

Range-wide reproductive consequences of ocean climate variability for the seabird Cassin's Auklet

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Abstract. We examine how ocean climate variability influences the reproductive phenology and demography of the seabird Cassin's Auklet (*Ptychoramphus aleuticus*) across ~2500 km of its breeding range in the oceanographically dynamic California Current System along the west coast of North America. Specifically, we determine the extent to which ocean climate conditions and Cassin's Auklet timing of breeding and breeding success covary across populations in British Columbia, central California, and northern Mexico over six years (2000–2005) and test whether auklet timing of breeding and breeding success are similarly related to local and large-scale ocean climate indices across populations. Local ocean foraging environments ranged from seasonally variable, high-productivity environments in the north to aseasonal, low-productivity environments to the south, but covaried similarly due to the synchronizing effects of large-scale climate processes. Auklet timing of breeding in the southern population did not covary with populations to the north and was not significantly related to local oceanographic conditions, in contrast to northern populations, where timing of breeding appears to be influenced by oceanographic cues that signal peaks in prey availability. Annual breeding success covaried similarly across populations and was consistently related to local ocean climate conditions across this system. Overall, local ocean climate indices, particularly sea surface height, better explained timing of breeding and breeding success than a large-scale climate index by better representing heterogeneity in physical processes important to auklets and their prey. The significant, consistent relationships we detected between Cassin's Auklet breeding success and ocean climate conditions across widely spaced populations indicate that Cassin's Auklets are susceptible to climate change across the California Current System, especially by the strengthening of climate processes that synchronize oceanographic conditions. Auklet populations in the northern and central regions of this ecosystem may be more sensitive to changes in the timing and variability of ocean climate conditions since they appear to time breeding to take advantage of seasonal productivity peaks.

Key words: California Current System; Cassin's Auklet; climate change; climate variability; demography; ocean; phenology; *Ptychoramphus aleuticus*; range; reproduction; seabird.

INTRODUCTION

Climate variability has been documented to have marked effects on the phenology, demographic rates, and abundance of many species (Stenseth et al. 2002, Walther et al. 2002, Parmesan 2006). However, most studies that examine the effects of climate variability on population processes focus on single populations over

time but do not assess these relationships across species' ranges (Frederiksen et al. 2005, Parmesan 2006). The limited number of studies that examine multiple populations have shown that population responses to climate conditions can vary across space (Sæther et al. 2003, Visser et al. 2003, Grosbois et al. 2006, Cheal et al. 2007), and determining the spatial scale over which populations respond similarly to climate has conservation relevance. For example, when demographic rates of populations covary similarly in response to the same climate conditions, unfavorable climate conditions across species' ranges can produce declines across multiple populations, reducing the probability of recolonization of depleted populations and increasing the risk of population extinction (Morris and Doak 2002). In addition, understanding spatial variation in climate

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forcing on population parameters is increasingly needed to inform range-wide predictions of how anthropogenic climate change will affect species (Hannah et al. 2002).

Many studies that examine climate-related variation across populations have used large-scale climate indices that integrate climate processes over broad spatial scales (Stenseth et al. 2002, Forchhammer and Post 2004). Indices of large-scale processes such as the El Niño Southern Oscillation and the North Atlantic Oscillation are readily available and easy to use (Stenseth et al. 2003). However, these large-scale indices may not be at the appropriate scale to capture mechanistic links between climate processes and the local ecology of study species (Coulson et al. 2001). In theory, local climate processes at finer temporal scales should better explain climate-related population variation since local physical processes should be more closely linked to local resource variability (Forchhammer and Post 2004, Hallett et al. 2004). Thus where possible, both local and large-scale climate indices should be assessed. In addition, the vast majority of studies that have examined multiple populations focus on the effects of climate variability on phenology and abundance (Stenseth et al. 1999, Post and Forchhammer 2002, Sanz 2002, Saether et al. 2003, Visser et al. 2003, Grotan et al. 2005, Parmesan 2006, Cheal et al. 2007, Sæther et al. 2007; but see Grosbois et al. 2006, Frederiksen et al. 2007), while few examine effects on the demographic rates that underlie population dynamics.

Here we examine how local and large-scale ocean climate variability influence the reproductive phenology and demography of the planktivorous seabird Cassin's Auklet (*Ptychoramphus aleuticus*; see Plate 1) across ~2500 km of its breeding range in an oceanographically dynamic marine ecosystem along the west coast of North America, the California Current System. Specifically, we investigate whether timing of breeding and breeding success of populations in British Columbia, central California, and northern Mexico covary and are similarly influenced by local and large-scale climatic variables over six years (2000–2005). Our study is one of the first to investigate latitudinal variation in climate forcing on demographic rates of geographically independent populations using both local and large-scale climate indices.

Cassin's Auklets have proven to be sensitive indicators of ocean climate conditions (Hyrenbach and Veit 2003, Bertram et al. 2005, Sydeman et al. 2006, Lee et al. 2007). Because they feed primarily upon zooplankton (e.g., krill, copepods), they are more directly linked to primary production and associated ocean climate processes than are predators with more diverse diets foraging higher in the trophic web. Long-term studies of Cassin's Auklets in the central California Current System, the Farallon Islands, have found that reproductive phenology and breeding success fluctuate from year to year in relation to oceanographic conditions (local sea surface temperature and the large-scale

Southern Oscillation Index, respectively), presumably because these processes influence the availability of their prey species (Abraham and Sydeman 2004, Lee et al. 2007). However, how auklet reproductive phenology and demography respond to local and large-scale ocean climate processes across the California Current System has yet to be investigated. This question holds high conservation relevance because the Farallon Islands auklet population has declined in size by 75% or more during the past three decades (Lee et al. 2007) and experienced unprecedented breeding failures in 2005 and 2006 (Sydeman et al. 2006; Point Reyes Bird Observatory Conservation Science and USFWS, W. J. Sydeman, *unpublished data*), which have been linked to ocean climate conditions. Thus understanding how auklet populations throughout the California Current System respond to ocean climate conditions is an important component of assessing the range-wide vulnerability of auklets to ocean climate change.

