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Covariation among demographic and climate parameters in whiskered auklets *Aethia pygmaea*

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Annual survival rate and other demographic parameters of whiskered auklets *Aethia pygmaea*, a small planktivorous seabird, were measured at Buldir Island Alaska during 1992–2003 to provide comparative information for auk life history studies and to test for links among climate, age, productivity and survival. Using two 9 m mistnets, we captured and recaptured 384 adult and 193 sub-adult (one year old, a known-age component of our sample) birds as they arrived at the colony after dark during May and June (1,730 capture events). The best fitting model indicated a lower initial survival rate over the first year following marking (0.708 ± 0.036 SE), and subsequent survival (mean 0.835 ± 0.029) covarying with the Aleutian Low Pressure climate Index, with higher auklet survival in years with weak low pressure over the Aleutian Islands. Annual survival rate varied from 0.726 ± 0.127 in 1998–99 to 0.994 ± 0.077 in 1994–95, rates similar to those previously reported for least *A. pusilla* and crested auklets *A. cristatella*. A model based only on recaptures of known-age birds indicated a lower local survival estimate over the first year following marking (age one to two years), with no other age-effects on survival. Breeding propensity by age inferred from recaptures of birds with fully-developed brood patches that were originally marked as sub-adults (one year olds) indicated 53% breeding at age two, 94% breeding at age 3, 97% breeding at age 4 and 100% breeding thereafter. The sex ratio of the sampled birds was significantly male biased (60/40), likely due to differences in behaviour between males and females during the incubation stage. Taken together, our data indicate that whiskered auklet survival and productivity covaried with continuous variation in large-scale climatic conditions, the mechanism being either negative effects of stormy North Pacific weather or indirect effects on food supplies.

Adult survival is a crucial demographic parameter determining population dynamics of most seabird species (Gaston and Jones 1998). Because most seabirds raise at most only a single chick each year, their populations remain stable only with sustained high survival rates. Although studies have rigorously quantified adult survival rates for several seabird species (e.g. Croxall et al. 1990, Wooller et al. 1992, Coulson and Strowger 1999, Ratcliffe et al. 2002), relatively few have identified environmental factors that affect auk adult survival rate, or examined the interrelationships among annual rates of survival, reproductive success, and climate change, even though it is these complex interactions that determine population dynamics.

Growing evidence indicates links between seabird demographic parameters and climate variability in ocean environments (e.g. Thompson and Ollason 2001, Jones et al. 2002, Weimerskirch 2002, Gjerdrum et al. 2003, Grosbois and Thompson 2005, Sandvik et al. 2005); especially ENSO-like variation in climate and related oceanographic conditions in the North Atlantic (Hurrell et al. 2003), and Pacific oceans (Trenberth and Hurrell 1994, Mantua et al. 1997, Zhang et al. 1997, Beamish et al. 1997). In the Pacific, during the 'warm phase' of this 'Pacific Decadal Oscillation' sea surface temperatures (SSTs) tend to be anomalously cool in the central North Pacific (our study area, 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 weather-generated nutrient availability, associated primary productivity and resulting zooplankton abundance in zones of cool SST. Links of this climatic and oceanographic variability to production of commercial fish have been documented (Beamish et al. 1997, Mantua et al. 1997). Taken together, the limited available data also support this indirect (i.e. through ocean production) link between climate and seabird survival (e.g. Jones et al. 2002, Sandvik et al. 2005). However, because low SSTs and higher primary productivity are associated with more intense low air pressure over the North Pacific near the Aleutian Islands (Beamish et al. 1997), weather conditions are likely to be stormier during years of 'favorable' conditions for ocean production. Thus, further work is required to evaluate whether variation in climate could frequently have a direct effect on seabird survival rates, through mortality caused by severe weather (e.g. Morris and Chardine 1995). Fortunately, using recently developed capture-mark-recapture data analysis programs such as program MARK (White and Burnham 1999), it is now relatively easy to test for relationships between survival rates and environmental covariates such as climate indexes.

Whiskered auklets *Aethia pygmaea* are small (mean body mass 118 g), monogamous, sexually monomorphic, planktivorous seabirds that have a clutch size of one egg (Hunter et al. 2002). Compared with other auklets of the tribe Aethiini, whiskered auklets forage close to land in active tide rips, roost on land during the non-breeding season, and apparently remain near their breeding colonies year round (Byrd and Williams 1993, Zubakin and Konyukhov 1999, Williams et al. 2003). Unlike least *A. pusilla* and crested auklets *A. cristatella*, that breed at only nine large colony sites in the Aleutian Islands, whiskered auklet colonies are widely dispersed on many (possibly hundreds of) sites on more than 20 islands (Williams et al. 2003). Activity at whiskered auklet colonies takes place almost entirely at night, with most individuals entering and leaving breeding crevices and delivering food loads to chicks in darkness (Zubakin and Konyukhov 1999). Their diet is more variable, including a wider taxonomic range of invertebrates than least auklets (Day and Byrd 1989, Hunt et al. 1993, Hunter et al. 2002). Although the behaviour and general breeding biology of whiskered auklets is now well-studied, no information is available on survival rates and population regulation. With the removal of introduced Arctic foxes *Alopex lagopus* from many Aleutian Islands, this species may be recovering through recolonisation and population increases on fox-free islands (Williams et al. 2003) – hence the need for a better understanding of population processes. The survival of least auklets was previously shown to correlate with large scale climatic conditions of the North Pacific Ocean, with higher survival in years with low air pressure, high winds and high ocean productivity in the central North Pacific (Jones et al. 2002).

