

Ian L. Jones · Fiona M. Hunter  
Gregory J. Robertson

## Annual adult survival of Least Auklets (*Aves*, *Alcidae*) varies with large-scale climatic conditions of the North Pacific Ocean

Received: 21 September 2001 / Accepted: 28 May 2002 / Published online: 10 August 2002  
© Springer-Verlag 2002

**Abstract** We evaluated whether annual adult survival of Least Auklets (*Aethia pusilla*), a small planktivorous seabird, covaried with large-scale oceanographic conditions in the North Pacific ocean during 1990–2000. Adult Least Auklets ( $n=358$  total) were captured near their nest sites, marked with plastic color bands, and survival estimates were based on color band resightings at their breeding colony. Survival estimates and relationships between survival and three large-scale indices of climatic conditions that correlate with oceanography: the Pacific Decadal Oscillation Index (PDO), Aleutian Low Pressure Index (ALPI), and North Pacific Index (NPI) were evaluated using program MARK. The best models included: (1) two groups of birds, defined by ease of resighting, that differed in recapture rate ( $p$ ) but not survival rate ( $\phi$ ); and (2) models that allowed for survival rates to differ in the year immediately after first capture from all subsequent years (structurally an age-model). Both of these model structures effectively explained (i.e. removed) sources of heterogeneity in the data set. For Least Auklet survival, the best fitting model was a two-age model incorporating the covariate NPI (average value for the period auklets were at sea, August – April), [ $\phi(\text{age}1, \text{age}2 \times \text{NPI}), p(g)$ ]. The annual survival rate varied from  $0.747 \pm 0.075$  SE in 1992–1993 to  $0.953 \pm 0.052$  in 1991–1992 (based on the model [ $\phi(\text{age}1, \text{age}2 \times t), p(g)$ ]) and averaged  $0.873 \pm 0.037$  over the study period. Least Auklet annual survival covaried with continuous variation in large-scale climatic conditions. Our results point to oceanographic conditions that relate to climate

change as crucial to the status of auklet populations, notwithstanding conservation measures taken to control introduced predators, oil spills, human disturbance and other anthropogenic sources of mortality.

**Keywords** *Aethia pusilla* · Climate change · Demography · Oceanography · Seabird

### Introduction

Like other long-lived marine animals, auks (*Aves*, *Alcidae*) are vulnerable to factors that influence their normally high adult survival rates (Gaston and Jones 1998). However, few studies have evaluated the effect changing climatic and related oceanographic conditions have on annual survival rates of adult seabirds. Cairns (1987) suggested that seabird survival rates are low only when their prey is extremely scarce, rise quickly with slightly improved feeding conditions, and are constant in moderate to good feeding conditions. Seabirds are believed to respond most strongly to changing oceanographic conditions with variation in their diet and breeding success rather than adult survival rate (Cairns 1987; Furness and Nettleship 1991; Montevecchi 1993). In several instances, extreme El Niño Southern Oscillation (ENSO) events were accompanied by catastrophic reproductive failure and likely adult mortality at tropical seabird colonies (e.g., Barber and Chavez 1983; Schreiber and Schreiber 1984). However, the degree to which annual adult survival rates respond to routine continuous variation in large-scale oceanographic conditions has not been quantified and is poorly understood.

There is growing evidence for ecologically important ENSO-like variation in climate and related oceanographic conditions in the North Pacific (Trenberth and Hurrell 1994; Beamish et al. 1997; Mantua et al. 1997; Zhang et al. 1997). During the ‘warm phase’ of this ‘Pacific Decadal Oscillation’ sea surface temperatures (SSTs) tend to be anomalously cool in the central North Pacific coincident with unusually warm SSTs along the west

I.L. Jones (✉)  
Department of Biology, Memorial University of Newfoundland,  
St. John's, Newfoundland, A1B 3X9, Canada  
e-mail: ijones@morgan.ucs.mun.ca  
Tel.: +1-709-7377666, Fax: +1-709-7373018

F.M. Hunter  
Dept of Animal and Plant Sciences, University of Sheffield,  
Sheffield, S10 2TN, U.K.

G.J. Robertson  
Canadian Wildlife Service, 6 Bruce St., Mount Pearl,  
Newfoundland, A1N 4T3, Canada

coast of North America (Mantua et al. 1997). In the ‘cool phase’ of the cycle, conditions are reversed and SSTs are warm in the central Pacific and cool along the west coast of North America. Ecological effects linked to this North Pacific climate variation are thought to be determined by nutrient availability, associated primary productivity and resulting zooplankton abundance in zones of cool SST. Links of this climatic and oceanographic variability to production of salmon and other commercial fish have been documented (Beamish et al. 1997; Mantua et al. 1997). Pacific decadal oscillation (so-called because it normally remained in one phase for >10 years before switching; Trenberth and Hurrell 1994) has predominantly remained in the warm phase during the period 1977–2000 with a few anomalous years of cool phase conditions.

