

Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change

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Summary

1. We performed demographic analyses on Cassin's auklet *Ptychoramphus aleuticus*, a zooplanktivorous seabird inhabiting the variable California Current System, to understand how temporal environmental variability influences population dynamics.
2. We used capture–recapture data from 1986 to 2002 to rank models of interannual variation in survival, breeding propensity, breeding success, and recruitment.
3. All demographic parameters exhibited temporal variability. Interannual variation in survival was best modelled as a nonlinear function of the winter Southern Oscillation Index (SOI). Breeding propensity was best modelled as a threshold function of local sea surface temperature. Breeding success and recruitment were best modelled with year-dependent annual variation.
4. Changes in the SOI force El Niño/La Niña events, which in turn alter prey availability to seabirds in this system. Demographic responses varied during El Niños/La Niñas. Survival diminished substantially during the 1997–98 El Niño event, while breeding propensity was affected during both the 1992 and 1998 El Niños. Breeding success was reduced during the 1992, 1993, and 1998 El Niños, but was unusually high in 2002. Recruitment was higher at the beginning and end of this time-series.
5. While demographic responses varied interannually, parameter values covaried in a positive fashion, a situation conducive to rapid population change. During the 11 years study period, the Farallon auklet breeding population declined at $6.05 \pm 0.80\%$ (SE) per year, a cumulative decline of 49.7%. This study demonstrates how climate variability has influenced key demographic processes for this diminished marine bird population.

Key-words: Alcidae, breeding success, El Niño, marine bird, population biology, recruitment, Southern Oscillation Index, survival.

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Introduction

Understanding how temporal environmental variability influences demographic parameters is central to interpreting change in animal populations (Emlen 1984; Croxall & Rothery 1991; Ratcliffe *et al.* 1998; Caswell 2001). For iteroparous vertebrates, such as marine birds, key demographic parameters include adult survival, breeding propensity (the proportion of a population attempting to reproduce in a given year given they have

reproduced in an earlier year), reproductive performance (breeding success), recruitment and net immigration (Nur & Sydeman 1999a; Thompson & Ollason 2001). Therefore, quantifying climate-induced temporal variation in these demographic parameters is critical to understanding population-level responses to climate change (Jenouvrier, Barbraud & Weimerskirch 2003; Jenouvrier *et al.* 2005; Sandvik *et al.* 2005).

Most demographic analyses for seabirds in the eastern North Pacific come from the California Current System (CCS), an upwelling-dominated, eastern boundary current ecosystem stretching from British Columbia, Canada to Baja California, Mexico. The CCS can be extremely productive, but is highly variable, dominated

by the El Niño Southern Oscillation (ENSO) phenomena (Goericke *et al.* 2004). The CCS has undergone substantial environmental changes over the past 30 years, with general intensification of warm, El Niño years (McGowan, Cayan & Dorman 1998; Fiedler 2002). In a key paper, Roemmich & McGowan (1995) demonstrated a 90% reduction in zooplankton biomass concomitant with ocean warming in this system. Another striking pattern has been a major decline in the pelagic abundance of migrant seabirds during the same period of time (Veit, Pyle & McGowan 1996). Populations of many locally breeding seabirds also declined from the early 1970s to the late 1990s (Ainley *et al.* 1994; PRBO unpublished data). The Cassin's auklet *Ptychoramphus aleuticus* (Pallas), an obligate zooplanktivore (Sydeman *et al.* 1997), declined at the Farallon Islands by roughly 50% from the early 1970s to the late 1980s (Ainley *et al.* 1994), with similar population decreases elsewhere in the CCS (Gaston & Jones 1998; Bertram *et al.* 2000). For seabirds, high elasticities in adult survival probabilities indicate that small variation in survival can have large effects on population dynamics (Croxall & Rothery 1991; Nur & Sydeman 1999a; Frederiksen *et al.* 2004). Previous studies have also clearly demonstrated that changes in fecundity and breeding propensity are, in general, related to climate variability (Aebischer & Coulson 1990; Croxall *et al.* 1990; Barbraud & Weimerskirch 2001a,b), but this has yet to be adequately investigated for the Farallon Cassin's auklet population.

This work was executed to investigate the role of climate variability in determining interannual changes in demographic traits of this declining population. We evaluate climate-induced annual variation of survival, breeding propensity, breeding success, and recruitment by estimating year-specific values, then by fitting models describing annual variation as a function of seasonal metrics of ocean climate at the local scale [sea surface temperature (SST) measured at the Farallon Islands] and basin-wide scale [Southern Oscillation Index (SOI), applied across the Pacific Ocean]. Conceptually, models were formulated to examine effects of season and spatial scale in identifying functional relationships between climate indices and demographic parameters. The two ocean climate metrics were computed for spring (breeding season) and winter (pre-breeding seasons) and included linear, nonlinear and threshold functions. Finally, we calculate temporal covariation among demographic parameters.

Methods

STUDY AREA AND DATA COLLECTION

PRBO Conservation Science (PRBO, formerly Point Reyes Bird Observatory) has studied the population biology of Cassin's auklet on South-east Farallon Island (SEFI), California (37°42'N 123°00'W) since the late 1960s (Manuwal 1974a,b; Ainley & Boekelheide 1990; Abraham & Sydeman 2004). Cassin's auklets on SEFI

nest in rock crevices and in burrows excavated in soil. Between 1978 and 1983, PRBO and collaborators installed 446 nest boxes to facilitate data collection on individually marked auklets (see Pyle 2001 for details).