Local ocean climate conditions that influence productivity and prey abundance for auklets are heterogeneous across the California Current System. Specifically, wind-driven coastal upwelling (i.e., the upwelling of nutrient-rich waters to the ocean surface) is the dominant physical process influencing ocean productivity (Huyer 1983), and upwelling timing and strength vary locally by latitude. Upwelling is seasonal and weak in the northern current (inhabited by the British Columbia study population), seasonal and strong in the central current (inhabited by the central California study population), and year-round and moderate strength in the southern current (inhabited by the northern Mexico study population) (Legaard and Thomas 2006, Schwing et al. 2006). Thus we expected that mean reproductive parameters and their functional relationships to ocean climate conditions would differ among Cassin's Auklet populations breeding across this system.

Local heterogeneity in ocean climate conditions in the California Current System is moderated and homogenized by the large-scale El Niño Southern Oscillation (ENSO). The ENSO produces periodic El Niño events, which transport warm water poleward through the California Current, driving high temperatures, high coastal sea levels, and low productivity conditions, as well as periodic cold water, high productivity La Niña events (Legaard and Thomas 2006). Because auklet ocean foraging environments are differentially shaped by local and large-scale climate forcing, it was less clear whether ocean conditions and auklet reproductive parameters would covary similarly across widely spaced sites and whether local or large-scale climate processes would be more strongly linked to auklet reproductive parameters. We predicted the following: (1) auklet demographic rates would covary strongly when the synchronizing effects of large-scale oceanographic processes (e.g., ENSO events) were also strong; (2) reproductive phenology and demography would be linked to ocean climate conditions across sites, but

functional relationships would differ; and (3) local-scale oceanographic indices would better explain variance in reproductive phenology and demography than large-scale indices, since they would be more strongly linked to auklet prey availability.

METHODS

Study areas.—We studied Cassin's Auklet reproductive ecology at the breeding islands of three of the largest populations in the California Current System: Triangle Island, British Columbia, Canada (50.87° N, 129.08° W) in the northern California Current System; Southeast Farallon Island (SE Farallon Island), California, USA (37.70° N, 123.00° W) in the central California Current System; and West San Benito Island (San Benito Island), Baja California, México (28.30° N, 115.57° W) in the southern California Current System (see Appendix A map).

Ocean climate conditions.—To characterize local ocean climate conditions at each study site, we chose three fine-scale indices related to oceanic productivity and one direct index of productivity: upwelling intensity, sea surface temperature, sea surface height, and chlorophyll *a* surface concentration, respectively. We used satellite imagery at the highest spatial and temporal resolutions available to construct monthly mean indices of these variables (see Appendix B for detailed information on data sources). While satellite-derived sea surface temperature reflects the heat content of the uppermost layer, satellite-derived sea surface height integrates the heat content of the water column at all depths as well as current flow; negative sea surface height values reflect colder water and offshore water movement, which occur during periods of upwelling. We used Bakun's upwelling index to estimate local upwelling intensity (Schwing et al. 1996); positive values indicate upwelling, whereas negative values indicate downwelling. Local ocean climate conditions were averaged within a 100-km radius of each study site based on an estimated maximum foraging distance of 80 km for breeding auklets (Yen et al. 2004, Boyd et al. 2008).

We chose the Northern Oscillation Index (NOI) as the large-scale index of ocean climate conditions across study sites, since it effectively integrates the atmospheric circulation patterns that influence the west coast of North America (Schwing et al. 2002). The NOI is dominated by interannual variation associated with El Niño and La Niña events forced by the El Niño Southern Oscillation, and measures the difference in the monthly sea level pressure anomaly of the North Pacific High in the Northeast Pacific and that of the low pressure system in the western tropical Pacific near Darwin, Australia (Schwing et al. 2002).

We measured covariation in local ocean climate conditions across study sites with two approaches. First, we calculated Pearson correlation coefficients (r) for pairwise site comparison of monthly mean values for

each climate variable across the six-year study period ($n = 72$ per variable per site; 6 yr \times 12 months). Next, we measured covariation of local ocean climate conditions after removing long-term trends and seasonal trends in climate variables. We detrended time series data for each variable with a linear least squares regression to remove long-term trends and with a linear least squares regression using month as the independent variable to remove seasonal trends. The covariation between detrended variables was estimated from the r^2 values of linear least squares regressions using pairwise site comparisons of residuals.

In testing relationships between ocean climate conditions and auklet reproductive parameters, ocean climate variables were averaged over three time periods for each population: egg-laying (beginning two standard deviations [SD] before and ending two SD after the mean egg-laying date across 2000–2005), breeding (beginning two SD before the mean egg-laying date and ending two SD after the mean fledge date), and chick-rearing (beginning two SD before the mean hatch date and ending two SD after the mean fledge date) (see Appendix C for exact time periods). Because the values of ocean climate variables often spanned different ranges for each population (e.g., sea surface temperatures were colder at higher latitudes and warmer at lower latitudes), annual means of ocean climate variables for each time period (i.e., egg-laying, breeding, and chick-rearing) were recalculated as standardized anomalies as follows: (annual mean – average of means for 2000–2005)/SD of means for 2000–2005.