Auklets (*Aethia* spp. and *Ptychoramphus* sp., Alcidae) include five small (75–300 g), cavity nesting, socially monogamous, sexually monomorphic seabirds that are widely distributed in the North Pacific ocean (Gaston and Jones 1998). Auklet diet includes a variety of zooplankton. The smallest and most abundant auklet species, Least Auklet (*Aethia pusilla*) preys preferentially on Calanoid copepods (Hunt et al. 1993; Jones 1993). Least Auklets come to land only during their short breeding season (May–August) and are non-migratory but remain at sea in the North Pacific for the remainder of the year (Jones 1993). Least Auklets are a suitable species for testing for a relationship between adult survival rate of a long-lived marine animal and oceanography because individuals can easily be marked and observed at breeding colonies (Jones 1992a,b) and their relatively (for a seabird) low trophic position suggests a close link to primary productivity.

In summary, the objectives of our study were to: (1) quantify variation in annual adult survival in a marked population of Least Auklets, a small planktivorous seabird, at a western Aleutian Island colony over the period 1990–2000; and (2) using modeling, evaluate whether auklet survival related to continuous variation in North Pacific climate and oceanography.

## Materials and methods

### Study area

Fieldwork was carried out at a mixed colony of more than 200,000 Least, Crested and other auklet species at Main Talus, Buldir Island, western Aleutian Islands, Alaska (52°22.577'N 175°54.326'E; Byrd et al. 1983; Byrd and Day 1984) during mid-May to early-August of 1990–2000. Buldir Island is located in the central North Pacific about 3,500 km west of the west coast of North America and is free of introduced mammalian predators (foxes, rats) that have affected seabirds on other Aleutian Islands (Bailey 1993).

### Auklet captures

Auklets were captured using noose carpets set on the colony surface within a single 100 m<sup>2</sup> (surface area) study plot over talus occupied by more than 1,000 nesting pairs of Crested Auklets and

**Table 1** Least Auklet (*Aethia pusilla*) capture and resighting effort at Main Talus, Buldir Island, Alaska, 1990–2000

Year	Individuals newly marked	Individuals resighted	Number of resightings
1990	66	28	61
1991	30	54	476
1992	33	72	541
1993	12	60	344
1994	0	48	204
1995	41	88	655
1996	16	74	506
1997	92	139	1,213
1998	60	202	1,256
1999	0	169	1,347
2000	14	145	1,206
Totals:	364		7,809

100 pairs of Least Auklets (I.L.J., unpublished data, Table 1). We believe noose carpets selected breeding and non-breeding auklets (distinguished by the presence of a fully-developed brood patch during June in breeding birds) randomly from the population (Jones 1992a, b, 1993). Each captured adult auklet was given a numbered stainless steel leg band and a unique combination of three Darvik plastic color bands. The age (other than as adults >2 years old) and sex of each individual in our sample was unknown. Subadult birds (2-year-olds, identified by criteria described by Jones 1993; Jones and Montgomerie 1992) were not color banded and not included in survival analysis.

### Auklet resightings

Resighting of color marked auklets were made daily (except during the most severe weather conditions) during mid-May to early August of 1990–2000 (Table 1), encompassing the birds' laying, incubation and chick-rearing periods. We observed birds attending the study plot from a plywood blind during their morning activity period (0900–1300 hours) and during the brief evening activity period at dusk (2300–0030 hours, mostly during early chick-rearing period when activity occurred during daylight conditions) and recorded the color band combinations of all marked individuals present. We kept track of the number of times each individual was resighted each year. It was evident that topography of the study plot, varying nest-site location and behavior of individuals created heterogeneity in our ability to resight individuals. Therefore, individuals were classified into two groups according to ease of resighting. Individual birds were classified as ‘hard to see’ by default, and classified as ‘easy to see’ if they exhibited a pattern of frequent resightings within years that matched the following criterion: resighted at least 3 times in each year they were recorded excepting the year of banding and the last year they were observed (e.g., resightings of a hard to see individual during 5 years, 1 0 3 0 4; resightings of an easy to see individual, 3 7 5 9 2). Each bird was assigned only one classification, which fit the pattern of resightings. We used the two-group criterion because we believe more complex grouping methods or use of an individual covariate for resightability would be unnecessarily complex and overparameterize the models, making it more difficult to make inferences about survival.