The principal aim of this study was to measure annual adult survival rate of whiskered auklets over an eleven year period at one colony, and to identify individual (e.g. age) and environmental (e.g. climate and oceanographic) factors correlated with survival. To reveal what factors might be most important to population regulation, we also examined the relationships among survival, recruitment, productivity and environmental variation at our study site at Buldir Island.

Methods

Study area

Fieldwork was carried out at one 45 m by 10 m trapping area near Crested Point, Buldir Island, western Aleutian Islands, Alaska (52° 22.58′N, 175° 54.33′E; Byrd et al. 1983, Byrd and Day 1986), an isolated fragment of the larger dispersed colony of thousands of whiskered auklets nesting in beach boulders and adjacent cliffs and rocky hillsides of this island. The trapping site was delimited by a sandy beach to the west (unsuitable habitat), and an abrupt headland to the east, together limiting trapping to a discrete area of the overall colony. Trapping occurred during mid-May to early-August of 1990–2003. Buldir Island, part of the Alaska Maritime National Wildlife Refuge, is located in the central North Pacific about 3500 km west of continental North America and is free of introduced mammalian predators (foxes, rats) that have negatively affected seabirds on other Aleutian Islands (Bailey 1993).

Capture-mark-recapture

Using two 12 m mistnets, we captured adult and subadult whiskered auklets between 00.00 h and 03.00 h ADT as they arrived at their nesting colony at Crested Point during May and June of 1992–2003 (Table 1). Because hatching commenced on 16–27 June (Hunter et al. 2002), nearly all of our trapping effort took place during the period when birds were incubating. In selecting nights for mist-netting, we avoided nights with

Table 1. Whiskered auklets captured at Buldir Island, Alaska, 1992–2003.

Year	Capture dates (trapping nights)	New birds			Retraps		Total captures
		Adults	Sub-adults (%)	Juveniles	Within year	Between year	
1992	May 18–June 20 (7)	89	5 (3.4)	–	53	–	147
1993	June 2–June 15* (6)	50	17 (19.1)	6	22	37	132
1994	June 3–June 16 (6)	12	9 (17.3)	–	31	66	118
1995	May 22–June 13 (8)	22	26 (29.5)	–	40	62	151
1996	May 31–June 28** (9)	23	27 (25.7)	–	55	97	204
1997	May 25–June 14*** (11)	40	20 (18.3)	2	49	76	198
1998	May 24–June 13**** (10)	24	27 (31.4)	–	35	92	178
1999	June 30–July 27 (3)	5	0	1	2	32	40
2000	May 28–July 22 (9)	47	24 (23.1)	–	33	61	166
2001	May 26–June 8 (10)	26	29 (27.9)	–	49	76	180
2002	June 2–July 25 (7)	21	2 (4.5)	–	21	64	109
2003	June 2–July 26 (7)	19	7 (17.9)	–	13	68	107
	Grand totals	378	193	9	403	731	1730

* Also July 9 and July 14; ** Also July 10 and July 25; *** Also June 28, July 12 and 26.

high wind and rain. We believe our nets captured birds more or less randomly from among birds frequenting our study area during the first of two nightly activity peaks (Zubakin and Konyukhov 1999), when most birds were arriving at the colony site. However, it was possible that breeding and non-breeding auklets' behaviour differed in some way that might have affected their trapability – we were not able to test for or otherwise measure this. We marked each captured individual with a numbered USFWS stainless steel band and scored its age as adult or sub-adult. Sub-adults were identified by extensive pale brown (due to weathering and wear) contour feathering on their forehead, chin, and neck, and by similarly worn secondaries and greater coverts (Bedard and Sealy 1984, Pitocchelli et al. 2003). Feather ornaments (forehead crest, sub- and superorbital plumes, auricular plumes) were diminutive or lacking in sub-adults. We opportunistically captured and banded a few fledglings as they roosted on nearby low cliffs at night during July and August.

Individuals identified as adults at first capture were scored as 'unknown age'. Individuals captured as juveniles (fledglings – age 0) and subadults (age one year) were considered to be of known age. We checked most captured birds for the presence of a brood patch starting in 1993. Individuals with complete, fully vascularized brood patches about 25 mm in diameter present during the incubation period (15 May to 15 June) were scored as 'breeders'. Other individuals, with unvascularized bare patches less than 25 mm diameter, were scored as 'non-breeders' and the size of the bare patch relative to 25 mm recorded (0.1–0.9). Other birds, that showed signs of heat stress after capture, and those caught simultaneously with >10 other birds and thus were likely to show heat stress symptoms, were released with the brood patch unscored. During 2000–2001 we took a 0.3 mL blood sample from the brachial vein of 102 adult and 49 subadult birds. To estimate a sex ratio for our study population, these individuals were later sexed using the molecular technique described by Fridolfsson and Ellegren (1999). Because whiskered auklets breed in mostly inaccessible rock crevices, are nocturnal, and are sexually indistinguishable by morphology, this was the only direct method of sex ratio determination available to us.

