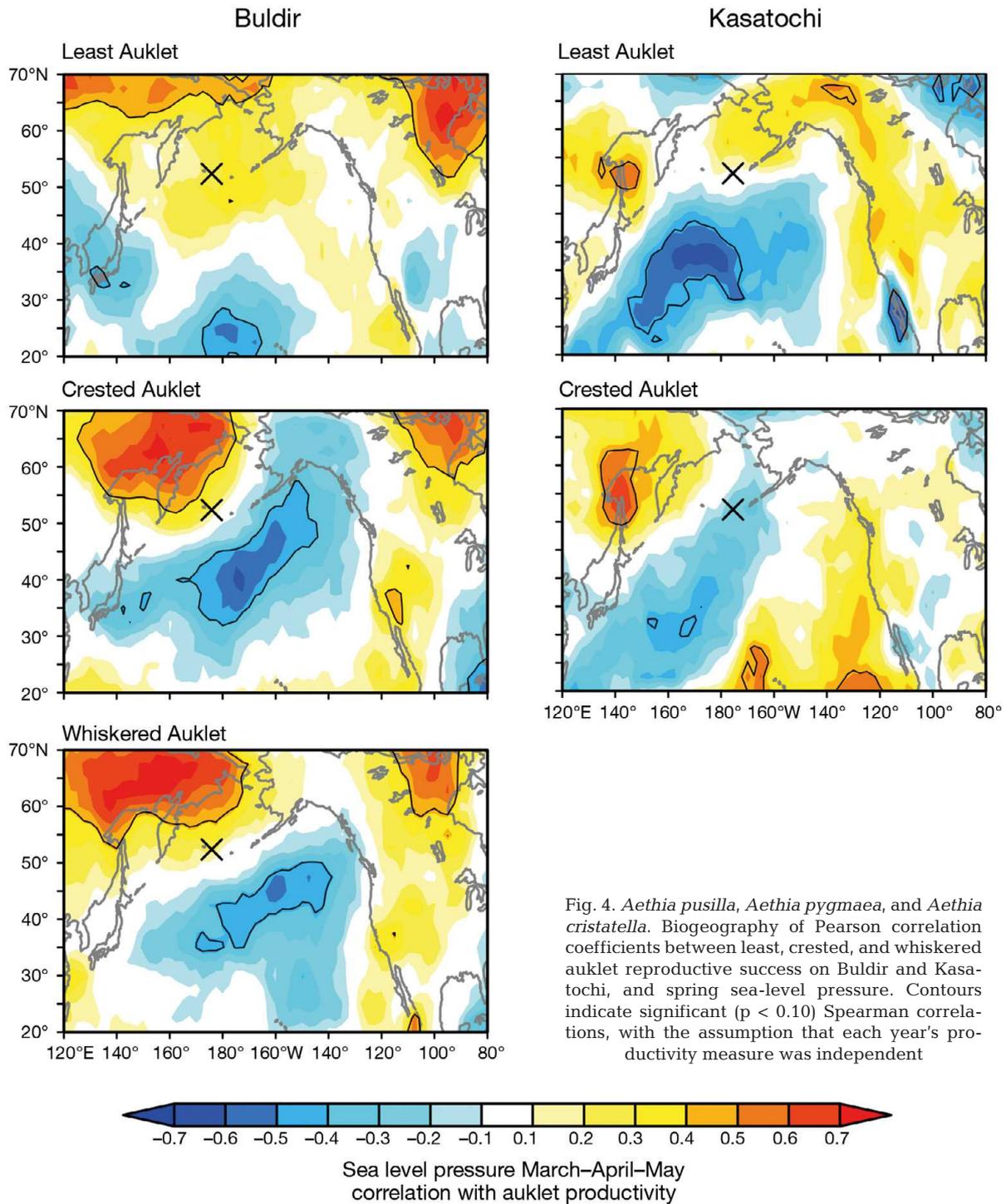


Fig. 4. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. Biogeography of Pearson correlation coefficients between least, crested, and whiskered auklet reproductive success on Buldir and Kasatochi, and spring sea-level pressure. Contours indicate significant ($p < 0.10$) Spearman correlations, with the assumption that each year's productivity measure was independent

ing for $\hat{c} = 5.62$ (Table 4). Parameter estimates are presented in Table 5.