### Environmental covariates

To test the hypothesis that auklet adult annual survival covaried with large-scale oceanographic variability we tested three recently derived North Pacific climatic indices. We used standardized values for the Pacific Decadal Oscillation Index (PDO; Zhang et al. 1997; Mantua et al. 1997; Table 2), derived as the leading princi-

**Table 2** Values for the environmental covariates used in the analysis

Year	Pacific Decadal Oscillation Index (August–April) (PDO)	Aleutian Low Pressure Index (ALPI)	North Pacific Index (August–April) (NPI)
1990	-0.22	-0.92	13.2
1991	-1.01	0.36	12.9
1992	0.42	2.09	11.4
1993	0.76	-1.1	13.2
1994	1.29	-0.64	11.8
1995	-0.63	1.52	12.7
1996	0.61	0.8	11.0
1997	0.23	0.54	11.8
1998	1.56	4.71	12.2
1999	-0.61	0.01	13.0
2000	-1.18	0.15	12.8

pal component of monthly SST anomalies (difference from mean SST) in the North Pacific ocean north of 20°N. The PDO index provides a single monthly index of SST anomaly over this entire region, based on monthly averaged SST anomalies from 4° latitude by 6° longitude blocks (Zhang et al. 1997). In this index, the monthly mean global average SST anomalies were removed to separate this pattern of variability from any ‘global warming’ signal present in the data (Zhang et al. 1997; Mantua et al. 1997). We used mean values over August–April preceding auklet resighting periods (May–July). We also examined the effect of the Aleutian Low Pressure Index (ALPI; Beamish et al. 1997; Table 2) that measures the relative intensity of the Aleutian low pressure system of the north Pacific (December–March). ALPI is based on the mean area (km<sup>2</sup>) of sea surface with sea level atmospheric pressure less than 100.5 kPa and expressed as a difference from the 1950–1997 mean. A positive index value reflects a relatively intense Aleutian Low. We used ALPI values for the calendar year preceding auklet resighting periods (May–July). We also examined the effect of the mean North Pacific Index (NPI; Trenberth and Hurrell 1994; Table 2) values for August–April preceding auklet resighting periods. NPI is derived from the area-weighted sea level atmospheric pressure over the region 30°–65°N, 160°E–140°W (Buldir Island is close to the centre of this region). In summary, PDO is based on PC 1 of SSTs of the entire North Pacific north of 20°N, ALPI is based on the mean area of the North Pacific with sea level atmospheric pressure less than 100.5 kPa, and NPI is based on SSTs over a limited area in the central North Pacific. Low values of NPI, and high values of PDO and ALPI, are coincident with relatively low air pressure, cool SST and high oceanic primary productivity near the western Aleutian Islands (Trenberth and Hurrell 1994; Beamish et al. 1997; Mantua et al. 1997; Zhang et al. 1997).

#### Survival rate estimation and model selection procedure

Local adult annual survival ( $\phi$ ) and recapture ( $p$ ) rates were estimated using methods described in Lebreton et al. (1992) and Burnham and Anderson (1998), with program MARK (White and Burnham 1999). We began by first defining a global model (Burnham and Anderson 1998; Anderson and Burnham 1999a). Heterogeneity in resight rate can create problems in estimating survival rates (Prévot-Juilliard et al. 1998); therefore we included a group effect in recapture rates, with hard-to-see individuals and easy-to-see individuals treated in different groups in our global model. Recapture rates were also allowed to vary over time (i.e., the years of our study). Since our marking technique is known to catch both non-breeding and breeding adult birds, we expected that some individuals (‘prospectors’) might show lower site fidelity, and hence lower local survival rates, after their first capture (Pradel et al. 1997; Prévot-Juilliard et al. 1998; Bertram et al. 2000). We allowed survival rates in the

year after the initial capture to be modeled independently of survival in subsequent years. Structurally, this is similar to age models (Lebreton et al. 1992). In these models, apparent survival after first year of capture is a combined estimate of true survival and permanent emigration rates (because the sample of marked individuals includes transient birds), while survival in subsequent years (of resident individuals) is a better approximation of true survival (Pradel et al. 1997). In summary, for our global model, we used a two-age class survival model with time dependence in both the year after initial capture and in subsequent years, and a recapture model with a group effect (ease of sighting) and time dependence. We used notation similar to Lebreton et al. (1992), where the parameterization of each class was explicitly described ( $a1 =$  first age class,  $a2 =$  all subsequent age classes); this model was  $\phi(a1 \times t, a2 \times t), p(g \times t)$ , using  $t$  for time (year) effects and  $g$  for group (easy versus hard to see) differences.