The recapture probability of species with high breeding site tenacity, such as auklets, is biologically interesting to the extent that it incorporates the conditional probability that an individual will breed in a particular year given that it has survived to that year (Lebreton *et al.* 1990; Clobert *et al.* 1994). Thus, capture–recapture data may be used to infer breeding propensity, a parameter that is often ignored and difficult to measure (Nur & Sydeman 1999b). There is evidence from recent studies that recapture probability is a reliable index of breeding propensity in seabirds (Jenouvrier *et al.* 2003).

In 1978, we began to mark adults and chicks with individually number-coded stainless steel leg rings. Ring loss was estimated at < 0.1% per year (Pyle 2001), so this factor was considered negligible to our estimates. From 1986 to 2002, we captured and resighted birds annually in nest boxes. For this study, we selected, from among all ringed individuals, those known-age and known-sex birds with an age-at-first-breeding of 2–5 for analysis. We selected known-age birds so that age and temporal effects could be examined for the same data set, though here we focus on temporal effects. We analysed the sexes separately because we expected survival probability and breeding propensity could be sex-specific. In a socially monogamous species such as Cassin's auklet, where incubation and chick-provisioning responsibilities are apparently fully shared (Manuwal 1974a,b; Sydeman *et al.* 1996), we expected no difference in reproductive success among the sexes, however, temporal variation in survival and breeding propensity could be sex-specific. Sex was determined by the relative bill depth of mates, assuming the male was larger than the female (Nelson 1981). We desired our data set to be composed of complete histories for all individuals. The age-at-first-breeding selection criterion omitted birds that entered the nest box population later in life, omitting 22 birds (7.7%) with possible incomplete histories. The year when a known-age, previously ringed bird was first resighted was considered the first capture occasion and first breeding attempt; subsequent years' breeding efforts were treated as recaptures. It is possible that some of our sample began breeding in natural burrows before they were resighted in nest boxes; however, our criterion of age-at-first-breeding, < 6, eliminated much of this concern, so we do not consider variation in age-at-first-breeding to be a significant confounding factor in our analyses. The probability of failing to identify a bird breeding in a nest box was apparently very low. Few egg-laying pairs abandoned their nest before both mates were captured (this was the case for 3.7% of the study sample) and this figure includes unringed birds; hence the actual proportion of missed, previously breeding, ringed birds must be lower than this.

Beginning on 2 March each year, we checked nest boxes every 5–15 days for breeding auklets. When a bird

was found, we monitored the site every 5 days to determine breeding success (Abraham & Sydeman 2004). Each individual auklet was assigned an annual breeding success score of 0, 1 or 2 indicating the number of chicks fledged in each year. The first year > 30 known-age birds returned to breed in nest boxes was 1986; consequently, the time period considered in this analysis was 1986–2002, except for recruitment, which examined cohorts that hatched between 1984 and 1999.

POPULATION ESTIMATION

There have been no estimates of absolute population size for this population since those made in 1989 (Carter *et al.* 1992). Instead, we analysed an index of population size, based on the number of occupied burrows and crevices per unit area, in a manner similar to Manuwal (1974a). Twelve 10 × 10 m 'index plots' were established by one of us (WJS) during winter 1991 in areas representative of available Cassin's auklet habitat (described in Ainley & Boekelheide 1990). This included deep and shallow soil areas on a broad marine terrace where most of the auklets establish nesting burrows (Manuwal 1974a), and plots in areas of combined small rocks and soil. We did not establish plots on cliffs, as few auklets breed in this habitat type. To enumerate burrows/crevices occupied each year, during the peak of the incubation phase we placed marking 'flags' at the entrance to each site and then retrieved and counted them. Each potential nest site was inspected for faecal material and depth to ascertain occupation.

For each year, we calculated the geometric mean burrow density among plots and its associated confidence interval. To estimate population trend over time, we analysed log-transformed burrow densities, controlling for plot effects, using a linear model. We analysed the linear trend over time, common to all plots, weighting by average density for each plot during the study period, similar to the approach of Geissler & Sauer (1990). Analysis of log-transformed burrow densities allowed us to estimate the constant, annual proportional change in breeding population density. All analyses were carried out using STATA 8.2 (Stata Corporation 2005).

MARK–RECAPTURE ANALYSIS FOR SURVIVAL AND BREEDING PROBABILITIES

We analysed capture–recapture data from known-age birds to model and estimate apparent survival probability (ϕ) and recapture probability, a measure of breeding propensity (p). All birds were marked when 20–30 days old in their year of birth. In analyses of ϕ and p presented here, age was treated as a constant during model selection procedures. In a separate analysis of ϕ and p in relation to age, we found that male ϕ and p was best modelled as a constant with age and that no simple linear or nonlinear model (with 1 or 2 d.f.) adequately described age-related variation in female p or ϕ (DEL, unpublished data). To avoid overfitting the female model,

and make comparisons between sexes easier, age was treated as a constant during model selection procedures for temporal variation in ϕ and p . We used program U-CARE 2.2 (Choquet *et al.* 2005) for goodness-of-fit testing of the Cormack–Jolly–Seber (CJS) model relative to the data ($CJS = \phi(t) p(t)$), following notation of Lebreton *et al.* (1992).