Using data from only Buldir and Kasatochi, the top 2 models included effects of Species and ALPI, with one model including their interaction. These models were almost equally supported, but were more than 7 times

more supported than the third-ranked model after correcting for $\hat{c} = 4.23$ (Table 6).

Based on EMMs from the full dataset, Buldir and Kasatochi had similar reproductive success rates during the study, and both were higher than Kiska. Among islands, crested and whiskered auklets had

Table 4. Summary of the model set for predicting productivity of least, crested, and whiskered auklets on Buldir, Kiska, and Kasatochi, Aleutian Islands, Alaska from 1990 to 2008. Models are sorted by increasing QAIC_c (quasi Akaike's information criteria 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, S: species, 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 $\hat{c} = 5.62$. Δ QAIC_c is the difference from the top-ranked model

Model	No. of parameters	QAIC _c	Δ QAIC _c	w_i
I + S + ALPI + I × ALPI	8	1818.624	0.000	0.72
I + S + ALPI + I × ALPI + S × ALPI	11	1820.790	2.166	0.24
I + S + ALPI	6	1825.154	6.529	0.03
I + S + ALPI + S × ALPI	8	1826.500	7.876	0.01
I + S + NPGO-DJF	7	1832.111	13.486	0.00
I + S + NPGO-MAM	7	1839.563	20.939	0.00
I + S	5	1844.406	25.782	0.00
I + S + SST	6	1845.380	26.756	0.00
I + S + I × S	8	1847.243	28.619	0.00
S	3	1854.478	35.854	0.00
I	3	1856.643	38.018	0.00
Intercept only	1	2496.983	678.359	0.00

Table 5. Parameter estimates from the top-ranked generalized linear model (Table 7) for productivity of least, crested, and whiskered auklets on Buldir, Kiska, and Kasatochi, Aleutian Islands, from 1990 to 2008

Parameter	β	SE	— 95% CI —		Wald χ^2	df	p-value
			Lower	Upper			
Intercept	0.391	0.1009	0.193	0.588	14.975	1	<0.001
Crested auklet	0.203	0.0794	0.047	0.358	6.508	1	0.011
Least auklet	-0.274	0.0784	-0.428	-0.121	12.246	1	<0.001
Whiskered auklet	0 ^a	—	—	—	—	—	—
Buldir	0.200	0.0824	0.039	0.362	5.903	1	0.015
Kasatochi	0.148	0.0849	-0.018	0.315	3.049	1	0.081
Kiska	0 ^a	—	—	—	—	—	—
ALPI	-0.273	0.0263	-0.325	-0.222	108.252	1	<0.001
Buldir × ALPI	0.168	0.0317	0.106	0.230	27.926	1	<0.001
Kasatochi × ALPI	0.220	0.0330	0.155	0.285	44.490	1	<0.001
Kiska × ALPI	0 ^a	—	—	—	—	—	—

^aThis parameter is set to 0 because it is redundant

Table 6. Summary of the model set explaining productivity of least, crested, and whiskered auklets in the Aleutian Islands from 1990 to 2008 using only data from Buldir and Kasatochi. For model sorting information and abbreviations, see Table 4. Model corrected for $\hat{c} = 4.23$

Model	No. of parameters	QAIC _c	Δ QAIC _c	w_i
S + ALPI + S × ALPI	6	1942.986	0.000	0.49
S + ALPI	4	1943.267	0.281	0.43
S + NPGO-DJF	4	1947.378	4.391	0.05
S + NPGO-MAM	4	1949.853	6.866	0.02
S	3	1951.288	8.302	0.01
S + SST	4	1952.190	9.203	0.00
I + S + I × S	5	1953.267	10.281	0.00
Intercept only	1	1964.425	21.439	0.00
I	2	1965.426	22.440	0.00

higher reproductive success than least auklets (Table 7). An increased ALPI was associated with decreased productivity among all species on all islands ($\beta = -0.273 \pm 0.0263$ [SE]) (Fig. 5).

DISCUSSION

Our results indicate that auklet reproductive success varied with large-scale climate indices, and that even with a short time series for multi-island comparisons (7 yr), the majority of correlations (9 of 10) were in phase. The combination of only 7 years' data from Kiska and the potentially confounding effect of introduced Norway rats complicates the interpretation, but performing analysis using data from only Buldir and Kasatochi, combined with independent spatial correlation analysis, yielded similar patterns. We note, however, that the oscillation between 'warm' and 'cold' phases of the Pacific Ocean may be masked or accentuated by increasing global temperatures (d'Orgeville & Peltier 2009), and so our correlations should be treated as minimum estimates.