The goodness-of-fit of this global model to the data was determined using a parametric bootstrap approach, based on 100 bootstraps, described in Cooch and White (2001). From these bootstraps, we extracted a mean of the model deviances and a mean  $\hat{c}$ .  $\hat{c}$  is a measure of overdispersion, or extra-binomial variation, in the data. It arises when some model assumptions not being met, such as heterogeneity in survival or recapture rates among individual animals (Burnham and Anderson 1998). The observed deviance and  $\hat{c}$  were divided by the mean of bootstrapped values, and the higher of the two values were taken as an estimate of  $\hat{c}$  (Cooch and White 2001).

We restricted our candidate models to the global model, plus a series of reduced parameter models, including Cormack-Jolly-Seber (Lebreton et al. 1992) models (time and group dependent, no age structure) to assess whether age-structure was appropriate. We did not construct every reduced parameter model, as this would have led to 64 models with the two-age class structure, and 8 additional models without age-structure (basic Cormack-Jolly-Seber and reduced parameters models) many of which had very poor fit. Instead, we used the approach in Lebreton et al. (1992) by first modeling recapture rates to determine the best structure for recapture rates and then modeling survival rates.

Relationships among factors were indicated using standard linear models notation. Model selection was based on comparison of the QAICc, where the models with lowest QAICc values suggest the best compromise between good fitting models and models with relatively fewer explanatory variables (i.e., parsimonious; Anderson and Burnham 1999a; Burnham and Anderson 1998). QAICc, instead of AICc was used to rank models, as an acknowledgment of the extra-binomial variation in the data set, represented by  $\hat{c}$  (Burnham and Anderson 1998, 1999b). QAICc weights were also calculated, as they provide a relative measure of how well a model supports the data compared with other models (Anderson and Burnham 1999a).

Finally, once an appropriate set of models was constructed, we modeled climatic covariates by treating them as an annual covariate in program MARK. We modeled the covariates with survival only after the initial capture period, as we were not interested in the influence of oceanographic conditions on birds not resident in the study area. Also, as with the candidate model set above, we did not model the covariates with every parameterization possible. Rather, we modeled these covariates with the second age class ( $a2$ ) within models with the best fitting parameterizations of  $\phi(a1)$  and  $p$  determined from models previously constructed.

## Results

A total of 358 Least Auklets was captured at Main Talus, of which 314 were resighted at least once (Table 1). The data provided a reasonably good fit to our global model with two age classes and time dependence in survival rates and two groups and time dependence in recapture rates. From the parametric bootstrap  $\hat{c}$  was calculated to

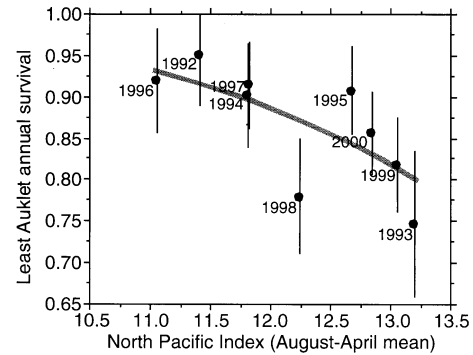
**Table 3** The best ten models among those referred to in the text, and the global model for Least Auklet survival at Buldir Island, Alaska 1990–2000 ( $\hat{c}$  adjusted to 1.434)

Model	QAICc	$\Delta$ QAICc	QAICc weight	Number of parameters	Deviance
$\phi(a1, a2 \times \text{NPI}), p(g)$	1,075.93	0	0.73	5	471.87
$\phi(2a), p(g)$	1,079.19	3.26	0.14	4	479.45
$\phi(a1, a2 \times \text{PDO}), p(g)$	1,081.00	5.07	0.06	5	479.15
$\phi(a1, a2 \times \text{ALPI}), p(g)$	1,081.02	5.09	0.06	5	479.17
$\phi(a1, a2 \times t), p(g)$	1,084.08	8.16	0.01	12	463.12
$\phi(\cdot), p(g)$	1,089.94	14.02	0.00	3	497.76
$\phi(t), p(g)$	1,090.18	14.25	0.00	12	471.86
$\phi(a1 \times t, a2 \times t), p(g)$	1,090.24	14.32	0.00	19	451.19
$\phi(g), p(g)$	1,091.88	15.95	0.00	4	497.64
$\phi(g \times t), p(g)$	1,093.86	17.93	0.00	22	447.39
$\phi(a1 \times t, a2 \times t), p(g \times t)$	1,114.18	38.26	0.00	36	433.82

be 1.434, suggesting the presence of some, but not major amounts, of extra-binomial variation. This value of  $\hat{c}$  was used to adjust all QAICc values. Without the two groups,  $\hat{c}$  was calculated to be 1.768.