Cassin's Auklet reproductive parameters.—We studied Cassin's Auklets reproductive ecology in natural burrows at Triangle Island using methods described in Bertram et al. (2001) and in nest boxes at SE Farallon Island and San Benito Island using similar methods described in Abraham and Sydeman (2004). We measured the following reproductive parameters for each population: egg-laying dates, breeding success (i.e., number of chicks fledged) for first and all attempts, and chick fledging masses (g), where chick fledging masses served as a proxy for the quality of the annual breeding effort. In all populations, Cassin's Auklets will relay if the first breeding attempt fails; at SE Farallon Island and southward, Cassin's Auklets are able to rear a second chick after fledging the first chick in some years. Timing of egg-laying and chick fledging masses were based on each pair's first breeding attempt.

During several years of our study, we arrived at San Benito Island after incubation had begun. If we did not observe the egg-laying date of a pair, we back-calculated lay date to be hatch date minus 39 d, using the mean 39-d incubation period observed for Cassin's Auklets (Ainley et al. 1990). When pairs failed during incubation, we were not able to back-calculate their lay dates; therefore, we estimated these lay dates as the mean egg-laying date of successful pairs that laid during the unobserved period. We did not obtain chick fledging

mass from 2002 at San Benito Island due to a reduced sampling effort or from 2005 at SE Farallon Island because no chicks were produced, so we analyzed fledging mass data for four years.

For each reproductive parameter, we tested for differences across populations and years and estimated the variance associated with population vs. year. To test for differences in egg-laying dates and chick fledging masses, we used a random effects variance components analysis with Type III ANOVA estimation, in which population and year were random categorical factors. Chick fledging masses were standardized by dividing each value by the mean adult mass specific to each population, since adult mass increases with latitude. To test for differences in breeding success, we used logistic regression where the nominal dependent variable was fledged chick (1) or unfledged chick (0) and explanatory variables were population and year. We approximated whether relatively more variance in breeding success was explained by population vs. year by comparing the goodness of fit G^2 deviance statistic of models with population or year as the categorical predictor variable. Since the deviance G^2 statistic measures the unexplained variability after fitting the model, the model with the lower deviance statistic was judged to better explain variability in breeding success.

We measured the covariation of egg-laying, breeding success, and scaled chick fledging mass across populations by calculating Pearson correlation coefficients for annual mean values of pairs of populations, although sample sizes were small ($n = 6$ for lay date and breeding success, $n = 4$ for fledging mass).

Relationships between ocean climate and auklet reproductive parameters.—We used General Linear Models (GLMs) to test for relationships between auklet reproductive parameters, including annual mean lay date, annual mean breeding success, and annual mean scaled fledging mass (response variables), and ocean climate conditions (predictor variables). For each auklet response variable, we tested relationships across populations using population identity as a categorical predictor and either local ocean climate conditions expressed as standardized anomalies or the large-scale NOI as continuous predictor variables. We followed these analyses by testing population-specific relationships between each auklet reproductive parameter and significant predictor variables identified in the population-wide analyses to assess the strength and shape of functional relationships for each population.

RESULTS

Ocean climate conditions.—Local ocean climate conditions and productivity differed across study sites in the monthly means and variance of all measured variables, indicating that local foraging environments for auklet populations were heterogeneous (Fig. 1). The local oceanographic environment shifted from seasonally variable upwelling and high productivity conditions at

the British Columbia and central California sites to more aseasonal year-round upwelling and lower productivity conditions at the northern Mexico site (see Appendix D for comparative data). Monthly means of upwelling intensity, sea surface temperature, and sea surface height were significantly correlated across study sites, suggesting that ocean climate conditions covaried similarly across the California Current System, while chlorophyll *a* surface concentrations were not well correlated across sites (Appendix E). When year trends were removed, significant correlations across sites remained, indicating that upwelling intensity, surface temperature, and surface height covaried despite long-term trends during the study period (Appendix E). When seasonal trends were removed, only monthly means in surface temperature and surface height were significantly correlated across sites, suggesting that covariation in these variables was driven by both local and large-scale climate forcing (Appendix E).

Cassin's Auklet reproductive parameters.—Cassin's Auklet timing of breeding differed significantly across populations and years ($F[\text{population}]_{2,1156} = 187.20$, $P < 0.0001$; $F[\text{year}]_{5,1156} = 2.82$, $P = 0.074$; Fig. 2); a significant interaction ($P < 0.001$) indicated that the effect of year varied by population. Most of the variance in lay date was associated with population (72.9%) rather than year (1.4%). Timing of breeding of the British Columbia and central California populations began in March to early April and spanned one to two months, with high covariance between mean egg-laying dates (Appendix F). In contrast, timing of breeding for the northern Mexico population began three to four months earlier and was more protracted, spanning four to six months with an early large peak (November–January) and late small peak (February–April).

Annual breeding success differed significantly across populations and years for first breeding attempts ($n = 1157$, $G^2 = 214.15$, $P < 0.001$; Fig. 2). A comparison of the G^2 statistic for the full model with explanatory variables of population and year ($G^2 = 214.15$) vs. reduced models with breeding success as a function of population ($G^2 = 37.57$) or year ($G^2 = 199.51$) suggests that population explains more of the variance than year. Annual breeding success for first attempts was significantly correlated between the British Columbia and central California populations and strongly correlated across all populations (Appendix F). When all breeding attempts were analyzed, breeding success differed significantly across populations and years, and average chick production during 2000–2005 was highest for central California auklets (breeding success [mean \pm SD]: Triangle, 0.56 ± 0.25 ; SE Farallon, 0.77 ± 0.42 ; San Benito, 0.54 ± 0.23 ; Fig. 2). Annual breeding success for all attempts was also strongly correlated across all populations (Appendix F).