Interestingly, we found no evidence of linear trends in our reproductive success or phenology data, contrary to that found in piscivorous seabirds in the Pribilof Islands (Byrd et al. 2008) and North Atlantic (Gaston et al. 2005, Moe et al. 2009). It is likely that our relatively short time series overall (19 yr) was insufficient to document potential climate-linked trends in productivity.

Reproductive success tended to be more correlated among species on the same island than for any single species among islands. Least and crested auklets tend to provision their chicks with diets consisting of euphausiids and calanoid copepods (Bédard 1969, Day & Byrd 1989, Hunt & Harrison 1990), so the observed pattern suggests that general prey availability differences among breeding sites were more important than species-specific factors. Several studies have now examined

Table 7. Estimated marginal mean (EMM) productivity for least, crested, and whiskered auklets on Buldir, Kiska, and Kasatochi in the Aleutian Islands, from 1990 to 2008 as derived from the top-ranked generalized linear model. Differences are considered significant when confidence intervals (CI) do not overlap

Parameter	EMM	95% CI
Least auklet	0.45	0.43–0.47
Crested auklet	0.60	0.56–0.64
Whiskered auklet	0.62	0.59–0.65
Buldir	0.62	0.60–0.63
Kiska	0.35	0.29–0.41
Kasatochi	0.61	0.59–0.63

the relationships between climate indices or local oceanographic conditions and timing of breeding in the Alcidae and found trends for earlier breeding (Gaston et al. 2005, Moe et al. 2009), later breeding (Byrd et al. 2008, Wanless et al. 2009), or no trend over time (Abraham & Sydeman 2004, Durant et al. 2004, this study). While snow cover, and consequently air temperature, may delay auklet nesting at northern colonies (Sealy 1975, Moe et al. 2009), breeding colonies in the Aleutian Islands are snow-free when auklets initiate nesting in late May or early June (data not shown).

Influence of climate on reproductive performance

Overall, a higher ALPI, which corresponded with a stronger, more intense Aleutian low-pressure system, was associated with decreased productivity in least, whiskered, and crested auklets across their range in the Aleutian Islands, Alaska, although the magnitude of this relationship was variable among species and islands. A stronger Aleutian low is supposed to correspond with a larger spring algal bloom in the Bering Sea (Iida & Saitoh 2007) but also possibly with a decrease in zooplankton biomass due to cold temperature limitation (Walsh & McRoy 1986, Huntley & Lopez 1992, Pinchuk et al. 2008). In the eastern Bering Sea, warmer SST (and positive values of PDO) were predicted to result in a decrease in zooplankton biomass in surface waters during the auklets' breeding season (Coyle et al. 2008, Jin et al. 2009), likely caused by the copepods' early descent in the water column to undergo diapause (Miller et al. 1984, Miller & Nielson 1988). In the northern Bering Sea, auklets are less selective in the prey species they choose when zooplankton abundance is low (Springer & Roseneau 1985, Hunt & Harrison 1990, Russell et al. 1999). Under these conditions, prey species that are not typically exploited by auklets because of their lower energy content (e.g. *Calanus marshallae*) are