Survival rate estimation and model selection procedure

Local adult annual survival (Φ) and recapture (P) rates were estimated using methods described by 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) in which recapture rates were allowed to vary over time. 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). Thus, 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, survival during the first year after initial capture is a combined estimate of true survival and permanent emigration rates, while survival in subsequent years 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 time dependence. We denoted this model as $\Phi(t/t) \times P(t)$, where t denotes time effects, while t/t represents time effects for the first and subsequent intervals after banding, before and after the slash, respectively. We applied this modeling technique to all individuals marked and recaptured at Crested Point.

Goodness-of-fit was first evaluated using Test 2 and 3 in program Release (Burnham et al. 1987), which specifically examines the data set for sources of heterogeneity due to first capture effects (Test 3) or previous trapping history effects (Test 2). If no systematic sources of heterogeneity were identified by Release, the overall goodness-of-fit of the 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 c-hat. The observed deviance and c-hat were divided by the mean of bootstrapped values, and the higher of the two values were taken as an estimate of c-hat (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 dependent, no age structure) to assess whether age-structure was appropriate. We did not construct every reduced parameter model, but rather we used the approach of Lebreton et al. (1992) by first modeling recapture rates to determine the best structure for recapture rates and then modeling survival rates. In addition to modeling recapture rate varying among all years, we also evaluated the fit of a model in which recapture rate varied among three groups of years: 1) 'normal' fieldwork years (1993–1998, 2001 and 2003), 2) the year 1999, when a vessel accident delayed fieldwork and reduced the number of captures, and 3) two other years with reduced trapping effort (2000 and 2002).

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; Burnham and Anderson 1998, Anderson and Burnham 1999a). QAICc, instead of AICc was used to rank models, as an acknowledgment of the extra-binomial variation in the data set, represented by c-hat (Burnham and Anderson 1998, Anderson and Burnham 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).

To further explore relationships between true age and local survival rates, we examined data for individuals of known age (captured and banded as subadults). We began modeling using the same global model as used for the entire data set; once suitable parameterizations for recapture rates and survival through the first age class (i.e. age 2) were determined, the number of unique age classes was increased to see if evidence of age specific variation in local survival rates existed in the 3rd and 4th year of life. We were not able to examine the relationship between sex and survival because our sample of known sex birds was small and most adults were blood-sampled several years after marking (i.e. sex identification and survival were confounded).

Oceanographic covariates

To evaluate whether oceanographic variability influenced whiskered auklet adult annual survival, we looked for relationships between survival and both summer (April–August) and winter (August–April) sea surface temperatures near Buldir, and with three North Pacific climatic indices. Mean sea surface temperatures in a 5° latitude by 5° longitude block centered on Buldir Island were obtained from the OAA Extended Reconstructed SST data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their web site at http://www.cdc.noaa.gov/. We used standardised values for the 'Pacific Decadal Oscillation Index' (PDO; Mantua et al. 1997, Zhang et al. 1997), derived as the leading principal component of monthly SST anomalies in the North Pacific ocean north of 20°N. We used mean PDO values for August–April preceding auklet recapture periods (May–June). We also examined the effect of the "Aleutian Low Pressure Index" (ALPI; Beamish et al. 1997) 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^2) with sea level atmospheric pressure less than 100.5 kPa and expressed as an anomaly from the 1950–1997 mean. A positive index value reflects a relatively intense Aleutian Low. We used ALPI values for the year preceding auklet resighting periods. 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°N–65°N, 160°E–140°W (Buldir Island is close to the center of this region). Low values of NPI, and high values of PDO and ALPI, are coincident with relatively low air pressure, high wind velocity, 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).

Once an appropriate set of models was identified, we modeled climatic covariates by treating them as an

Table 2. The best twelve models identified by program MARK and the global model, for whiskered auklet survival and recapture rates (all birds) at Crested Point, Buldir Island, Alaska 1992–2003 (c-hat adjusted to 1.614). In the model names, c denotes constant rates, t denotes full time variation, while the slash notation (x/y) represents parameterizations for the first (x) and subsequent (y) age classes. For the covariates, ALPI is the Aleutian Low Pressure Index, SST Aug-Apr and SST Apr-Aug are sea surface temperatures in the previous year, NPI is the North Pacific Index and PDO is the Pacific Decadal Oscillation. For recapture rates, 3 groups of years indicates 1993–1998, 2001 and 2003 estimated as one rate; 1999 estimated alone and 2000 and 2003 combined.