For scaled chick fledging masses analyzed in 2000, 2001, 2003, and 2004, a significant interaction ($P < 0.001$) between population and year indicated that

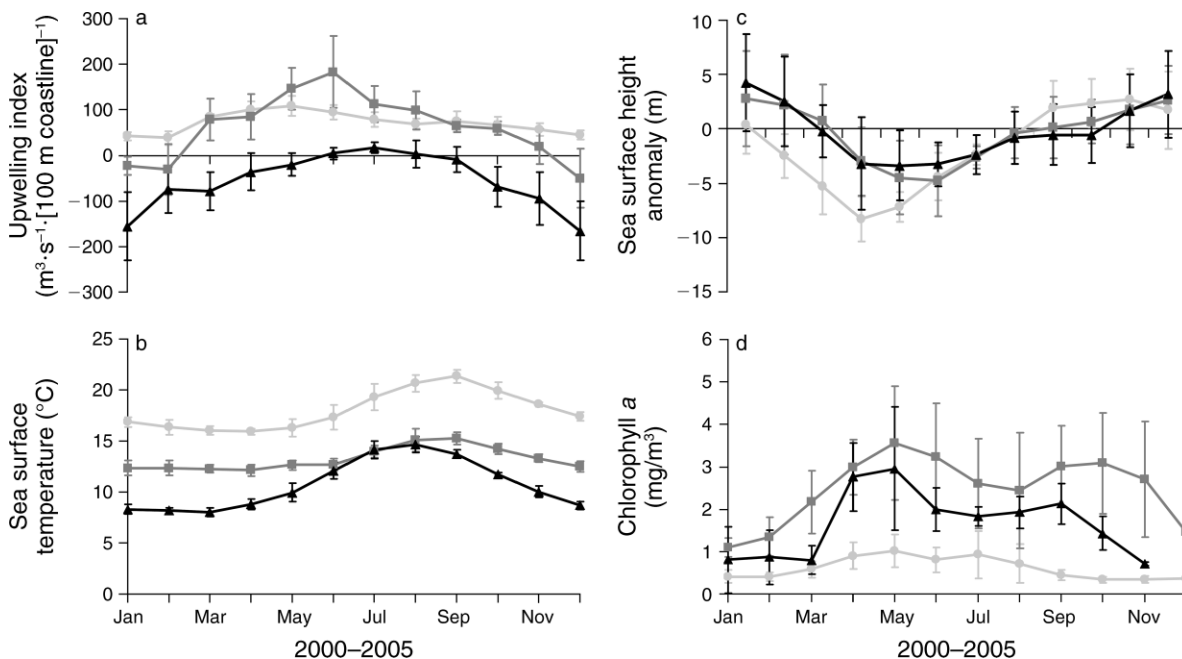


FIG. 1. Monthly values (mean \pm SD) of oceanographic and productivity parameters within a 100-km radius of each study site averaged across 2000–2005 for (a) upwelling index, (b) sea surface temperature, (c) sea surface height anomaly, and (d) chlorophyll *a* surface concentration. Values for Triangle Island are depicted as black triangles, SE Farallon Island as dark gray squares, and San Benito Island as light gray circles.

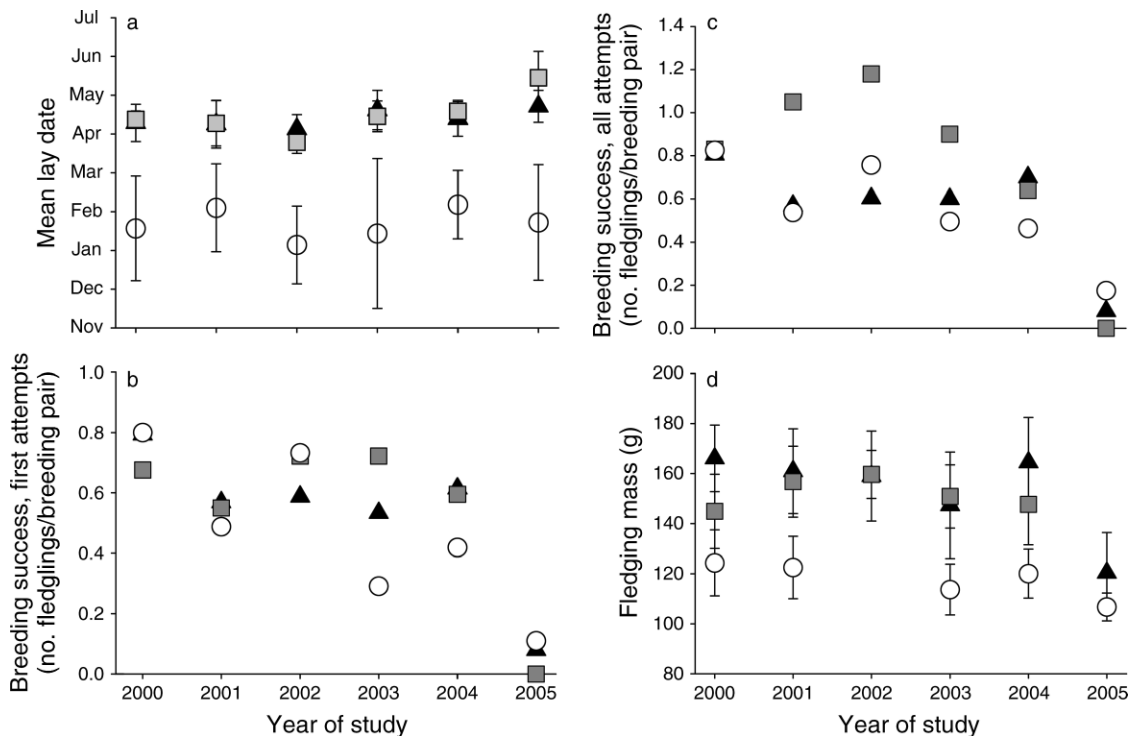


FIG. 2. Annual values (mean \pm SD) of (a) lay dates, (b) breeding success for first attempts, (c) breeding success for all attempts, and (d) chick fledging masses (unscaled) for each population. Triangle Island values are depicted as black triangles, SE Farallon Island as gray squares, and San Benito Island as open circles.