In our modelling and estimation procedures, we began by determining the best structure for breeding propensity while holding survival in its most highly parameterized form. Once we established the most parsimonious structure for breeding propensity, we modelled survival while holding recapture in its most parsimonious form. Finally, we ranked models of p with ϕ in its most parsimonious form to confirm earlier rankings (Lebreton *et al.* 1992; Burnham & Anderson 2002). We used the logit link function and 2nd part variance estimation throughout these analyses. We determined model parsimony using Akaike Information Criterion corrected for small sample size (AICc). We calculated $\Delta AICc$ = the difference between the AICc for a model and the AICc for the minimum (preferred) AICc model; for the latter, $\Delta AICc = 0$, by definition.

The key to understanding model selection results lies within the AICc Weights column. AICc Weights are a measure of the strength of evidence that a given model is best, given the data. Owing to model selection uncertainty, information from all models in the set with AICc Weight > 0.01 should be considered when making inferences (Burnham & Anderson 2002). We also used AICc Weights as importance values for covariates. Importance values are the sum of AICc Weights across all models that contain a given variable and indicate the descriptive power of that variable relative to the others in the set (Burnham & Anderson 2002). The variable with the largest summed AICc Weight is estimated to be the most important, and the variable with the smallest summed AICc Weight is estimated to be the least important. When each variable is in the model set only once, AICc Weight = importance. The ratio of AICc Weights between two models computes how many times stronger is the evidence for the numerator model compared with the denominator model (Burnham & Anderson 2002). We used analysis of deviance (ANODEV) to determine the significance of covariate effects, and to compute the proportion of total variance explained by covariate models, using the formula, F statistic = [(Deviance of the constant model – Deviance of the 'time' model) – (Deviance of the covariate model – Deviance of the 'time' model)] / [(Deviance of the covariate model – Deviance of the 'time' model) / (d.f. of the 'time' model – d.f. of the covariate model)], where 'time' refers to the fully time-varying model (Skalski, Hoffmann & Smith 1993).

MODEL SETS

We created our model set of annual variation with the purpose of evaluating the importance of local- vs.

basin-scale climate indices, seasonal importance, and the functional relationship between demographic parameters and climate indices. SOI is the difference in sea-level pressure between Darwin, Australia and Tahiti, French Polynesia (Trenberth 1984). SOI is a physical forcing mechanism and indicates the primary signal for the ENSO phenomenon. Positive SOI values indicate strong Pacific trade winds (La Niña), negative values indicate the reversal of Pacific trade winds (El Niño). SST is local sea surface temperature at SEFI expressed as a monthly mean of daily measurements. Seasons were defined as winter, pre-breeding season = January, February, and March; and spring, early breeding season = April, May, and June. Functional relationships we examined were: linear function of mean seasonal index values; nonlinear accelerating function of mean seasonal index values (mean seasonal index value – maximum observed index value)² for SOI and (mean index – minimum observed)² for SST; and binomial threshold functions defined by the most extreme 10% of index values (lowest 10% of SOI and highest 10% of SST, respectively). These functions provide the basis for determining the best 1 d.f. model. We chose these three function types to determine the best model of the El Niño phenomenon as it affects demography of Cassin's auklet, and we expected extreme El Niño events to impact the demographic rates more than smaller oscillations. Thus, transformed SOI values could range from 0 (extreme La Niña year) to 78.6 (for most extreme El Niño year), and transformed SST values ranged from 0 (very cold water) to 16.3 (very warm, El Niño-like conditions).

The specific a priori model set for analyses of annual variation included ϕ and p parameters: (1) as constants; (2) as a linear function of the mean seasonal value for the SOI during winter (January, February, March; SOI_{jfm}); (3) as a nonlinear accelerating function of winter SOI (SOI_{jfm}^2); (4) as a linear function of the mean seasonal value for the SOI during spring (April, May, June; SOI_{amj}); (5) as a nonlinear accelerating function of spring SOI (SOI_{amj}^2); (6) as a linear function of the mean seasonal value for SST during winter (SST_{jfm}); (7) as a nonlinear accelerating function of winter SST (SST_{jfm}^2); (8) as a linear function of spring SST (SST_{amj}); (9) as a nonlinear accelerating function of spring SST (SST_{amj}^2); (10) as a threshold function for El Niño, defined when the winter SOI was *below* the 10th percentile of winter values from 1900 to the present (negative SOI indicates El Niño conditions; EN_{soiW}); (11) as a threshold function for El Niño defined by spring SOI, using the 10th percentile of spring values (EN_{soiSp}); (12) as a threshold function for El Niño defined as years when winter SST was *above* the 90th percentile of winter values from 1900 to the present (warm SST indicates El Niño conditions; EN_{sstW}); (13) as a threshold function for El Niño years defined by spring SST (EN_{sstSp}); and (14) fully time-dependent (Lebreton *et al.* 1992), year treated as a categorical variable. Note that $EN_{sstW} = EN_{sstSp}$ for breeding propensity analyses (same threshold years, 1992 and 1998,

identified by the two criteria) but that this was not the case for analyses of other parameters. This was because, in addition to 1992 and 1998, 1986 was an El Niño year by the $sstW$ criterion but not the $sstSp$ criterion. However, unlike analyses of survival, breeding success, and recruitment, which examined the effects of 1986 conditions on the respective parameter, the first year that could be analysed with respect to breeding propensity was 1987.