Model	QAICc	ΔQAICc	QAICc weight	Number of parameters	Deviance
Φ(c/ALPI) × P(3 groups of years)	1893.1	0	0.83	6	700.17
Φ(c/SST Aug-Apr) × P(3 groups of years)	1897.2	4.08	0.11	6	704.26
Φ(c/t) × P(3 groups of years)	1900.3	7.18	0.02	14	691.08
Φ(c/SST Apr-Aug) × P(3 groups of years)	1900.4	7.25	0.02	6	707.41
Φ(c/c) × P(3 groups of years)	1903.0	9.87	<0.01	5	712.07
Φ(c/NPI) × P(3 groups of years)	1903.9	10.79	<0.01	6	710.97
Φ(c/PDO) × P(3 groups of years)	1905.0	11.87	<0.01	6	712.04
Φ(c) × P(3 groups of years)	1907.6	14.45	<0.01	4	718.66
Φ(t) × P(3 groups of years)	1909.6	16.53	<0.01	14	700.42
Φ(c/t) × P(t)	1910.25	17.14	<0.01	22	684.54
Φ(c) × P(t)	1913.18	20.08	<0.01	12	708.06
Φ(t) × P(t)	1920.15	27.05	<0.01	21	696.52
Φ(t/t) × P(t)	1922.92	29.81	<0.01	31	678.39

[1] Three recapture rate parameters: 4, 1993–1998, 2001 and 2003; 5, 1999 only; 6, 2000 and 2003 (see Table 4).

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 within models with the best fitting parameterizations of Φ of the first age class and P determined from models previously constructed. To look for associations among annual survival with proportion of subadults present and productivity (data from Hunter et al. 2002), we modeled these covariates with the second age class, compared to the model Φ(c/t) × P(3 groups of years), see below. To look for associations among environmental covariates with proportion of subadults present and productivity we used simple correlation analysis.

Results

Aging birds, age at first breeding, age-dependent breeding, and sex ratio

Most birds were caught on the seaward side of the net (i.e., as they arrived). A few birds may have been netted as they departed the colony site, but because some arriving birds circled on approach, we were unable to be sure whether the birds caught on the landward side of the net were departing or arriving. The proportion of whiskered auklets captured in subadult plumage varied from year to year, with the greatest proportion captured in 1995 (24%) and the lowest proportion captured in 1992 (5%; Table 1). Among 54 birds caught and banded as subadults and recaptured in the following year, all were recaptured in adult plumage. Two birds banded as juveniles (recent fledglings) were recaptured the following year as subadults. From these data we deduced that whiskered auklets possessed subadult plumage for only one season (yr) and that subadults were one year old. All birds marked as subadults were thus classified as known age birds in our dataset, and the proportion of subadult birds trapped each year used as an index of recruitment.

The proportion of birds attempting breeding by age, as inferred from possession of a complete vascularized brood patch during the period May 15–June 15, was 3.5% at one year of age, 52.4% at two years of age, 94.0% at three years of age, 97.0% at four years of age, and 100% thereafter (Fig. 1). Among the 1,730 captures, 820 (47%) were scored as breeders, 297 (17% overall, and 27% of birds scored) were scored as

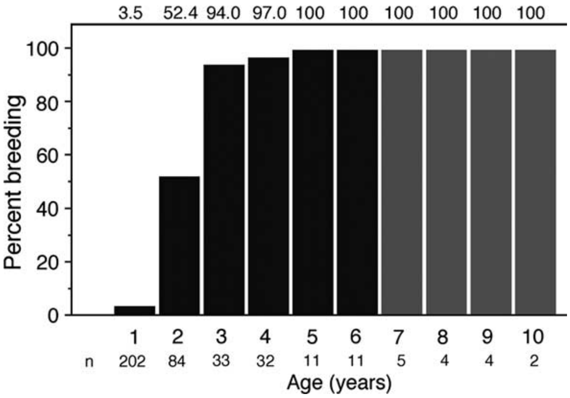

Fig. 1. Proportion of known age whiskered auklets breeding (as inferred from possession of a full brood patch during the incubation period) at Buldir Island Alaska during 1992–2003.

non-breeders, 524 (30%) were unscored because their brood patch area was not examined, and 89 (5%) were unscored because they were captured after 15 June.

The proportion of subadult (one year old) birds caught varied strikingly (and statistically significantly; $\chi^2 = 78.8$, df = 10, $P < 0.001$) among years from less than 5% in 1992 and 2002 to as high as 31% of birds captured in 1998 (Table 1).

Among 102 birds captured as adults and sexed genetically (Fridolfsson and Ellegren 1999), 40 (39%) were identified as females and 62 (61%) as males, indicating a significant male bias in the sampled adult population (Binomial, $Z = 2.2$, $P = 0.03$). In a smaller sample of subadults ($n = 49$), 20 (41%) were identified as females and 29 (59%) as males, a similar ratio (adult and subadult sex ratios compared, $\chi^2 = 0.04$, df = 1, $P = 0.86$) but not significantly different from 50/50 in the subadult population (Binomial, $Z = 1.3$, $P = 0.2$). Combining all sexed birds, 60 (40%) were identified as females and 91 (60%) as males, indicating a significant male bias in the overall sample (Binomial, $Z = 2.5$, $P = 0.01$).