TABLE 1. Linear relationships between ocean climate predictor variables and annual mean lay date and breeding success for first and all breeding attempts across populations.

Response variable	Predictor variables	β	t	P	Model r^2
Lay date (first)	SSH	0.51	2.80	0.014	0.46
	CHL	-0.40	-2.17	0.046	...
	NOI	-0.13	-0.51	0.615	0.00
Breeding success (first)	SSH	-0.17	-3.36	0.004	0.38
	NOI	0.09	1.37	0.189	0.05
Breeding success (all)	SSH	-0.21	-3.15	0.006	0.35
	NOI	0.03	0.36	0.722	0.00

Notes: Oceanographic variables are abbreviated as follows: sea surface height (SSH), surface chlorophyll *a* concentration (CHL), and Northern Oscillation Index (NOI). $N = 18$ for all predictor variables.

fledging masses differed among populations only in some years ($F[\text{population}]_{2,425} = 16.70, P < 0.01$; $F[\text{year}]_{3,425} = 1.87, P = 0.23$; Fig. 2). More of the variance in chick fledging mass was associated with population (27.8%) than year (1.2%).

Relationships between ocean climate conditions and auklet reproductive parameters.—Local sea surface height and chlorophyll *a* concentration were significant predictors of mean lay date across populations (Table 1; Fig. 3), indicating that auklets laid later when sea surface heights were higher and surface chlorophyll *a* concentrations were lower. In population-specific anal-

yses, sea surface height and chlorophyll *a* concentration were significant predictors of lay date for the British Columbia population (sea surface height, $\beta = 0.53, t = 4.83, P = 0.017$; chlorophyll *a* concentration, $\beta = -0.56, t = -5.12, P = 0.014, r^2 = 0.98, n = 6$), and sea surface height was a significant predictor for the California population (sea surface height, $\beta = 0.89, t = 3.83, P = 0.019, r^2 = 0.79, n = 6$). We found no significant relationships between ocean climate conditions and lay date for the Mexico population (Fig. 3). The large-scale Northern Oscillation Index (NOI) was not a significant

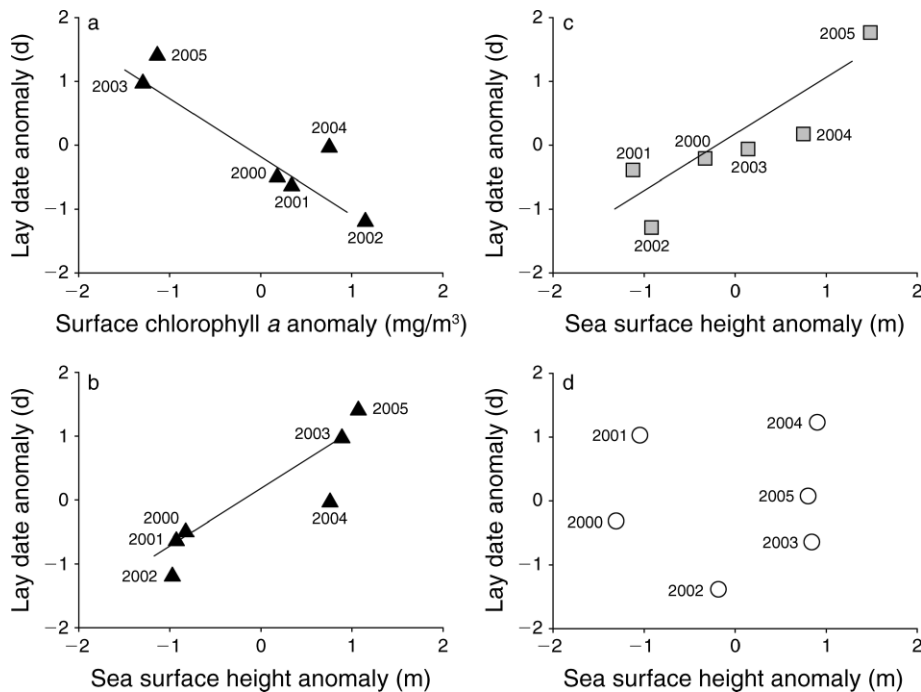


FIG. 3. Relationships between the annual mean lay date anomaly and standardized anomalies of (a) surface chlorophyll *a* concentration at Triangle Island (black triangles), (b) sea surface height at Triangle Island (black triangles), (c) sea surface height at SE Farallon Island (gray squares), and (d) sea surface height at San Benito Island (open circles). The lay date anomaly for each year was calculated as [(annual mean - average of annual means for 2000–2005)]/SD of annual means for 2000–2005, where the annual mean refers to the mean lay date each year. Using the same formula, the surface chlorophyll *a* anomaly and sea surface height anomaly were calculated for each year, where the mean refers to mean chlorophyll *a* or mean sea surface height during the egg-laying period for that year. Significant linear relationships are shown. Years 2000 to 2005 are indicated beside each data point.