BREEDING SUCCESS

Our modelling approach for breeding success was similar to that for modelling ϕ and p . We analysed the number of chicks fledged (i.e. that reached day 35 of life) per pair, scored 0, 1 or 2, which we refer to as the parameter rs , using STATA 8.2 (Stata Corporation 2005). We conducted Poisson regression with the global model, and used the POISGOF procedure to determine if the dependent variable was overdispersed (i.e. variation of the residuals exceeded that of a Poisson distributed variable); there was no overdispersion and therefore we used Poisson regression in our analyses (Kleinbaum, Kupper & Muller 1988). In an analysis of age effects on rs for this data set (NN, unpublished), we determined, using AICc, that the effect of age was most parsimoniously modelled as an inverse function ($invage = 1/age$) and that this function differed in slope and intercept for the two sexes. We therefore incorporated sex-specific age effects in our subsequent modelling of annual variation in rs . We ranked models using AICc and calculated AICc Weights for each of the 14 models, as described above for ϕ and p .

RECRUITMENT

Recruitment fraction was calculated as the proportion of ringed fledglings from year x that returned to breed in a nest box in subsequent years. We included only cohorts from 1984 to 1999 in order to ensure sufficient sample size ($n > 20$ ringed fledglings) from early cohorts, and that the majority of the individuals from later cohorts, and at least half of the 1999 cohort had begun breeding (i.e. median age of recruits = 3). Cohort-specific recruitment was modelled in STATA 8.2 (Stata Corporation 2005) using GLM with a binomial error distribution and logit link, with number of recruits as the response variable and total number of fledglings as the binomial denominator. We examined the same ocean-climate covariates described above for ϕ , p and rs , except that we examined ocean-climate covariates for: (1) the year of fledging (year x); (2) year $x + 1$; and (3) year $x + 2$; therefore, we ranked a total of 38 models in relation to recruitment probabilities (including time-constant model). Models were ranked using AICc as described above.

TEMPORAL COVARIATION

To examine temporal covariation among demographic parameters, we computed pair-wise correlation coefficients

Table 1. Index of breeding population size of Cassin's auklets *Ptychoramphus aleuticus* on South-east Farallon Island 1991–2002. Shown are the geometric means of burrow density (active burrows m^{-2}) and their 95% confidence intervals, based on 12 census plots per year.

Year	Density (burrows m^{-2})	Lower 95% bound	Upper 95% bound
1991	0.254	0.169	0.381
1992	0.232	0.163	0.330
1993	0.191	0.125	0.292
1994	0.211	0.143	0.311
1995	0.218	0.153	0.311
1996	0.179	0.113	0.283
1997	0.215	0.140	0.330
1998	0.087	0.061	0.126
1999	0.109	0.064	0.185
2000	0.105	0.058	0.189
2001	0.128	0.078	0.209
2002	0.160	0.108	0.237

and Spearman rank correlations of year-specific estimates of ϕ , p , rs and recruitment fraction. Survival is from year $x - 1$ to year x , breeding propensity, and breeding success estimates are for year x , and recruitment is for the cohort hatched in year $x - 1$.

Results

The density of occupied burrows declined at an annual rate of 6.05% (SE = 0.80%, $P < 0.001$; Table 1). The estimated finite growth rate, $\lambda = 0.9395 \pm 0.0080$, implies a cumulative decline of 50.8% over 11 years. Densities were lowest for the years 1998–2000, and showed some recovery in 2001 and 2002.

From 1986 to 2002, 149 individual males and 114 individual females that were ringed as chicks returned to breed at least once in the monitored nest boxes. Effective sample sizes by sex for capture–mark–recapture analysis were: males = 480, females = 375. U-CARE goodness-of-fit testing found no evidence of systematic lack-of-fit (Global Test $\chi^2_{72} = 64.7$, $P = 0.72$), nor were any of the component tests of transience or trap-dependence significant (Test 3.SR males: $\chi^2_{14} = 14.3$, $P = 0.43$; females: $\chi^2_{13} = 14.4$, $P = 0.34$; Test 3.SM males: $\chi^2_{11} = 6.5$, $P = 0.83$; females: $\chi^2_9 = 4.4$, $P = 0.88$; Test 2.CT males: $\chi^2_{10} = 12.3$, $P = 0.26$; females: $\chi^2_9 = 12.6$, $P = 0.18$). No variance inflation factors were applied.

ANNUAL VARIATION

Annual variation in apparent survival probability (ϕ) of both sexes was most parsimoniously modelled as a nonlinear function of winter SOI (male $\beta = -0.0264$, 95% CI = -0.0370 to -0.0158 , female $\beta = -0.0178$, 95% CI = -0.0304 to -0.0052). The quadratic SOI^2 model was a significant covariate (males: $F_{1,13} = 14.4$, $P = 0.002$; females: $F_{1,13} = 5.3$, $P = 0.039$), accounting for 53% of annual variation in male survival and 29% of annual variation in female survival (Fig. 1; ANODEV). The