Local survival rate estimation and model selection procedure

The complete dataset (including all known age and unknown age birds) provided a reasonably good fit to our global model with two age classes and time dependence in survival rates and time dependence in recapture rates. No consistent sources of heterogeneity were detected by Release (Test 2, $\chi^2 = 32.7$, df = 34, $P = 0.57$; Test 3, $\chi^2 = 41.3$, df = 37, $P = 0.29$). From the parametric bootstrap c-hat was calculated to be 1.614, suggesting the presence of some, but not major amounts, of extra-binomial variation. This value of c-hat was used to adjust all QAICc values for this dataset.

After constructing Cormack-Jolly Seber models and reduced parameter models, it was clear that recapture rate was best modeled without complete time dependence, but instead with three time parameters that included groups of years with similar recapture rates (high: 1993–1998, 2001, and 2003; very low: 1999; moderate: 2000 and 2002; Table 2). Therefore, only this recapture rate parameterization (P(3 groups of years)) was used in building subsequent models. Models with two-age-structure were well-supported by the data (Table 2), and models with a constant survival rate after initial capture (denoted c) were ranked higher than models with time dependent rates (Table 2). Therefore, we used survival rate after the first interval and recapture in three groups of years to model climatic covariates: $\Phi(\text{c/climatic indices}) \times P(3 \text{ groups of years})$.

The most parsimonious model in the final candidate model set was a two-age class model in which survival covaried with the climate index ALPI $\{\Phi(\text{c/ALPI}) \times P(3 \text{ groups of years})\}$; Table 2, Fig. 1). This model was 7.6 times (0.83/0.11; Table 2) better supported by the data than the next most parsimonious model. The second-best model was a two-age class model in which survival covaried with mean sea surface temperature near Buldir Island during the preceding August–April ($\Phi(\text{c/SST August–April}) \times P(3 \text{ groups of years})$); Table 2). The slope β (based on a logit-linked analysis) of the relationship between survival and the ALPI was -0.3119 ± 0.0816 SE (95% CI = -0.4719 to -0.1520; note that 0 is not within the 95% CI). Models with the other two climatic indices were ranked below a two-age model with a constant survival (Table 2), suggesting that these indices were not as useful in explaining variation in survival.

It was not possible to provide a mean survival rate after first capture from the best fitting model as it included a covariate, but by using a method that takes

Table 3. Parameter estimates for the model: $\Phi(\text{c/t}) \times P(3 \text{ groups of years})$ corrected for c-hat = 1.614, for whiskered auklets at Crested Point, Buldir Island, Alaska 1992–2003.

Parameter			95% CI	
		SE	lower	upper
Survival, first occasion	0.708	0.036	0.633	0.774
Survival 1993–1994	0.873	0.079	0.628	0.966
Survival 1994–1995	0.948	0.061	0.619	0.995
Survival 1995–1996	0.994	0.077	0.000	1.000
Survival 1996–1997	0.798	0.075	0.613	0.908
Survival 1997–1998	0.857	0.086	0.603	0.960
Survival 1998–1999	0.726	0.132	0.421	0.907
Survival 1999–2000	0.745	0.135	0.420	0.922
Survival 2000–2001	0.836	0.113	0.502	0.963
Survival 2001–2002	0.865	0.116	0.402	0.831
Recapture rate, 1993–1998, 2001 and 2003	0.517	0.025	0.481	0.553
Recapture rate, 1999 only	0.149	0.041	0.116	0.240
Recapture rate, 2000 and 2003	0.374	0.048	0.305	0.425

Table 4. The best ten models identified by program MARK and the global model, for survival of 193 known-age whiskered auklets marked and recaptured at Crested Point, Buldir Island, Alaska 1992–2003 (c-hat adjusted to 1.756). In the model names, c denotes constant rates, t denotes full time variation, while the slash notation (x/y) represents parameterizations for the first (x) and subsequent (y) age classes. For recapture rates, 3 groups of years indicates 1993–1998, 2001 and 2003 estimated as one rate; 1999 estimated alone and 2000 and 2003 combined.

Model	QAICc	ΔQAICc	QAICc weight	Number of parameters	Deviance
Φ(c/c) × P(3 groups of years)	467.5	0	0.65	5	228.83
Φ(c/c/c) × P(3 groups of years)	469.4	1.89	0.25	6	228.64
Φ(c/c/c/c) × P(3 groups of years)	471.3	3.80	0.10	7	228.47
Φ(c/c) × P(t)	478.1	10.59	<0.01	13	222.49
Φ(c) × P(c)	478.8	11.29	<0.01	2	246.27
Φ(c/c/c) × P(t)	479.9	12.40	<0.01	14	222.13
Φ(c) × P(t)	482.0	14.46	<0.01	12	228.53
Φ(t) × P(c)	491.9	24.38	<0.01	12	238.44
Φ(c/t) × P(t)	493.5	25.94	<0.01	22	217.78
Φ(t) × P(t)	499.3	31.72	<0.01	21	225.85
Φ(t/t) × P(t)	510.6	43.10	<0.01	31	213.73

into account annual variance and sampling variance in survival rate (based on the model (Φ(c/t) × P(3 groups of years)), see Table 3 for estimates) our mean estimate of whiskered auklet adult survival rate at Crested Point during 1992–2003 was 0.835 ± 0.029.