After constructing Cormack-Jolly Seber and reduced parameter models, it was clear that recapture rate was best modeled with differences between the two groups, but with no time dependence. Therefore, only this parameterization was used in building subsequent models. Our index of ease of sighting was not biasing our efforts to model survival rate: we found no evidence for a difference in survival rate between the easy and difficult to resight groups, as indicated by the relatively poor fit of the model  $\phi(g), p(g)$ . Therefore, we believe our method of identifying easy and hard to see birds proved useful in reducing unexplained heterogeneity in  $p$  while not biasing estimates of  $\phi$ . Models with two-age structure were also well-supported by the data (Table 3), and models with a constant rate for the survival rate after initial capture were ranked higher than models with time dependent rates (Table 3). Therefore, we used a model with survival rate after the first interval and a recapture that allowed for two groups (ease of sighting) to model climatic covariates:  $[\phi(a1, a2 \times \text{climate indices}), p(g)]$ .

The most parsimonious model in the final candidate model set was a two-age class model in which survival covaried with the climatic index NPI during the preceding August–April and recapture rate differed between the previously classified ‘hard to see’ and ‘easy to see’ groups  $[\phi(a1, a2 \times \text{NPI August–April}), p(g)]$ ; Table 3, Fig. 1). This model was 5.1 times (0.73/0.14; Table 3) better supported by the data compared to the next most parsimonious model. The second-best was the simple ‘two-age class’ (2a) model with two survival rate parameters, one for the first interval following initial capture/markings and the second for constant survival thereafter, in which recapture rate varied between the hard and easy to see groups  $[\phi(2a), p(g)]$ ; Table 3]. The slope  $\beta$  (based on a logit-linked analysis) of the relationship between survival and the NPI was  $-0.539 \pm 0.246$  SE (95% CI,  $-1.022$  to  $-0.056$ ; note the 95% confidence limits do not bound 0). Models with the other two climatic indices were ranked below a model with a constant survival (Table 3), providing little support that these indices were useful in explaining variation in survival.



**Fig. 1** Trends in annual adult survival (for  $a2$ ,  $\pm$ SE) of Least Auklets (*Aethia pusilla*) at Buldir Island, Alaska 1990–2000 and North Pacific oceanography as indicated by mean annual North Pacific Index (NPI) for the period August–April. Survival rates from model  $[\phi(a1, a2 \times t), p(g)]$ ; line based on point estimates from model  $[\phi(a1, a2 \times \text{NPI August–April}), p(g)]$

For this final model, recapture rates were  $0.669 \pm 0.029$  SE for the hard-to-see group, and  $0.996 \pm 0.004$  for the easy to see group. Apparent survival rate after first capture was  $0.728 \pm 0.032$ . This value includes both true survival and emigration from the site. It was not possible to provide a mean survival rate after first capture from the best fitting model as it includes a covariate, but by using a method that takes into account annual variance and sampling variance in survival rate (based on the model  $[\phi(a1, a2 \times t), p(g)]$ ) our mean estimate of Least Auklet adult survival rate at Main Talus 1991–2000 was  $0.873 \pm 0.037$ .

## Discussion

Our best fitting model suggested that: (1) Least Auklets show variability in the ability of observers to resight them; (2) after initial capture some individuals permanently left the study site; and (3) a major index of climate explained some variation in annual survival rate. The first two findings were mostly related to the techniques used in the study. Individuals using areas close to our observation blind would be expected to be seen more often than individuals farther away, and our separation of the data set into two groups appeared to have the desired

effect of reducing this resighting heterogeneity. This grouping technique was effective in reducing  $\hat{c}$  from 1.768 to 1.434, greatly aiding our ability to make inferences from the data. We suggest that the effect of such grouping on model selection deserves further theoretical attention, although in this case of Least Auklet survival at Buldir there is no indication it affected our conclusions. We also found that auklets showed a lower local survival rate after initial capture, and this rate rose in subsequent years. This result has been observed in a number of studies, and results from the fact that not all birds that are initially captured and marked remain in the study area (Pradel et al. 1997). We believe these individuals were prospecting birds not resident at our study site (most were non-breeders), although a disturbance effect due to handling could not be completely excluded.