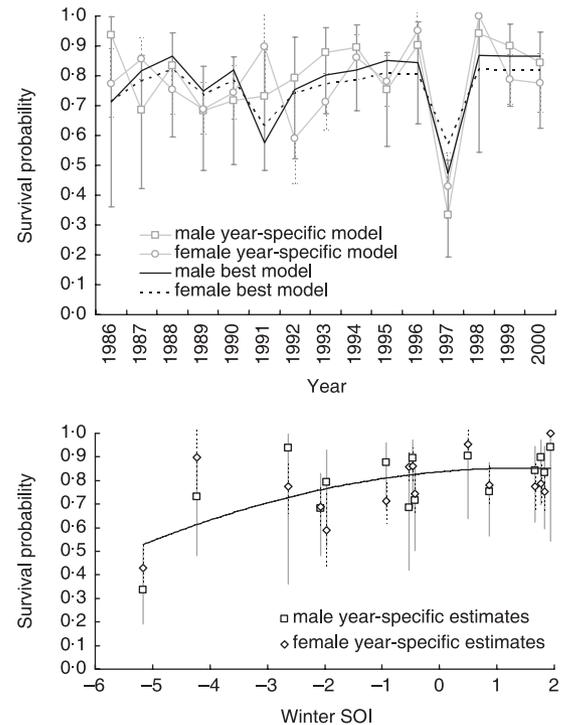


Fig. 1. Annual variation in apparent survival probability (top) and the relationship of survival to winter SOI (bottom) of male (□) and female (○) Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1986 to 2000. Survival estimates are for the time period from the breeding season in year x to the following year's breeding season. AICc-selected best model was a nonlinear function of winter SOI for each sex. Error bars denote 95% confidence intervals of annual estimates.

top-ranked SOI^2 model was 3.4 and 1.8 times better than the second-ranked model, for male and female data, respectively (Tables S1 and S2, bottom). Note that survival was depressed during the El Niño conditions of 1997/1998 (Fig. 1), but not during the El Niño conditions of 1992, explaining why an El Niño threshold model did not fit ϕ well.

Annual variation in breeding propensity was most parsimoniously modelled as a threshold function of SST, reflecting local ocean conditions during the El Niño phase of the ENSO cycle (Tables S1 and S2, top). The years identified in threshold models for spring and winter SST were identical, so only one was ranked. The EN_{SST} threshold model of p was essentially a constant with El Niño effects drastically reducing breeding propensity in 1992 and 1998 (Fig. 2; male $\beta = -2.030$, 95% CI = -2.844 to -1.216 ; female $\beta = -2.301$, 95% CI = -3.141 to -1.461). The EN_{SST} threshold model was a significant covariate (males: $F_{1,13} = 22.0$, $P = 0.0005$; females: $F_{1,13} = 25.5$, $P = 0.0002$), explaining 65% and 66% of interannual variation in breeding propensity for males and females, respectively (Fig. 2; ANODEV). The EN_{SST} threshold model was 1.6 and 4.1 times better than the second-ranked model, nonlinear spring SST (SST_{Amj}^2), for male and female data, respectively. The year-specific, and constant models of p both had zero

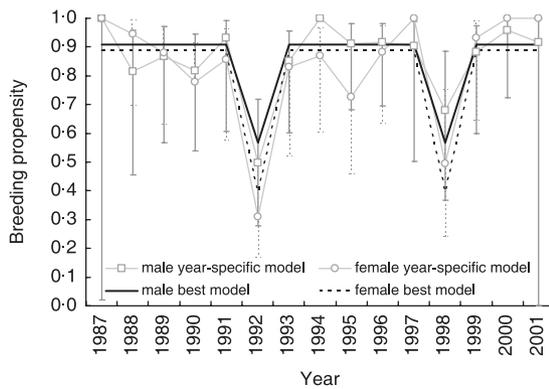


Fig. 2. Annual variation in breeding propensity of male (□) and female (○) Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1987 to 2001. AICc-selected best model was a threshold El Niño model based on local SST. Error bars denote 95% confidence intervals of annual estimates.

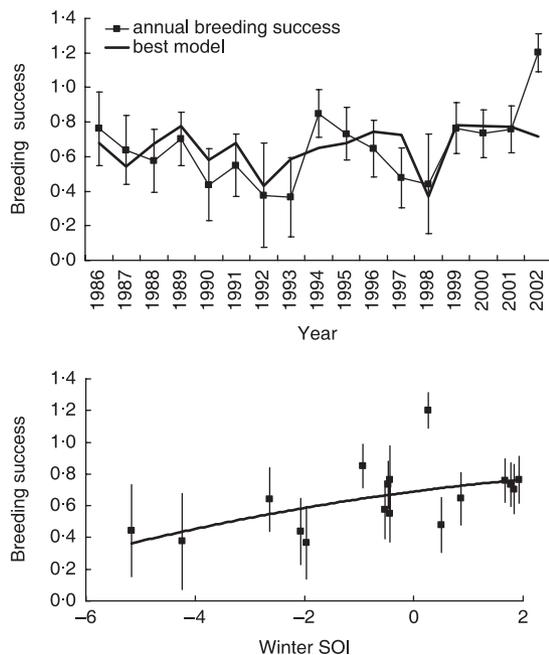


Fig. 3. Annual variation in breeding success (fledglings pair⁻¹ years⁻¹; top) and the relationship of breeding success to winter SOI (bottom) for Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1986 to 2002. Error bars denote SE of annual estimates.

AICc Weight for both sexes indicating the clear superiority of temporal covariate models.