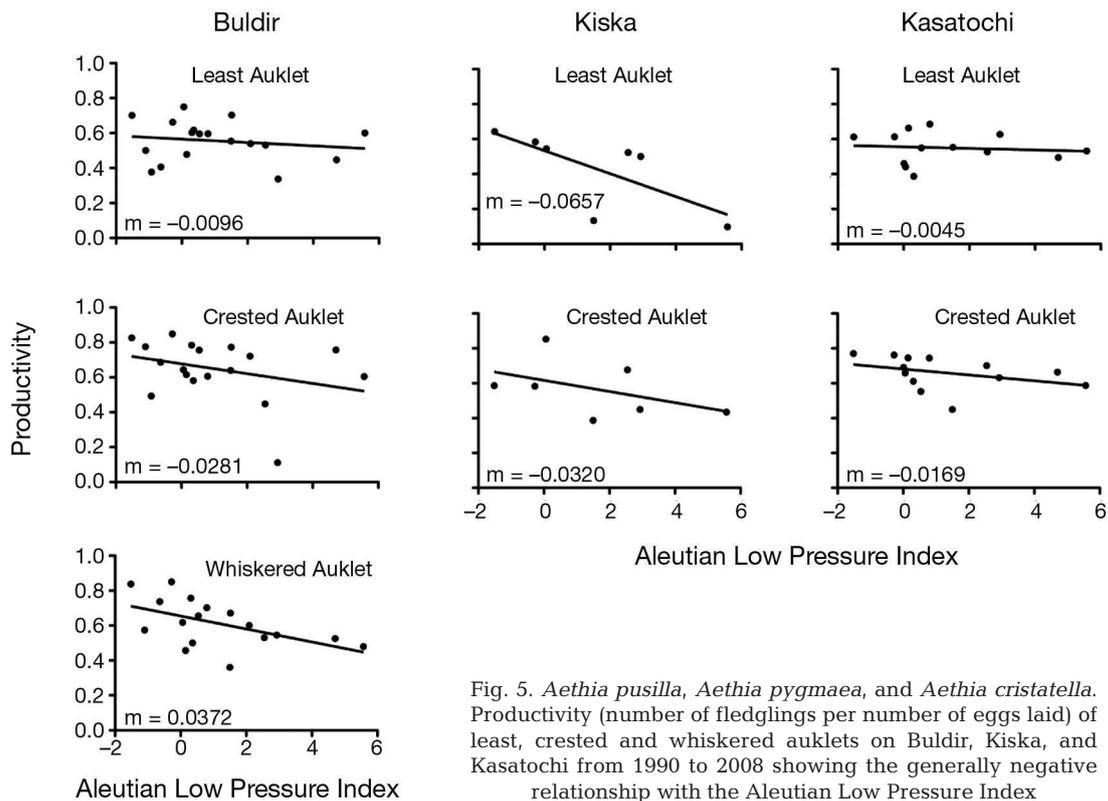


Fig. 5. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. Productivity (number of fledglings per number of eggs laid) of least, crested and whiskered auklets on Buldir, Kiska, and Kasatochi from 1990 to 2008 showing the generally negative relationship with the Aleutian Low Pressure Index

more prevalent in adult and chick diet. The same could be true in the Aleutian Islands during a stronger Aleutian low, leading to a decrease in productivity. Survival of auklet chicks is related to the quality of prey items delivered by their parents (Gall et al. 2006). In the northern California Current System, Cassin's auklets have low reproductive success in warm years when biomass of their main prey species *Neocalanus cristatus* peaked early and was consequently not abundant in chicks' diet (Sydeman et al. 2006). We do not believe that such a mismatch occurred with *Aethia* auklets in the Aleutian Islands, as chick diet composition has been relatively constant over our study period (data not shown).

Aside from indirect effects of ocean climate via impacts on productivity, direct effects are also possible and non-mutually exclusive to indirect effects (Jones et al. 2007). Heavy rainfall during early chick rearing can flood nesting crevices, resulting in chick death (Bond A.L., Jones I. L. pers. obs). The relative importance of such local, atypical effects compared to prey availability is unknown.

Another direct effect of stormy weather could operate via increased wave action, which is thought to decrease availability of zooplankton to predators (Wroblewski & Richman 1987). Unfortunately, land-based field observational studies (such as ours) alone do not provide direct information on plankton availability, and are therefore inadequate to confirm the relative roles of direct and indirect effects of ocean climate on auklet breeding success.

ALPI and NPGO

Conveniently, our 3 study islands lie nearly at the centre of the geographic area used for ALPI calculations. ALPI is also measured over the period December to March, and other studies have found significant relationships between seabird reproductive performance and winter climate (Abraham & Sydeman 2004, Durant et al. 2006, Byrd et al. 2008, Sandvik et al. 2008), presumably through climate-mediated controls on prey development, abundance, and distribution (Kitaysky & Golubova 2000, Frederiksen et al. 2006, Byrd et al. 2008). We previously found that adult survival in whiskered auklets covaried with ALPI as well, through either direct (negative effects of a stormy North Pacific) or indirect effects (i.e. bottom-up control of food supplies) (Jones et al. 2007). This contrasts partly with recent findings that reproductive success in Cassin's auklet *Ptychoramphus aleuticus* is driven by local factors rather than large-scale climatic variables (Wolf et al. 2009). Cassin's auklet chicks are fed only at night by their nocturnal parents, grow slower, and take

much longer to fledge than *Aethia* auklets (Ydenberg 1989), meaning that there is a larger timeframe over which nocturnal species' reproductive success may be affected by climatic variation. Cassin's auklets breed from southern California to the Aleutian Islands, so that large-scale climate variation is likely to be inherently more variable over their range than that of *Aethia* auklets in our study. Pacific-wide climate patterns affect the coasts of California, British Columbia, and Alaska differently and span several oceanic domains (California Current, North Pacific Current, Alaska Coastal Current). Our study of auklets in the Aleutian Islands spans one oceanic domain where large-scale climate effects would likely be more consistent than those experienced by Cassin's auklets in the study by Wolf et al. (2009).