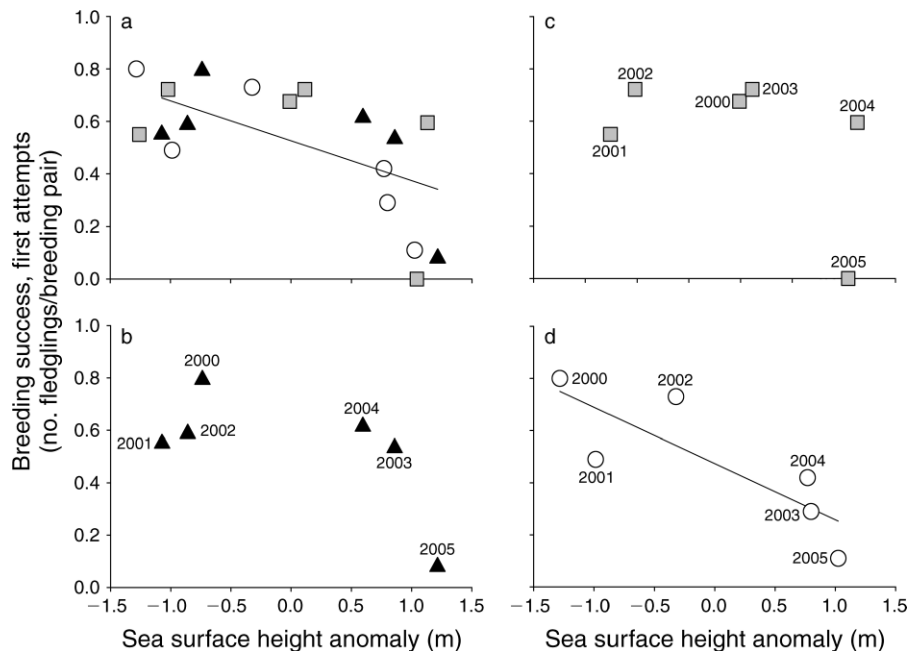


FIG. 4. Relationships between annual mean breeding success for first attempts and the sea surface height anomaly (a) across populations, (b) at Triangle Island, (c) at SE Farallon Island, and (d) at San Benito Island. Calculations use the same formula as for Fig. 3. Significant linear relationships are shown. Triangle Island values are depicted as black triangles, SE Farallon Island as gray squares, and San Benito Island as open circles. Years 2000 to 2005 are indicated beside each data point.

predictor of lay date across populations (Table 1) or on a population-specific basis.

In testing for relationships between ocean climate conditions and breeding success of first and all attempts, local sea surface height was a significant predictor across populations (Table 1; Figs. 4 and 5), indicating that auklets produced more chicks in years when sea surface heights were lower during the breeding season. Population was not a significant categorical predictor, and there was no significant interaction between population and sea surface height, indicating that the effect of sea surface height did not vary by population. In population-specific analyses, we found significant relationships for first breeding attempts only for the Mexico population (sea surface height, $\beta = -0.22$, $t = -2.92$, $P = 0.043$, $r^2 = 0.68$, $n = 6$), although the British Columbia and California populations followed similar trends (Fig. 4). For all breeding attempts, we found significant relationships only at the British Columbia and California populations (Triangle, $\beta = -0.18$, $t = -2.61$, $P = 0.06$, $r^2 = 0.63$; SE Farallon, $\beta = -0.31$, $t = -2.23$, $P = 0.09$, $r^2 = 0.55$, $n = 6$; Fig. 5). The large-scale NOI was not a significant predictor of success of first or all breeding attempts across populations (Table 1) or on a population-specific basis.

Scaled chick fledging masses across populations were significantly higher when sea surface heights during the chick rearing period were lower (all populations, $\beta = -0.74$, $t = -4.67$, $P < 0.001$, $r^2 = 0.61$, $n = 12$; Triangle, P

$= 0.133$; SE Farallon, $P = 0.088$; San Benito, $P = 0.062$, $n = 4$).

DISCUSSION

Although many studies have demonstrated that ocean climate strongly influences phenology and demography, few studies have examined these relationships across species' ranges. In the dynamic California Current System, long-term studies have linked annual variation in seabird demographic rates to variability in ocean climate conditions at single sites (Sydeman et al. 2001, Gjerdrum et al. 2003). However, how seabird phenology and demography, ocean foraging environments, and the relationships among them vary across this dynamic marine ecosystem is not well understood, but has significant conservation implications for seabirds in the context of future climate change. Our study found that Cassin's Auklet timing of breeding covaried strongly and was similarly related to climate conditions for populations in the northern and central regions of the current characterized by seasonal productivity. Breeding success covaried strongly across all populations and was consistently related to the same ocean climate variable (sea surface height) across the California Current System. Local ocean climate indices, particularly sea surface height, better explained timing of breeding and breeding success than a composite large-scale climate index, the Northern Oscillation Index (NOI). Overall, the significant relationships we detected between Cassin's Auklet breeding success and oceanographic condi-