Far more interesting, however, is the result that Least Auklet survival was related to an index of large-scale climatic variation in the North Pacific, the first such direct evidence for a Pacific auk species. The observed correlation between survival and the environmental covariate NPI may have resulted from both direct and indirect processes. Over-winter survival likely related to the availability of the birds' preferred zooplankton prey, which are short-lived and vary in abundance with primary productivity determined by oceanographic conditions and reflected by the indices NPI, PDO and ALPI (Trenberth and Hurrell 1994; Mantua et al. 1997; Zhang et al. 1997; Beamish et al. 1997). Least Auklet's low trophic position implies a potentially close direct relationship of oceanography and auklet demography, with only two links in the food chain (phytoplankton abundance and zooplankton abundance) separating oceanographic conditions and survival. An indirect effect could have contributed to the relationship of oceanography with variation in auklet survival because Glaucous-winged Gulls (*Larus glaucescens*) may have increased their take of auklets (I.L.J.) during years when their prey (e.g., small fishes) were scarce and they experienced reduced reproductive success (Jeff Williams, AMNWR, unpublished data). This would create an accentuated negative effect on auklet survival in years of unfavorable oceanography because of the combined effects of prey shortage and predation. Further work is required to determine the relative importance to auklet demography of mortality at sea during the non-breeding season (August–April) and mortality at the colony during breeding attempts (May–July).

We detected a correlation between survival and climatic conditions despite several factors that could have hampered our ability to detect such a relationship. First, our small sample size (initially only 66 birds marked, Table 1) reduced the power of our analysis to a degree that we would only be likely to detect a strong relationship. Secondly, because of the structure of the bird's rocky breeding habitat and due to behavioral differences among the marked birds in our study population, not every bird was equally likely to be resighted in each year, reducing the goodness of fit of our data to model assumptions ( $\hat{c}$  was adjusted to 1.434) and thus our ability

to detect weak relationships to environmental covariates. Thirdly, mortality caused by predators such as gulls at the colony during the breeding season may have been indirectly linked to oceanography as mentioned above, but equally could have varied from year to year related to varying local weather conditions and human disturbance. This would be expected to introduce noise into the data that would obscure the relationships between demography and oceanography. Fourthly, our 10-year study took place when the Pacific decadal oscillation was predominantly in the 'warm' phase (Mantua et al. 1997), with cool SSTs, high primary productivity and favorable conditions for auklet survival in the central North Pacific prevailing near the western Aleutian Islands. We thus had few oceanographically poor years (e.g., 1993) to contrast with good years in our analysis. One aspect of our modeling approach that might have tended to create the opposite effect (i.e., an increased possibility of detecting effects) was that because we rated a number of models, the confidence limits on our survival estimates may be slightly too small. This is an ongoing issue in capture-mark-recapture analysis methodology (Burnham and Anderson 1998).

Our data indicate a continuous response of survival rate to variable climate and oceanography (Fig. 1), even during a period of predominantly favorable conditions. Cairns (1987) suggested that seabird survival rate would remain high and constant across almost the entire range of natural variation in food availability, decreasing only in the most severely poor conditions. Our data (Fig. 1) indicate a more gradual and variable response of auk survival within changing (and mostly favorable) environmental conditions.

Among the climate and oceanographic indices we considered, NPI had the best fit to Least Auklet survival at Buldir Island, followed by PDO and ALPI (Table 3). The best fit of NPI was not surprising because among the three covariates, NPI reflects climatic conditions closest to our marked auklet population at Buldir Island (52°N, 175°E), which lies near to the center of the area (30°–65°N, 160°E–140°W) over which NPI indexes sea level atmospheric pressure (Trenberth and Hurrell 1994). Furthermore, NPI is based on a simple averaging of sea level pressure over the region. In contrast, the PDO index is based on the first principal component of SST anomalies over all the North Pacific ocean north of 20°N (Zhang et al. 1997; Mantua et al. 1997), and ALPI reflects the relative size anomaly of the Aleutian low over the entire North Pacific ocean (Beamish et al. 1997).