The NPGO is an index of sea surface height and temperature anomalies over 110 to 180°W and 25 to 62°N (Di Lorenzo et al. 2008) and tends to explain more of the SST anomaly than the PDO (Bond et al. 2003). It is controlled largely by basin-wide variations in upwelling and advection in the ocean and therefore influences nutrient abundance and salinity directly (Di Lorenzo et al. 2009), which in turn affects the abundance of plankton (Di Lorenzo et al. 2008). In all cases where the relationship between Aleutian auklet productivity and either winter or spring NPGO was significant, the relationship was negative, such that a higher NPGO index corresponded with lower reproductive success. A high NPGO is associated with a stronger Aleutian Gyre in the Gulf of Alaska and a stronger North Pacific Current, the main warm-water current that runs west to east along the south of the Aleutian chain at about 40 to 50°N. Furthermore, the NPGO mode has been strengthening since about 1993 (Bond et al. 2003, Di Lorenzo et al. 2008) and may be the result of anthropogenic climate change (Di Lorenzo et al. 2008). Furthermore, the NPGO and the Aleutian low-pressure system are linked to ENSO dynamics. There is an atmospheric teleconnection between the Aleutian low and ENSO, and the North Pacific Oscillation (which is related to the NPGO) leads ENSO by approximately 8 to 12 mo (Di Lorenzo et al. unpubl. data). Biologically, this means that there should be concern about the Aleutian Islands' population of auklets, as both increased ALPI and NPGO are related to decreased reproductive success, likely through a bottom-up mechanism of limiting prey availability during either the pre-breeding period (Schroeder et al. 2009) or during chick rearing (Gall et al. 2006). Combined with vegetative succession (Roby & Brink 1986) and the detrimental effects of rats on Kiska (Major et al. 2006), the effects of oceanography or climate may be masked or dampened by colony effects.

Geospatial mapping of climate and reproductive success

The strongest geospatial correlations provided evidence based on winter SST correlations that reproductive success of least auklets on Buldir might be related to the PDO (Fig. 3). Similarly, the correlation map for whiskered auklet reproductive success on Buldir, and winter and spring SST (Fig. 3) resembled the Victoria mode of SST anomalies (Bond et al. 2003). The Victoria mode is the atmospheric expression of the NPGO in the North Pacific Oscillation, an atmospheric SLP pattern. We again found only weak correlations, possibly because of our short time scale.

The negative relationship between auklet productivity and winter SST in the Gulf of Alaska further suggests a bottom-up mechanism. Warmer SST is related to earlier timing of life history events by copepods (Mackas et al. 2007), including diapause, which may render the copepods unavailable to auklets (Goldblatt et al. 1999, Richardson 2008). Data from continuous plankton recorders in the North Pacific showed a marked decrease in copepod abundance in winter (December to March), although smaller numbers may remain accessible to seabird predators (Fort et al. 2010).

Critical to an understanding of geospatial patterns of demography-oceanography relationships in seabirds is an understanding of the birds' spatial distribution during the time of interest, which in our case is winter and spring. Knowledge of the non-breeding distributions of *Aethia* auklets, especially from the ice-free Aleutians, is poor. Whiskered auklets are believed to be non-migratory, spending winters in the vicinity of the breeding colony (Stejneger 1885, Konyukhov & Zubakin 1994, Zubakin & Konyukhov 1994, Gibson & Byrd 2007). Crested auklets winter in the eastern Aleutians, particularly in productive upwelling areas such as Unimak Pass (Renner et al. 2008, Sydeman et al. 2010). Least auklets are more abundant in the western Pacific during the winter and spring (Vyatkin 1981, Sydeman et al. 2010), while some winter in the Sea of Japan off the coast of Primoye, Russia (Shuntov 1965, Velizhanin 1977, Kondratyev et al. 2000), although the extent of mixing between Russian and North American populations is unknown. Nevertheless, large-scale climate patterns would be expected to influence the species differently during the winter, but as the relationships between ALPI and productivity among all species on all islands was similar, the differing effects may manifest themselves in a similar way.