Age-dependence in survival

The known age dataset (193 birds marked as one-year-old subadults) again provided a reasonably good fit to a global model with two age classes and time dependence in survival rates and time dependence in recapture rates. No consistent sources of heterogeneity were detected by Release (Test 2, $\chi^2 = 9.5$, df = 20, P = 0.98; Test 3, $\chi^2 = 24.6$, df = 31, P = 0.78). From the parametric bootstrap c-hat was calculated to be 1.756, suggesting the presence of some extra-binomial variation. This value of c-hat was used to adjust all QAICc values for this dataset. The most parsimonious model was a two-age class model (i.e. only two survival rates, across first interval after capture (age one to age two) and annually across all subsequent occasions (year two and above; Φ(c/c) × P(3 groups of years)); Table 4). The survival rate estimates for this model were 0.611 ± 0.073 for age one to age two and 0.813 ± 0.039 for all subsequent years. Recapture rates were 0.150 ± 0.067 for 1999, 0.373 ± 0.075 for 2000 and 2002, and 0.494 ± 0.053 for the rest of the years. This model was 2.6 times (0.65/0.25; Table 4) better supported by the data compared to the next best model, a three-age class model in which survival varied between ages one-two (0.597 ± 0.077), two-three (0.865 ± 0.129) and all subsequent age groups lumped (0.803 ± 0.046).

Covariation in demographic parameters across years

A positive relationship was present between survival rate and productivity ($\beta = 3.14 \pm 1.05$, 95% CI: 1.07 to 5.20) while the positive relationship between survival rate and proportion of subadults present ($\beta = 0.076 \pm 0.041$, 95% CI: −0.005 to 0.158) was only weakly supported by the data (Table 5). Besides the association between survival rate and ALPI, the only statistically significant correlations we found among other demographic and environmental parameters considered was between whiskered auklet productivity and sea surface temperature near Buldir (r = +0.84, P = 0.007, Fig. 3). There was no association between productivity and ALPI (r = −0.38, P = 0.4) and the proportion of

Table 5. Models examining relationships between survival and other demographic parameters, for whiskered auklets at Crested Point, Buldir Island, Alaska 1992–2003 (c-hat adjusted to 1.614). In the model names PROD is productivity and SUB% is the percentage of subadults in the population. The model: Φ (c/t) × P(3 groups of years) is retained for comparison. For the models including the covariate, the Φ for 1998–1999 was estimated separately, as a covariate was not available for 1999. For recapture rates, 3 groups of years indicates 1993–1998, 2001 and 2003 estimated as one rate; 1999 estimated alone and 2000 and 2003 combined.

Model	QAICc	ΔQAICc	QAIC weight	No. of parameters	Deviance
Φ(c/PROD) × P(3 groups of years)	1894.10	0.00	0.751	7	699.14
Φ(c/SUB%) × P(3 groups of years)	1896.60	2.50	0.215	7	701.64
Φ(c/t) × P(3 groups of years)	1900.29	6.19	0.034	14	691.08

subadults captured was not correlated with productivity in the previous year (r = +0.04, P = 0.9).

Discussion

Our study provided a comprehensive preliminary analysis of demographic processes in a whiskered auklet population. The general picture that emerged was of whiskered auklets having survival rates very similar to least and crested auklets, but lower than those of larger alcids such as murres (*Uria* spp., e.g. Sandvik et al. 2005, Robertson et al. in press), and we found evidence for a direct negative effect of climate rather than an indirect effect operating through ocean productivity.

We observed a rapid increase in the proportion of known-age birds possessing a fully developed brood patch, from about 50% at age two years to over 90% by three years of age to 100% at five years of age and beyond. Although our inference of breeding status based on fully vascularized brood patches was indirect, and such inferences are open to further discussion (e.g. McFarlane Tranquilla et al. 2003), we believe our data is consistent with the idea that some whiskered auklets breed at two years of age and that most birds are breeding by age five. This fits with some other small alcid species in which some individuals start breeding at two years and most are breeding at age four (e.g. ancient murrelet *Synthiboramphus antiquus*, Gaston 1994; Cassin's auklet *Ptychoramphus aleuticus*, Pyle 2001). This also fits with whiskered auklets' lower survival rate compared with large alcids, because earlier age at first breeding would be favoured by their lower life span. With most individuals breeding by age three, whiskered auklets might be able to recover more rapidly than large auk species from population crashes.