Several authors have suggested that seabirds may be useful 'indicator species' that could provide information about otherwise difficult to measure variation in the marine environment (Cairns 1987; Furness and Nettleship 1991; Montevecchi 1993). Considering survival rate only, Least Auklets are a poor candidate for an ecologically important indicator species. Although their annual survival rate is responsive to changing oceanographic conditions, survival is difficult to measure because robust estimates for a particular year require several subsequent

years of recapture/resighting data. Survival estimates thus provide a historical perspective of past events and correlations rather than a useful predictive tool. Least Auklets fail to meet key criteria required for useful indicator species (Landres et al. 1988) because their distribution and biology at sea are poorly known and large-scale climatic conditions can be easily assessed quantitatively using remote sensing. Auklet survival data do not provide information on the state of environmental quality unobtainable in other ways. Rather than this seabird species' demography being a useful indicator of environmental change, the reverse is true: easily measured climatic conditions as indexed by NPI, PDO and ALPI impact on and are likely useful predictive indicators of the status of auklet and possibly other seabird populations. The difficulty in measuring auklet population trends at colonies that arises because they nest in concealed crevices (Jones 1992b) points to the need for an alternate signal of favorable or unfavorable conditions.

In most years of our study at Buldir, adult Least Auklets experienced high annual adult survival rates expected for a stable or increasing population of a long-lived seabird species (5 of 9 years with survival  $>0.85$ , 2 years with survival  $>0.90$ ; estimates from the model  $[\phi(a1, a2 \times t), p(g)]$ . High auklet survival at Buldir was consistent with the persistence of mostly favorable oceanographic conditions in the central Pacific during the 1990s. In contrast, the coast of North America from California to British Columbia (hereafter referred to as 'NE Pacific Coast') experienced the brunt of the warm phase of Pacific decadal oscillation during this period. It is not surprising that during 1994–1997, Cassin's Auklets (*Ptychoramphus aleuticus*), another small planktivorous alcid, experienced low annual adult survival ( $0.672 \pm 0.047$ ) at their largest colony at Triangle Island, British Columbia, a rate indicative of a declining population (Bertram et al. 2000). This low rate of annual survival was approached by that indicated by the model  $[\phi(a1, a2 \times t), p(g)]$  for auklets at Buldir in the years of the worst oceanographic conditions ( $0.747 \pm 0.075$ ; 1992–1993). Low adult survival rates of auklets at Triangle Island (Bertram et al. 2000) were likely caused by similar unfavorable oceanographic conditions that were responsible for previously documented population declines of this species at the Farallon Islands, California (Ainley et al. 1994; Nur et al. 1998). We predict that ongoing long-term demographic studies of auklets in the Aleutians and the NE Pacific coast should confirm an inverse relationship of auklet survival between these areas.

We detected one anomalous year (1998) in which Least Auklet survival deviated substantially from the rate expected based on overall oceanographic conditions (Fig. 1). The outlying survival estimate of 0.78 (95% CL, 0.71–0.85) for 1998 was the second lowest of any year of our study. We observed no unusual activity of avian predators at the Buldir Island breeding colony study area during the 1997 or 1998 breeding seasons, nor were there any earthquakes during this period that could have killed birds in their nesting crevices, so we believe

the usual mortality occurred at sea. For the Least Auklet population at Buldir (ca.50,000 birds, I.L.J.), this translates into a mortality during the winter of 1997–98 of about 3,500 birds in excess of that predicted from large-scale environmental conditions ( $\phi$  of 0.85, Fig. 1). Two possible explanations for the event are an oil spill or a severe storm in which birds died of exposure.

It appears both ironic and significant that notwithstanding conservation measures taken to protect seabird populations in the Aleutian Islands and NE Pacific coastal areas from introduced predators, oil spills, human disturbance and other anthropogenic sources of mortality, the status of auklet populations may ultimately be determined by oceanography and climate change. Our results underline the need to consider the state of local and larger-scale climatic conditions when interpreting productivity and population trends at seabird colonies. Furthermore, our study indicates a need for investigation of the role of climate-induced changes in oceanographic conditions in determining the fate of seabird populations.

**Acknowledgements** We thank Christine Adkins, Laura Cowen, Gail Fraser, Mark Hipfner, Karen Kriesel, Elizabeth Mayock, Alejandra Nunez de la Mora, Jeff Williams, Nicole Winter, Ian Stevenson and Allison Veit for assistance in the field, and Vernon Byrd for logistic support and permission to conduct research on the Aleutian Island Unit of the Alaska Maritime National Wildlife Refuge. We are especially grateful to the captains and crews of the vessels R.V. "Tiglax", F.V. "American Empire", F.V. "Resolute", and USCGS "Jarvis", and to the U.S. Fish and Wildlife Service, Empire Seafoods, Arctic King Fisheries, and the U.S. Coast Guard for providing vessel transportation to Buldir Island, to the National Geographic Society Committee for Research and Exploration for providing major funding, and to Kevin Trenberth and Jim Hurrell for helpful comments on the manuscript. During the study, I.L.J. was supported by NSERC Canada and F.M.H. by NERC UK.