Other factors affecting reproductive success

In general, all species' reproductive success was negatively related to the ALPI across all islands, but

local factors must also have been important. These factors included variable abundance and predation by avian predators such as the glaucous-winged gull *Larus glaucescens*, the peregrine falcon *Falco peregrinus*, and the bald eagle *Haliaeetus leucocephalus*. In addition, auklet reproductive success was affected by rainstorms during peak hatching periods when chicks were vulnerable to chilling, and earthquakes collapsing auklet breeding crevices. An extreme example of local effects was the August 7, 2008, eruption on Kasatochi, which buried the entire auklet colony site under thousands of tons of hot volcanic ash, entombing late auklet chicks and any accompanying adults (Williams et al. 2010). Another example is introduced Norway rat population that has been present on Kiska since the 1940s (Murie 1959). The rats were implicated in causing severe reproductive failure in least auklets on Kiska in 2001 and 2002 (Major et al. 2006). Auklets form a considerable portion of the rats' diet, and caches of dead birds were found annually, being especially large in the years of breeding failure (Major et al. 2007).

CONCLUSIONS

Our results indicated that ocean climate and associated effects on ocean productivity and frequency and intensity of storms influence variation in Aleutian *Aethia* auklet reproductive performance. Colony-specific effects, such as variation in the abundance and behaviour of naturally occurring and introduced predators, vegetative succession, and even seismic and volcanic activity must also be considered.

Acknowledgements. We thank the many field workers who collected this abundance of data over 20 yr. Especially noteworthy are the multi-year efforts of several people indicated with an asterisk (*): E. Andersen*, M. Barrett, D. Barton, G. Beyersdorf*, C. Brake, K. Brennehan, R. Buchheit, D. Clutter, J. Daniels, E. Drew, B. Drummond*, A. Durand, J. Dussureault*, C. Eggleston*, K. Elkin, J. Fischer*, J. C. Ford, S. Freeman*, C. Gray, M. Grinnell, J. M. Hipfner*, S. Hootman, N. Jones, T. Joyce*, P. Kappes, B. Keller, S. Kissler, H. Knechtel*, N. Konyukhov, S. Lantz, A. Larned, K. Lindquist, G. Loh, S. Lorenz, J. Marais, M. McClintock, L. Meehan, J. Mueller, M. Murphy*, R. Orben, M. Ortwerth, A. Palmer, L. Parker, K. Payne, J. Petersen, D. Rehder, H. Renner*, A. Ritchie, N. Rojek*, K. Russell, P. Ryan, G. Samson, S. Sabora, C. Schlawe, N. Seferovic, K. Shea, E. Sommer, L. Spitzer*, A. Stoertz, A. Stover, S. Syria*, G. Thomson, C. VanStratt, R. Walder, and H. Walsh. The MV 'Tiġlaġ' and her crews provided logistical support. The North Pacific Research Board (grant no. 638), Natural Sciences and Engineering Research Council of Canada, Alaska Maritime National Wildlife Refuge, and Northern Scientific Training Program of Indian and Northern Affairs Canada provided financial support for this research. This is publication no. 283 of the North Pacific Research Board. A. R. Breton, A. P. Lusignan, and

G. J. Robertson gave statistical advice, G. W. Humphries assisted with the remotely sensed data, and T. W. Chapman, E. H. Miller, G. J. Robertson, M. Frederiksen, R. P. Wilson, and 3 anonymous reviewers provided improvements on previous drafts of this manuscript.