The AICc-preferred model for annual variation in breeding success was the fully time-dependent, *year* model (Deviance = 1745.0, $k = 20$, AICc = 1785.9). In order to identify the most parsimonious ocean climate model we ranked the remaining 13 models (including the time-constant model). The most parsimonious ocean climate model was a nonlinear function of winter SOI (Table S3; $\beta = -0.0098$, 95% CI = -0.0152 – 0.0044 ; AICc = 1796.2), the same model of annual variation that was most parsimonious for ϕ (Fig. 3). The *SOIjfm*² model accounted for 26% of annual variation in breed-

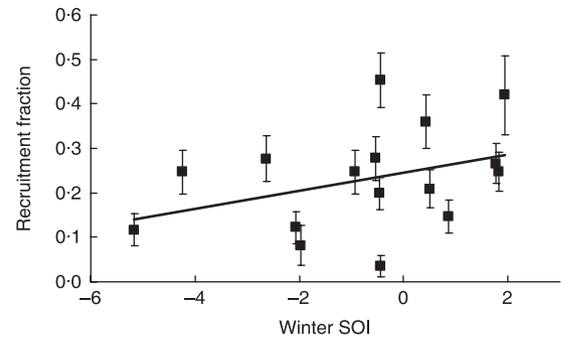
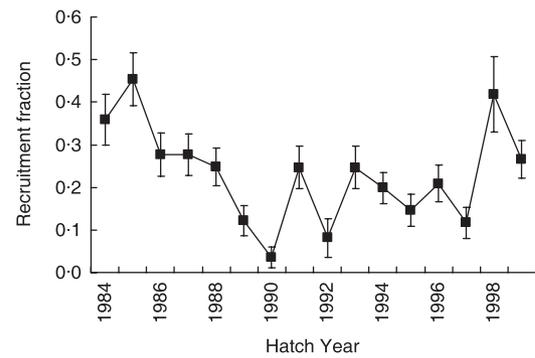


Fig. 4. Annual variation in recruitment fraction (top; recruits fledgling⁻¹) and the relationship between recruitment and winter SOI in the first year post-fledging (bottom) for Cassin's auklet *Ptychoramphus aleuticus* cohorts fledged on South-east Farallon Island, California from 1984 to 1999. Error bars denote SE of annual estimates.

ing success, was significant (ANODEV $F_{1,16} = 5.53$, $P = 0.032$), and was 2.2 times better than the next best covariate model, *SOIjfm*. However, the *year* model was > 100 times better than even the top-ranked temporal covariate model, *SOIjfm*².

RECRUITMENT

The recruitment probability for the 1984–99 cohorts averaged 0.229 (SD = 0.120) with large interannual variation (Fig. 4). The recruitment fraction of each cohort was best modelled with the fully time-dependent *year* model of cohort-specific effects (Deviance = 1237.8, $k = 15$, AICc = 1268.2). To identify the most parsimonious ocean-climate model we ranked the remaining 37 models, including the time-constant model (Table S4). The best ocean climate model was a linear function of winter SOI in the first year after fledging (*SOIjfm* + 1, $\beta = 1.271$, 95% CI = -0.667 – 3.209), only a little better than the nonlinear model *SOIjfm*² + 1 (Table S4). However, even the *SOIjfm* model explained only 9% of cohort variation in recruitment and was not significant (ANODEV, $P = 0.27$); the *year* model was > 1000 times better than the top-ranked covariate model.

IMPORTANCE AND COVARIATION

For both male and female survival, importance values for winter parameters far exceeded those of spring (male:

Table 2. Correlation matrix for mean year-specific estimates of survival, breeding propensity, breeding success, and recruitment of Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1986 to 2000. Survival is from year $x - 1$ to year x , breeding propensity, and breeding success estimates are for year x , and recruitment for cohort year $x - 1$. Above the diagonal are Spearman rank correlations, below the diagonal are correlation coefficients. *P*-values are given in parentheses.

	Breeding propensity	Survival	Breeding success	Recruitment
Breeding propensity	1	0.339 (0.216)	0.532 (0.041)	0.484 (0.080)
Survival	0.458 (0.086)	1	0.539 (0.038)	0.712 (0.004)
Breeding success	0.580 (0.021)	0.500 (0.052)	1	0.561 (0.037)
Recruitment	0.185 (0.526)	0.657 (0.011)	0.555 (0.039)	1

winter = 0.99, spring = 0.01; female: winter = 0.87, spring = 0.14). However, for breeding propensity, results differed by sex: for female *p*, winter was more important (winter = 0.93, spring = 0.71), while the converse was the case for males (winter = 0.66, spring = 0.85). Summed seasonal importance values across all six demographic parameters found the winter, pre-breeding season more important overall. Comparing SOI and SST importance values, SOI importance was higher than SST importance for ϕ (female: SOI = 0.73, SST = 0.27; male: SOI = 0.91, SST = 0.09). However, SST importance values were higher than SOI for *p* (female: SOI = 0.25, SST = 0.74; male: SOI = 0.15, SST = 0.85). Summed importance values across all demographic parameters found SOI was more important than SST due to the superiority of SOI in explaining variation in breeding success and recruitment fraction.