## References

- Ainley DG, Sydeman WJ, Hatch SA, Wilson UW (1994) Seabird population trends along the west coast of North America: causes and the extent of regional concordance. *Stud Avian Biol* 15:119–133
- Anderson DR, Burnham KP (1999a) General strategies for the analysis of ringing data. *Bird Stud* 46:261–270
- Anderson DR, Burnham KP (1999b) Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Stud* 46:14–21
- Bailey EP (1993) Introduction of foxes to Alaskan Islands – history, effects on avifauna and eradication. US Fish and Wildlife Service, Washington, D.C.
- Barber RT, Chavez FP (1983) Biological consequences of El Niño. *Science* 222:1203–1210
- Beamish RJ, Neville CE, Cass AJ (1997) Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Can J Fish Aquat Sci* 54: 543–554
- Bertram D, Jones IL, Cooch E, Cooke F (2000) Survival rates of Cassin's and rhinoceros auklets at Triangle Island, British Columbia. *Condor* 102:155–162
- Burnham KP, Anderson DR (1998) Model selection and inference - a practical information-theoretic approach. Springer, Berlin Heidelberg New York
- Byrd GV, Day RH (1984) The avifauna of Buldir Island, Aleutian Islands, Alaska. *Arctic* 39:109–118

- Byrd GV, Day RH, Knudtson EP (1983) Patterns of colony attendance and censusing of auklets at Buldir Island, Alaska. *Condor* 85:274–280
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biol Oceanogr* 5:261–271
- Cooch EG, White GW (2001) Using MARK – a gentle introduction, 2nd edn. Available at <http://www.phidot.org/software/mark/docs/book/>
- Furness RW, Nettleship DN (eds) (1991) Seabirds as monitors of changing marine environments. *Proc Int Ornithol Congr Symp* 41
- Gaston A J, Jones I L (1998) *The auks*. Oxford University Press, Oxford
- Hunt GL Jr, Harrison NM, Piatt JF (1993) Foraging ecology as related to the distribution of planktivorous auklets in the Bering sea. In: Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds) *The status, ecology and conservation of marine birds of the North Pacific*. Canadian Wildlife Service, Ottawa, pp 18–26
- Jones IL (1992a) Factors affecting survivorship of least auklets (*Aethia pusilla*) at St. Paul Island, Alaska. *Auk* 109: 576–584
- Jones IL (1992b) Colony attendance of Least Auklets (*Aethia pusilla*) at St. Paul Island, Alaska: implications for population monitoring. *Condor* 94:93–100
- Jones IL (1993) Least Auklet (*Aethia pusilla*). In: Poole A, Gill F (eds) *The birds of North America*, No. 69. The Birds of North America, Philadelphia, Penn.
- Jones IL, Montgomerie RD (1992) Least auklet ornaments: Do they function as quality indicators? *Behav Ecol Sociobiol* 30:43–52
- Landres PB, Verner J, Thomas JW (1988) Ecological uses of vertebrate indicator species: a critique. *Conserv Biol* 2:316–328
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62: 67–118.
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteorol Soc* 78:1069–1079
- Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJD (eds) *Birds as indicators of environmental change*. Chapman and Hall, London, pp 217–266
- Nur N, Sydeman WJ, Hester H, Pyle P (1998) Survival of Cassin's Auklets on Southwest Farallon Island: temporal patterns, population viability and the cost of double brooding. *Pac Seabirds* 25: 38
- Pradel R, Rioux N, Tamsier A, Lebreton J-D (1997) Individual turnover among wintering teal in Camargue: a mark-recapture study. *J Wildl Manage* 61: 816–821
- Prévot-Juilliard A-C, Lebreton J-D, Pradel R (1998) Re-evaluation of adult survival of Black-headed Gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk* 115:85–95
- Schreiber RW, Schreiber EA (1984) Central Pacific seabirds and the El Nino Southern oscillation: 1982 to 1983 perspectives. *Science* 225:713–716
- Trenberth KE, Hurrell JW (1994) Decadal atmosphere-ocean variations in the Pacific. *Clim Dyn* 9:303–319
- White GC, Burnham KP (1999) Program MARK – survival estimation from populations of marked animals. *Bird Stud* 46:120–139
- Zhang Y, Wallace JM, Battisti DS (1997) ENSO-like interdecadal variability: 1900–93. *J Clim* 10:1004–1020