We observed a 60/40 male-biased sex ratio in whiskered auklets trapped at our study area at Crested Point, raising the question of whether this reflected a true population wide sex ratio or a sampling bias. We believe our nocturnal mist netting technique representatively sampled all auklets attempting to come ashore in the study area during the incubation period, because the net was both invisible to the birds and high enough to preclude subgroups of colony attending birds avoiding capture (i.e. the nets missed some birds during netting periods, but there was no reason to believe these belonged to a particular age or sex category). Thus the biased sex ratio suggests an inter-sexual difference in behaviour at this stage of the breeding season (e.g. males arriving predominantly during the first of two nightly peaks of activity, Zubakin and Konyukhov 1999). Our results are also consistent with another possibility, that the whiskered auklet population at Buldir Island had a 60/40 male-biased sex ratio, but this seems less likely. Among 134 whiskered auklet chicks (nestlings) sexed from study crevices at nearby Main Talus, 59 (44%) were males and 75 (56%) were females (Binomial, Z = 1.4, P = 0.2), no deviation from 50/50 at the chick stage (Dawson et al. 2001). Our findings indicate the need for further quantification of sex-ratios of whiskered and other auklet species, and perhaps a re-evaluation of the assumption of even sex ratios in auks and other seabirds. Ideally, in studies of sexually indistinguishable species, all individuals should be blood or feather sampled at time of marking and sexed genetically (i.e. Fridolfsson and Ellegren 1999). In our study this was not done systematically and we were thus unable to measure inter-sexual differences in survival rate. There is little information on sex ratios in adult auk populations, likely due to the indistinguishability of auk sexes by visual observation alone, and the difficulty of obtaining representative samples. Counts of known sex alcids have either involved individuals that are paired (i.e. visible breeding birds on cliff ledges), are affected by sex differences in behaviour (e.g. Fraser et al. 2002, Bradley et al. 2002), or result from beach bird surveys of dead birds (e.g. killed in oil spills) that may not be representative of entire populations. Population models (e.g. Wiese et al. 2003) normally assume an even sex ratio for auk populations, but the consequences of uneven sex ratios could be very significant to population processes.

Our best fitting models for local survival and recapture rate indicated that after initial capture some individuals (transients) permanently left the trapping area, and that survival varied with a major index of North Pacific climate. Local survival during the first interval after marking was 0.71 ± 0.04, while survival thereafter averaged 0.84 ± 0.03, suggesting that about 13% of newly-marked individuals in any year were transients. This mean whiskered auklet survival rate during our study was slightly less than (but not statistically significantly different from) that measured for least auklets (0.87 ± 0.04, Jones et al. 2002) and crested auklets (0.86 ± 0.02, Jones et al. 2004) during the same time span. Most interesting was our finding that the best survival model incorporated the Aleutian Low Pressure Index (ALPI, Beamish et al. 1997) as a climate covariate (Table 2). Whiskered auklet survival at Buldir was highest in years with slightly negative or neutral ALPI (a weak Aleutian Low pressure anomaly, e.g. 1994) and survival was lowest in years with positive ALPI index (a relatively strong or intense Aleutian Low pressure anomaly, e.g. 1998 and 2002, Fig. 2; Beamish et al. 1997). Coincidentally, 1998 was an unusually anomalous year for ENSO, a climate index for more southern parts of the Pacific Ocean. This may indicate a role for ENSO that extends to the Aleutian Islands. The second best model indicated survival positively correlated with sea surface temperature (August–April) near Buldir (Table 2; i.e. higher survival following periods of

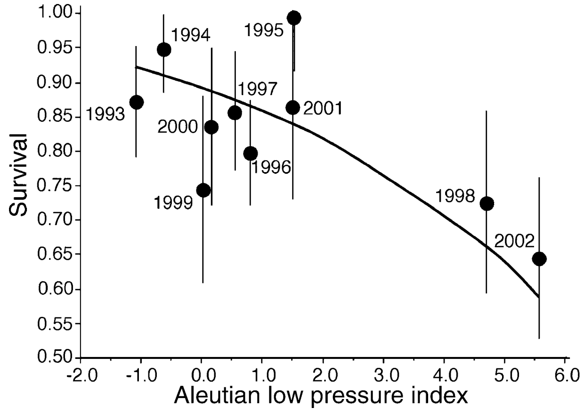

Fig. 2. Correlation between annual adult survival (±SE) of whiskered auklets at Buldir Island, Alaska 1993–2002, and North Pacific climate, as indicated by the Aleutian Low Pressure Index. Survival rates from model: $\Phi(c/t) \times P$(3 groups of years); line based on point estimates from model: $\Phi(c/ALPI) \times P$(3 groups of years).