The correlation coefficients and Spearman rank correlations for the annual estimates of survival, breeding propensity, breeding success, and recruitment are given in Table 2. All pair-wise correlations were positive. Four of six pair-wise Spearman rank correlations were significant at the $P < 0.05$ level. The strongest correlation was between adult survival from year $x - 1$ to year x and recruitment of the cohort fledged in year $x - 1$. An interesting finding was the positive correlation between survival from year $x - 1$ to year x and breeding propensity in year x (Table 2).

Discussion

CLIMATE AND DEMOGRAPHY

Although annual variation in demographic parameters has been documented in virtually all seabirds studied to date (Wooller, Bradley & Croxall 1992; Nur & Sydeman 1999a; Weimerskirch 2002), few have simultaneously explored the influence of climate variability on multiple parameters (but see Jenouvrier *et al.* 2003). We have shown how annual variation in ocean climate synchronously affected multiple demographic parameters including survival, breeding propensity, breeding success, and recruitment for SEFI Cassin's auklets. The winter SOI was the best predictor, explaining a high proportion of the between-year variation in survival and breeding success and some variation in recruitment.

In the dynamic CCS, recurrent large-scale oceanographic events (e.g. ENSO) and low-frequency ocean climate 'regime' shifts result in new vital rates for auklets, and other top marine predators (Nur & Sydeman 1999b; Peterson & Schwing 2003). Changes in the SOI drive other physical oceanographic conditions that affect zooplankton and larval fish abundance, key prey items for the auklets (Sydeman *et al.* 1997, 2001; Abraham & Sydeman 2004). The SOI may be viewed as an integrated index of the smaller-scale physics that affect local food webs. This predator-prey linkage (reflecting changes in prey abundance, distribution and/or availability) is likely the primary mechanism by which SOI influences auklet demographic values. However, given that climate indices explained only a portion of the variability in these demographic attributes, other factors, such as predation and disease, also warrant further investigation.

Vital rates for this population undergo reductions associated with El Niño, reflected in all four parameters. It should be noted that the time-series we examined included two El Niño events that were among the top three most-extreme annual events in the past 150 years (1991–92 and 1997–98). However, during the El Niño event of winter 1992, Cassin's auklet survival did not drop, in contrast to 1997–98. Breeding propensity dropped similarly in both 1992 and 1998, with a reduction of *c.* 35%.

It is noteworthy that the wintertime and basin-scale climate indices were the most important predictors of demographic variation. Jenouvrier *et al.* (2003) found that winter SST and sea ice extent best explained variation in adult survival of southern fulmars *Fulmarus glacialisoides*. These findings are consistent with the idea that adult survival of seabirds is influenced mainly by wintertime conditions (Lack 1968; Fretwell 1972; Newton 1998), but breeding season conditions have also been shown to affect adult survival (Davis, Nager, & Furness 2005). Least auklet *Aethia pusilla* adult survival in the North Pacific Ocean also varies with large-scale ocean climate conditions indicated by the North Pacific Index (Jones, Hunter & Robertson 2002). The North Atlantic Oscillation, another basin-scale atmospheric pressure climatic index, has also been shown to affect seabird survival in the North-eastern Atlantic (Thompson & Ollason 2001; Sandvik *et al.* 2005).

POPULATION CHANGE

The Farallon population demonstrated a strong decline over the 11-year study period, averaging -6.1% per year. Apparently, the population has been declining markedly at least since the 1970s (Ainley *et al.* 1994). Manuwal (1974a) estimated the SEFI breeding population at 105 000 in 1971 while Carter *et al.* (1992) estimated fewer than 30 000 in 1989. Though the two estimates may not be strictly comparable (due to methodological differences; Ainley *et al.* 1994), taken at face value they suggest an annual average decline of 6.7% per year, a value that is within 1 SE of the annual decline observed in this study. Thus, our results, when combined with earlier studies, indicate a cumulative decline of 75% or more between 1971 and 2002.

COMPARISONS AND CAVEATS

Our estimates (mean \pm SE) of annual survival probabilities were 0.789 ± 0.040 for males, 0.774 ± 0.036 for females. These compare well with estimates from others (Gaston 1992; Bertram, Harfenist & Smith 2005). One potential source of bias in survival probabilities is permanent emigration from the nest box study areas. We have no estimate of how many previously nest box-breeding birds move permanently to an unmonitored burrow, or depart the island altogether, but both situations would be confounded with mortality in our data set. Another possible source of bias in survival is the exclusion of unsexed birds from the data set, but only seven birds were thus excluded, so any bias associated with these birds should be small.

Our estimate of breeding propensity was 0.864 ± 0.033 for males and 0.834 ± 0.051 for females. Breeding propensity from Triangle Island averaged 0.60 (Bertram *et al.* 2005). Recapture probabilities from Gaston's (1992) study varied from 0.42 to 0.66, but his estimates could be lower due to either the presence of nonbreeding birds in his net-trapped sample, or trap-shyness. Owing to our use of nest boxes as the capture site, which homogenizes variation in observability, we did not expect nest box-captured birds to exhibit trap-shyness. However, temporary emigration of birds to natural burrows could reduce true recapture probability to less than unity, making p an underestimate of breeding propensity. We feel this bias is small, and should be constant because the rate of movement between boxes is not year-dependent (Pyle 2001), making annual variation in p a reliable index of annual variation in breeding propensity. However, we have no estimate of true recapture probability, so cannot know how large this component of p is relative to breeding propensity. Breeding propensity is often overlooked in demography studies (but see Nur & Sydeman 1999b), but modelling by Jenouvrier *et al.* (2005) demonstrated that despite low elasticities, large temporal fluctuations in breeding propensity and breeding success can drive population dynamics of seabirds.