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Editorial responsibility: Rory Wilson,
Swansea, UK

Submitted: March 10, 2010; Accepted: December 3, 2010
Proofs received from author(s): February 10, 2011

Reproductive success of planktivorous seabirds in the North Pacific is related to ocean climate on decadal scales

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Marine Ecology Progress Series 424:205–218 (2011)

Supplement. Sample sizes, and raw demographic and phenological data for auklets in the Aleutian Islands, Alaska

Table S1. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. The number of breeding pairs of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) studied on the Aleutian islands Buldir, Kiska, and Kasatochi from 1990 to 2008. ‘–’ indicates years in which no data were collected

Year	Buldir			Kiska		Kasatochi	
	LEAU	CRAU	WHAU	LEAU	CRAU	LEAU	CRAU
1990	61	67	–	–	–	–	–
1991	81	74	46	–	–	–	–
1992	89	79	55	–	–	–	–
1993	44	49	54	–	–	–	–
1994	64	67	57	–	–	–	–
1995	64	66	67	–	–	–	–
1996	57	66	57	–	–	54	43
1997	84	82	90	–	–	91	76
1998	76	70	78	–	–	95	104
1999	–	–	–	–	–	100	110
2000	69	78	70	–	–	89	110
2001	65	75	75	210	31	85	109
2002	50	81	100	205	23	94	109
2003	83	45	44	208	20	110	136
2004	81	67	66	197	31	91	107
2005	73	79	70	–	–	93	103
2006	84	73	68	180	34	77	88
2007	68	66	67	173	36	124	143
2008	67	75	68	157	29	98	109

Table S2. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. Reproductive success (number of chicks fledged per number of eggs laid) of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) on the Aleutian islands Buldir, Kiska, and Kasatochi from 1990 to 2008. Sample sizes are listed in Table S1. ‘–’ indicates years in which no data were collected

Year	Buldir			Kiska		Kasatochi	
	LEAU	CRAU	WHAU	LEAU	CRAU	LEAU	CRAU
1990	0.38	0.49	–	–	–	–	–
1991	0.62	0.58	0.50	–	–	–	–
1992	0.54	0.72	0.60	–	–	–	–
1993	0.50	0.78	0.57	–	–	–	–
1994	0.41	0.69	0.74	–	–	–	–
1995	0.70	0.77	0.67	–	–	–	–
1996	0.60	0.61	0.70	–	–	0.69	0.74
1997	0.60	0.76	0.66	–	–	0.55	0.55
1998	0.45	0.76	0.53	–	–	0.49	0.66
1999	–	–	–	–	–	0.46	0.69
2000	0.48	0.62	0.46	–	–	0.66	0.75
2001	0.55	0.64	0.36	0.13	0.39	0.55	0.45
2002	0.60	0.60	0.48	0.10	0.43	0.53	0.59
2003	0.34	0.11	0.55	0.50	0.45	0.63	0.63
2004	0.53	0.45	0.53	0.52	0.68	0.53	0.70
2005	0.60	0.78	0.76	–	–	0.39	0.61
2006	0.75	0.64	0.62	0.54	0.85	0.44	0.66
2007	0.66	0.85	0.85	0.58	0.58	0.61	0.76
2008	0.70	0.83	0.84	0.64	0.59	0.61	0.77

Table S3. *Aethia pusilla*, *Aethia pygmaea*, and *Aethia cristatella*. Timing of breeding (mean egg hatch date) of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) on the Aleutian islands Buldir, Kiska, and Kasatochi from 1990 to 2008. ‘–’ indicates years in which no data were collected

Year	Buldir			Kiska		Kasatochi	
	LEAU	CRAU	WHAU	LEAU	CRAU	LEAU	CRAU
1990	27 June	25 June	24 June	–	–	–	–
1991	30 June	29 June	27 June	–	–	–	–
1992	29 June	26 June	18 June	–	–	–	–
1993	26 June	27 June	22 June	–	–	–	–
1994	24 June	25 June	19 June	–	–	–	–
1995	29 June	29 June	25 June	–	–	–	–
1996	25 June	26 June	22 June	–	–	25 June	30 June
1997	27 June	28 June	24 June	–	–	28 June	01 July
1998	30 June	05 July	23 June	–	–	03 July	03 July
1999	–	–	–	–	–	30 June	29 June
2000	25 June	29 June	17 June	–	–	28 June	29 June
2001	26 June	29 June	22 June	28 June	–	28 June	30 June
2002	25 June	25 June	24 June	5 July	2 July	27 June	27 June
2003	27 June	02 July	25 June	2 July	–	25 June	29 June
2004	28 June	05 July	21 June	27 June	4 July	30 June	28 June
2005	25 June	25 June	18 June	–	–	29 June	29 June
2006	30 June	09 July	27 June	1 July	7 July	03 July	03 July
2007	27 June	23 June	17 June	28 June	28 June	30 June	01 July
2008	24 June	26 June	21 June	28 June	29 June	30 June	02 July