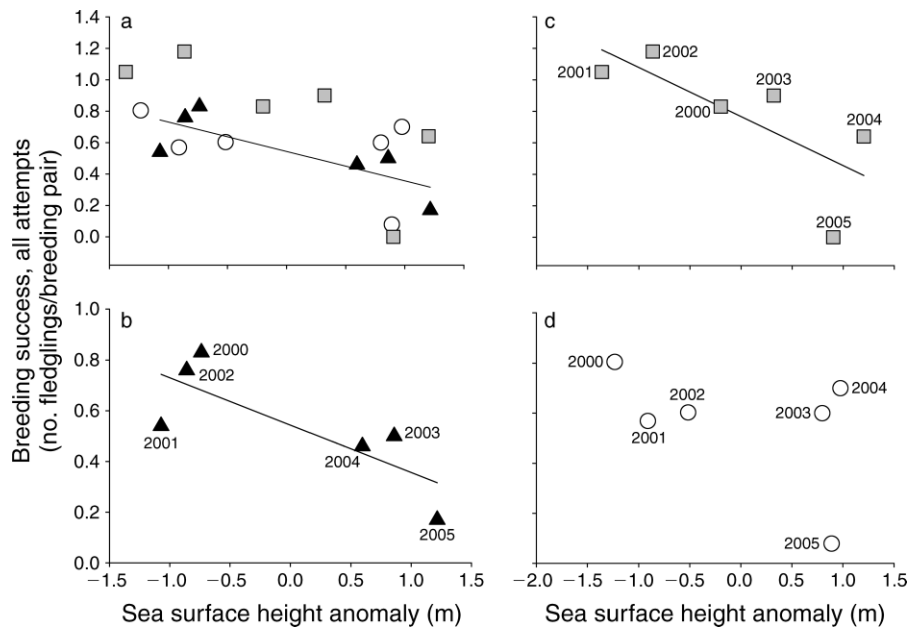


FIG. 5. Relationships between annual mean breeding success for all attempts and the sea surface height anomaly (a) across populations, (b) at Triangle Island, (c) at SE Farallon Island, and (d) at San Benito Island. Calculations use the same formula as for Fig. 3. Significant linear relationships are shown. Triangle Island values are depicted as black triangles, SE Farallon Island as gray squares, and San Benito Island as open circles. Years 2000 to 2005 are indicated beside each data point.

tions across widely spaced populations indicate that Cassin's Auklets are susceptible to climate change across the California Current System, especially by the strengthening of climate processes that synchronize oceanographic conditions.

Patterns of ocean climate conditions and auklet reproductive parameters across sites

We found that foraging environments used by Cassin's Auklets during the breeding season are influenced by a complex interplay between local climate processes that create oceanographic heterogeneity across sites and remote large-scale climate processes that synchronize sites. Local processes, particularly latitudinal gradients in upwelling-favorable winds and sea surface temperature (Fig. 1), resulted in different ocean foraging environments that varied from colder, seasonally variable upwelling, high-productivity conditions to the north to warmer, aseasonal upwelling, lower-productivity conditions to the south. Four large-scale climate events also influenced auklet foraging environments during our six-year study period: (1) a series of cooler La Niña-like years during 2000–2002; (2) the anomalous intrusion of cold subarctic water in spring and summer 2002 that permeated the entire system (Venrick et al. 2003, Pérez-Brunius et al. 2006); (3) the short-lived, mild El Niño event in winter 2002–2003 (Venrick et al. 2003); and (4) an unusual large-scale atmospheric circulation pattern that resulted in delayed upwelling in spring and summer 2005 (Schwing et al. 2006) and an anomalous interruption in upwelling-

favorable winds in early summer 2005 (Sydeman et al. 2006). This unusual event in 2005 was evident in local sea surface temperature and wind patterns at the central California site (Sydeman et al. 2006) and at the British Columbia and northern Mexico sites (S. G. Wolf, unpublished data). The signatures of large-scale El Niño Southern Oscillation (ENSO)-related climate events on local sea surface temperature and sea surface height are evident in the synchronized switch from cooler to warmer conditions in 2003 across study sites (Appendix G). Thus large-scale climate processes appear to have increased covariance in local ocean climate conditions across auklet foraging environments.

The significant differences in reproductive phenology and demography across Cassin's Auklet populations are consistent with increasing evidence that seabirds show pronounced spatiotemporal variation in their demographic parameters (Frederiksen et al. 2005, Frederiksen et al. 2007), and were expected based on the pronounced heterogeneity in auklet foraging environments. Auklet timing of breeding in northern Mexico began three to four months earlier than the northern populations, such that auklet timing of breeding across sites was asynchronous. Overall breeding success during the study period was significantly higher and more variable in the central California population (SE Farallon, 0.77 ± 0.42 ; compared to Triangle [0.56 ± 0.25] and San Benito [0.54 ± 0.23]), due in large part to its high success in rearing second broods in three years (2001–2003; S. G. Wolf, unpublished data). Breeding success of the central California population fluctuated between high produc-



PLATE 1. Cassin's Auklet adult at San Benito Island study site. Photo credit: S. G. Wolf.

tivity years during the cooler-water La Niña-like conditions in 2001–2002 when auklets reared nearly twice as many chicks as did the British Columbia and northern Mexico populations, to a catastrophic year of unprecedented breeding failure during the unusual oceanographic event in 2005 (Sydeman et al. 2006). Despite differences in mean breeding parameters, we detected strong covariation in timing of breeding across northern populations and in breeding success across all populations that appear to be linked to covariance in ocean climate conditions across sites and to consistent relationships between ocean climate conditions and breeding parameters.

Timing of breeding and ocean climate

Cassin's Auklets in the British Columbia and central California populations appear to adjust timing of breeding to local ocean climate conditions, since auklets on average laid earlier in years with lower March–April sea surface heights that indicate colder water with more upwelling. Our results are consistent with previous findings from the central California population that auklets began egg-laying earlier in years with colder mean spring sea surface temperatures (Abraham and Sydeman 2004). Seabirds are thought to rely on proximal cues from their marine foraging environment to time breeding with peaks in prey availability, as supported by multiple studies in seasonal environments that have detected relationships between spring sea surface temperature and seabird breeding phenology (Jaquemet et al. 2007). Our results suggest that the

pronounced transition in spring oceanographic conditions at the northern and central current sites provides cues to auklets to time breeding with periods of increased productivity that allow adults to reach breeding condition and that indicate that prey will be available during the chick-rearing period. In contrast, we detected no relationships between ocean climate conditions and timing of breeding for the northern Mexico population, which forages in an ocean environment that is markedly more aseasonal in upwelling and primary production. Low seasonal variability results in higher unpredictability of optimal ocean conditions and prey peaks, which may favor the lower observed seasonality in timing of breeding as noted in other seabird populations that breed in low variability environments (Jaquemet et al. 2007).