warmer water temperature). Our data are thus consistent with the idea that whiskered auklet survival was directly affected by climate, with low survival during stormy winters. Presumably cold water was churned up during stormy, positive ALPI conditions, explaining the weaker positive correlation between survival and sea temperature. Our data for whiskered auklets shows the opposite trend to that previously found for least auklet survival (1990–2000), in which high survival followed years with a positive North Pacific Index (i.e. high survival was correlated with low sea level air pressure over the North Pacific; Trenberth and Hurrell 1994, Jones et al. 2002). We previously speculated that for least auklets, survival was higher following low pressure (windy) conditions because these were associated with increased ocean productivity, an indirect effect of climate on survival rate (Trenberth and Hurrell 1994, Jones et al. 2002). The opposing trends for whiskered and least auklets may be explained by differences in their biology, with whiskered auklets foraging close to land and remaining near their breeding colonies and even roosting on land during the non-breeding season, while least auklets disperse widely in the North Pacific during winter. Possibly, whiskered auklets were less affected by annual variation in ocean productivity because they forage in reliable prey concentrations (tide rips) and on a wider range of prey taxa (Day and Byrd 1989, Hunter et al. 2002) including longer-lived species than the *Neocalanus* copepods preferred almost exclusively by least auklets (Jones et al. 2002). Whiskered auklets might be more directly affected by stormy low pressure conditions because foraging conditions in the tide rips in which they habitually feed themselves might be modified during storms to make foraging more difficult, possibly for days at a time in winter. However, there was another possibility – that warmer sea temperature actually favours populations of whiskered auklets' preferred prey taxa. This would be an indirect effect of climate on survival, but favouring whiskered auklet foraging in warm (not cold, as for least auklet) sea temperature conditions. Distinguishing between indirect versus direct effects on whiskered auklet survival will require further research on the biology and population dynamics of copepods and Euphausiids in relation to climate and oceanographic variability. Our study demonstrated that seabird survival may, for at least some species, be negatively affected by intense low pressure conditions, unlike previous studies that showed an association between high survival rate and climatic conditions favouring increased productivity of the oceans (Jones et al. 2002, Grosbois and Thompson 2005, Sandvik et al. 2005).

Analysis of the known age whiskered auklet population indicated that local survival differed only between the first occasion after marking (0.61) and all subsequent occasions (0.84, Table 4). Models with survival rates varying across wider age ranges were not supported (Table 4). These results were consistent with two possibilities: 1) there was constant true survival rate across all ages with one year old birds being more likely to leave the trapping area after marking, or 2) survival rate was lower between age one and two compared with all other ages. Although disentangling death and permanent emigration is inevitably problematical in capture-mark-recapture studies of free-living organisms, we believe our data were more consistent with the former possibility. One year old birds were non-breeders without mates and thus were likely prospectors and transients, so a lower local survival rate was expected.

Considering how our demographic measures covaried, it was interesting but not surprising that whiskered auklet survival rate and productivity (reproductive success) were positively correlated, although each was significantly correlated with a different important environmental variable (Tables 2 and 5). Presumably the correlation reflected the role of the same environmental conditions affecting both survival and productivity (in winter and summer, respectively) in the same year. Also notable was that whiskered auklet productivity was positively correlated with sea surface temperature near Buldir (Fig. 3), even though warm water is normally associated with poor feeding conditions for seabirds (e.g. Hatch 1987, Gjerdrum et al. 2003). Although a correlation between warmer water and productivity at first seems counterintuitive, research on krill (Euphausiids) has shown cases where abundance was high in warm sea conditions (e.g. Tanasichuk 1998), suggesting that whiskered auklet prey abundance might be affected more by shifts in ocean currents than by sea temperature per se (Siegel 2000), and that at Buldir some combination of factors led to higher prey abundance in warm

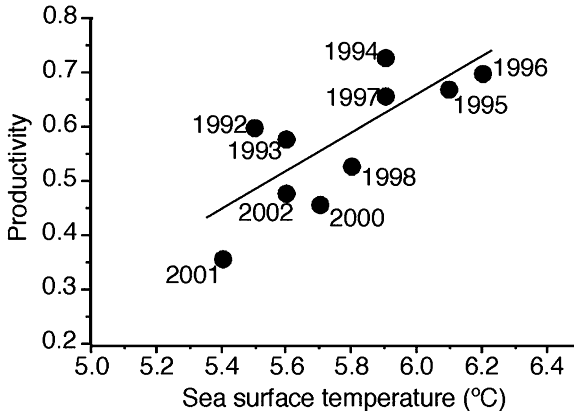

Fig. 3. Correlation between whiskered auklet productivity (number of chicks fledged per egg laid, Hunter et al. 2002) and mean sea surface temperature (SST) for the preceding August-April within a 5° latitude and longitude block surrounding Buldir Island, Alaska, during 1992–2003. $\text{Productivity} = 0.351 \times \text{SST} - 1.45$, $r^2 = 0.584$, $P = 0.007$ (productivity not measured in 1999).

water years. Although the proportion of subadults present varied highly among years, this was not correlated with productivity in the preceding year, suggesting that recruitment to the breeding colony did not depend on years with high breeding success, but perhaps with some factor determining yearling overwinter survival.

Taken together, our data provide quantification of population parameters of a small, poorly-studied planktivorous auk species. The information we obtained on sex-ratios indicates the need for further examination of sex ratios of auk species and how these might relate to population processes. Our data on survival, productivity and climatic conditions suggest that climate might operate on even closely related auk species in very different ways. Both of these results underline the need for further long term detailed investigations of seabird demography.

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