Our estimate of mean annual breeding success (fledglings pair⁻¹) was 0.648, similar to estimates from others

(Vermeer & Lemon 1986; Morbey & Ydenberg 1997). Sydeman *et al.* (2001) and Abraham & Sydeman (2004) describe temporal trends in annual breeding success from a 34-year data set of unknown age Cassin's auklets at SEFI, and highlight declining productivity for the study population, at least through 1997. Both papers assert that changes in the auklets' primary prey base, euphausiid crustaceans, appear responsible for this demographic response, but this has yet to be proven.

Recruitment was highly variable, but related to winter SOI in the first year after fledging. Interestingly, recruitment was male-biased, with almost twice as many males as females recruiting to SEFI nest boxes from every cohort (PRBO, unpublished data). Male bias was especially high for cohorts fledged in El Niño years (e.g. 1997). Natal philopatry in most birds is male-biased (Greenwood 1980), but Pyle (2001) found no sex difference in fine-scale natal dispersal distance of SEFI Cassin's auklet, although the probability of leaving the nest box study area or colony (permanent emigration) may be sex-specific.

COVARIATION AND POPULATION DYNAMICS

Covariation among demographic parameters has rarely been addressed in the literature. Saether & Bakke (2000) demonstrated that where data were available, large temporal covariation among demographic parameters was often found. For marine birds, Nur & Sydeman (1999b) and Jenouvrier *et al.* (2003) found that adult survival, recruitment and breeding propensity were all positively correlated for Brandt's cormorants *Phalacrocorax penicillatus* and southern fulmars, respectively. Covariation between demographic parameters should be expected when fluctuations in different demographic parameters are governed by the same external variables, such as climate. When demographic parameters positively covary, population fluctuations can be much larger than when parameters vary independently (Caswell 2001). Conversely, fluctuations will be dampened and population stability enhanced if parameters negatively covary. It is thus essential for accurate modelling of population dynamics to know whether environmental stochasticity affects all demographic parameters positively, negatively or independently (Burgman, Ferson & Akçakaya 1993). Demographic covariation, especially negative correlations, also greatly affects elasticity estimates (Brault & Caswell 1993; Benton, Grant & Clutton-Brock 1995; Reid *et al.* 2004).

For Cassin's auklet, the relationship with SOI indicates that strong El Niño events result in diminished cohorts of new breeders and reduced breeding effort and success, while strong La Niña years enhance survival and reproduction. Because these perturbations appear to be found elsewhere (Bertram, Mackas & McKinnell 2001; Bertram *et al.* 2005), suggesting that poor/good years are poor/good everywhere in the CCS, we would not expect diminished cohorts to be compensated by immigration. Climatic variation therefore creates transient population dynamics and possibly unstable age

structure for auklet populations (Caswell 2001; Harkonen, Harding & Heide-Jorgensen 2002).

It is clear that strong environmental forcing correlates with demographic variability for Cassin's auklet in the CCS (Bertram *et al.* 2001, 2005; Abraham & Sydeman 2004; this study). Such interconnections of demographic rates, and effects over much of its range, all linked to climate variability, indicates that this species is vulnerable to climate change. Indeed, the SEFI auklet population has declined during a period of warming and generally decreasing zooplankton biomass (Roemmich & McGowan 1995; McGowan *et al.* 1998). Off southern California, one of the primary prey species of Farallon Cassin's auklets *Euphausia pacifica* was found to be inversely related to the Pacific Decadal Oscillation (Brinton & Townsend 2003), indicating lower abundance during warmer periods, but this study was conducted c. 400 km to the south of the Farallones; information on the abundance of euphausiid species within the foraging range of the Farallon population is not available. Annual values of breeding success and recruitment in this population improved after 1998, when stronger upwelling-favourable winds, colder surface and subsurface temperatures, and elevated biological productivity characterized the CCS (Peterson & Schwing 2003; Goericke *et al.* 2004). For the most recent years of the study, the observed changes in demographic parameters were concordant with observed changes in the population index.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from

Table S1. Model selection results for annual variation in recapture (p), and survival (ϕ) probabilities of male Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1986 to 2002. Age-specific probabilities were modelled as constants (see text). Variance inflation factor (c) = 1.00.

Table S2. Model selection results for annual variation in recapture (p), and survival (ϕ) probabilities of female Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1986 to 2002. Age-specific probabilities were

modelled as constants (see text). Variance inflation factor (c) = 1.00.

Table S3. Model selection results for annual variation in breeding success of Cassin's auklet *Ptychoramphus aleuticus* breeding on South-east Farallon Island, California from 1986 to 2002. Models included an inverse-transformed age effect and a sex-effect. ΔAICc and AICc weights are compared among all models but 'year'. AICc for 'Year' model was 1785.9; AICc for SOIjfm^2 model was 1796.2; see text.

Table S4. Model selection results for best 20 models of recruitment fraction (recruits fledgling⁻¹) for Cassin's auklet *Ptychoramphus aleuticus* cohorts on South-east Farallon Island, California from 1984 to 1999. AICc for the year-specific model was 1268.2; AICc for $\text{SOIjfm} + 1$ model was 1303.6; see text.