Breeding success and ocean climate

It is noteworthy that Cassin's Auklet breeding success and chick fledging masses were similarly related to the same local ocean climate variable (sea surface height) across populations, since we expected that ocean processes would differentially influence reproductive parameters across oceanographically heterogeneous regions of the California Current. However, the strength and shape of relationships between breeding success and sea surface height differed across populations. While we found a significant linear relationship between breeding success and sea surface height for the northern Mexico population for first breeding attempts, the relationship was nonlinear in the British Columbia and central

California populations, where production of first chicks was relatively constant except for breeding failure during anomalous ocean climate conditions in 2005. However, we did find a linear relationship for the British Columbia and central California populations when all breeding attempts (relays and second broods) were considered. Relationships between seabird demography and ecosystem fluctuations are commonly thought to be nonlinear and characterized by threshold effects (Cairns 1987). In seasonally productive environments of the central and northern California Current, Cassin's Auklets may achieve relatively constant chick production in first attempts when oceanographic conditions are generally favorable and when they time breeding to correspond to peak productivity, leading to nonlinear relationships between chick production and ocean climate conditions, where chick production declines only in the worst years. Additional chick production from relays and second broods would further increase breeding success in years when ocean climate conditions continued to be favorable throughout the breeding season, leading to the linear relationships observed for all breeding attempts. In the more aseasonal oceanographic environment in northern Mexico, auklets may exhibit a more linear relationship between ocean climate and breeding success for first attempts, since auklets are not able to synchronize their breeding efforts with periods of higher productivity in all years. For example, during the 2002–2003 El Niño, auklets in the northern Mexico population initiated egg-laying in November 2002. Warm El Niño conditions peaked during December 2002 to February 2003 amidst incubation, and breeding pairs suffered low breeding success, whereas auklets in the central and northern current delayed breeding in 2003 and did not experience much reduction in chick production. Overall, auklets appeared to have higher breeding success in years with lower sea surface heights, but these relationships were moderated by population differences in timing of breeding and life history traits (e.g., ability to double-brood), and our inferences are constrained by our short six-year study period. It is also important to note that we examined mean ocean climate conditions, although timing and variability of oceanographic processes deserve more detailed examination as predictors of seabird reproductive success.

Local vs. large-scale indices

Local ocean climate variables proved to be significantly better predictors of auklet reproductive parameters than the large-scale NOI (Table 1). Local sea surface height was a particularly good predictor, most likely because it integrates both large-scale and local oceanographic processes that drive productivity. Colder La Niña conditions are reflected by lower sea surface heights, and the poleward coastal surge of warmer water during El Niño events is reflected by higher sea surface heights. Sea surface height may also provide a better

measure of local upwelling (e.g., the upward transport of cold water to the surface and the offshore transport of surface waters) than the upwelling index, which measures the strength of upwelling-favorable winds but not ocean temperature. Since the NOI and most other large-scale indices of Pacific basin climate are dominated by interannual variation associated with ENSO events (Schwing et al. 2002), these large-scale indices may not sufficiently capture important ocean dynamics when auklet phenology and demography are affected by climate processes other than ENSO. For example, remote large-scale forcing from the subarctic intrusion of cold water into the current in 2002 that enhanced productivity in the current was independent of ENSO, as was the delay and subsequent interruption in upwelling in 2005 that was precipitated by anomalous atmospheric forcing (Sydeman et al. 2006). As this study demonstrates, the best predictors of seabird demographic variation are likely local ocean climate variables or composite indices of local ocean climate variables that reflect local and large-scale climate processes.

CONCLUSIONS

The strong covariance of ocean climate conditions and Cassin's Auklet breeding success over a 2500-km range, and similar relationships between breeding success and ocean climate conditions across widely spaced populations, indicate that Cassin's Auklets are susceptible to climate change across the California Current System. Increases in frequency or magnitude of climate processes that synchronize ocean climate conditions important to productivity, such as El Niño Southern Oscillation (ENSO) events or shifts in atmospheric pressure fields influencing wind patterns, will likely increase demographic covariation and extinction risk for Cassin's Auklets across this oceanographic system. For example, the delayed timing and increased variability in upwelling-favorable winds leading to an interruption in upwelling in 2005 produced a range-wide breeding failure of Cassin's Auklets, marked by the lowest breeding success in 11 years and 35 years of monitoring at Triangle and SE Farallon Islands, respectively (Sydeman et al. 2006). Changes in timing and variability of local ocean climate conditions may be more problematic for northern and central auklet populations that appear to time their breeding to take advantage of seasonal peaks in productivity. Examining the covariation in demographic rates across its entire range in the Alaska and California Current Systems will be an important next step in predicting the future impacts of climate change on range-wide auklet population dynamics.

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APPENDIX A

A map of the study sites (*Ecological Archives* E090-051-A1).

APPENDIX B

Source, spatial resolution, and temporal resolution of ocean climate and ocean productivity variables (*Ecological Archives* E090-051-A2).

APPENDIX C

Time periods over which ocean climate and ocean productivity variables were averaged for each population (*Ecological Archives* E090-051-A3).

APPENDIX D

Rankings of mean and variance of local climate and ocean productivity variables at each study site relative to other study sites (*Ecological Archives* E090-051-A4).

APPENDIX E

Covariation of ocean climate and ocean productivity variables across study sites (*Ecological Archives* E090-051-A5).

APPENDIX F

Pairwise Pearson correlation coefficients (r) for comparisons of annual mean values of auklet egg-laying dates, breeding success for first and all breeding attempts, and chick fledging mass between populations (*Ecological Archives* E090-051-A6).

APPENDIX G

Anomalies of ocean climate and ocean productivity variables during the breeding season at the three study sites (*Ecological Archives* E090-051-A7).