

BREEDING BIOLOGY OF THE WHISKERED AUKLET (*AETHIA PYGMAEA*) AT BULDIR ISLAND, ALASKA

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ABSTRACT.—We quantified aspects of the breeding biology of Whiskered Auklets (*Aethia pygmaea*) at Buldir Island, western Aleutian Islands, Alaska, from 1993 to 1998 to provide a better understanding of this poorly known species' ecological relationship to other auklets (*Aethia* spp.). Whiskered Auklets nest in rock crevices in a range of habitats including talus slopes, cliffs, and beaches. No physical characteristic of nesting crevices predicted breeding success. Hatching dates varied among years; mean hatching dates averaged 20 June \pm 6.8 days (range 16–27 June). Chicks remained in the nest for 39 ± 2 days, with mean annual fledging from 27 to 29 July. Eggs were 44.1 ± 1.6 mm in length and 31.1 ± 1.61 mm in breadth, and varied significantly in size among years. Chicks weighed 17.4 ± 2.4 g (15.6% of adult mass) within two days of hatching and gained 3.8 g day^{-1} in mass and 3.2 mm day^{-1} in wing length during the linear growth period. Chicks fledged at 101.3 ± 11.3 g (90.5% adult mass) after a pre-fledging mass recession of 8.9% of peak mass, and a wing length of 102.2 ± 4.3 mm (93.5% adult wing length). Mass increase during the linear growth period and fledging mass varied among years, but wing growth and fledging wing length did not. Parents provisioned chicks after nightfall with copepods (*Neocalanus* spp.) and euphausiids (*Thysanoessa* spp.); the proportion of food types varied significantly among years. Eighty-nine percent of chicks that hatched survived to fledge; most of those that did not had died of starvation. Low-intensity monitoring underestimated breeding success but provided useful comparative information. Whiskered Auklets exhibited a suite of unique characteristics that make them an ecological outlier among *Aethia* auklets. Received 10 January 2001, accepted 17 July 2002.

RESUMEN.—Cuantificamos aspectos de la biología reproductiva de *Aethia pygmaea* en la Isla de Buldir, Islas Aleutianas Occidentales, Alaska, desde 1993 a 1998 con el fin de proporcionar un mejor entendimiento de la relación ecológica de esta especie pobremente conocida, con otras especies del género *Aethia*. *A. pygmaea* anida en grietas entre rocas en un rango de hábitats que incluye pendientes, acantilados y playas. Ninguna característica física de las grietas de nidificación predijo el éxito reproductivo. Las fechas de eclosión variaron entre años; la fecha media de eclosión fue el 20 junio \pm 6.8 días (con un rango entre el 16–27 de junio). Los polluelos permanecieron en el nido durante 39 ± 2 días, con un periodo promedio anual de emplumamiento entre el 27 al 29 de julio. Los huevos midieron 44.1 ± 1.6 mm de longitud y 31.1 ± 1.61 mm de ancho, y el tamaño varió significativamente entre los años. Los polluelos pesaron 17.4 ± 2.4 g (15.6% del peso de los adultos) dentro de los dos primeros días después de salir del cascarón y ganaron 3.8 g día^{-1} en el peso y 3.2 mm día^{-1} en la longitud del ala durante el periodo de crecimiento lineal. Los polluelos entraron a la etapa de emplumamiento cuando alcanzaron un peso de 101.3 ± 11.3 g (90.5% del peso de los adultos) luego de un retroceso pre-emplumamiento de un 8.9% del peso máximo, y una longitud del ala de 102.2 ± 4.3 mm (93.5% longitud del ala adulta). El aumento de peso durante el periodo de crecimiento lineal y el peso durante el periodo de volatón varió entre años, pero el crecimiento del ala y la longitud del ala de volatones no variaron. Los padres aprovisionaron a los polluelos después del anochecer con copépodos (*Neocalanus* spp.) y euphásidos (*Thysanoessa* spp.); la proporción de tipos de alimento varió significativamente entre

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años. Ochenta y nueve por ciento de los polluelos que eclosionaron sobrevivieron a la etapa de volantón; la mayoría de aquéllos que no lo hicieron murieron de inanición. Monitoreos de baja intensidad subestimaron el éxito reproductivo pero proveyeron de información útil para fines comparativos. *A. pygmaea* exhibió una colección de características únicas que la hacen una excepción ecológica entre las demás especies del género *Aethia*.

WHISKERED AUKLETS (*Aethia pygmaea*) are an enigmatic and intriguing member of the Alcidae, a distinctive family of seabirds comprising 23 extant species that exhibit a wide variety of behavioral, reproductive, and life-history strategies (Nettleship and Birkhead 1985, Ydenberg 1989, Nettleship 1996, Gaston and Jones 1998). The Whiskered Auklet is a small, socially monogamous seabird that is active at breeding colonies only at night. It is arguably the most exotically ornamented of all seabird species, having a long black forehead crest, three white facial plumes, and a red bill. Nevertheless, this species' biology remains poorly known relative to most other auk species.

Whiskered Auklets are of conservation concern because of their limited range and because of introductions of mammalian predators such as Arctic foxes (*Alopex lagopus*) and Norway rats (*Rattus norvegicus*) to many of their breeding islands (Bailey 1993). In addition, like other alcids that nest and forage in dense groups, Whiskered Auklets may be vulnerable to oil spills, entanglement in fishing nets, fatal attraction to ships' lights, and physical and anthropogenic factors that disrupt their prey base (Springer et al. 1987, Springer 1991, Burger and Gochfeld 1994, Duffy and Schneider 1994, Nisbet 1994). Once understood, the potential effects of those threats to Whiskered Auklets may be mitigated through habitat protection and other appropriate management actions. However, such actions must be based on sound knowledge of the species' breeding biology. As a result of the remote location of their breeding areas (Byrd and Williams 1993), previous studies of Whiskered Auklets have been largely descriptive and have been based on small sample sizes (Byrd and Gibson 1980, Knudtson and Byrd 1982, Day and Byrd 1989, Golovkin 1990, Hipfner and Byrd 1993, Byrd and Williams 1993, Zubakin and Konyukhov 1999).

We studied the breeding success of Whiskered Auklets at Buldir Island from 1988 to 1998 and investigated other aspects of their breeding biology from 1993 to 1998. Our objectives were to (1) define this species' breeding

habitat and characteristics of nesting crevices, (2) assess variation in breeding phenology among years, (3) quantify egg size and chick growth and variation in those attributes among years, (4) describe the prey types and quantity of food fed to chicks, (5) quantify variation in reproductive performance among years and identify the primary sources of chick mortality, and (6) assess the accuracy of a low-intensity method of monitoring breeding success.

STUDY AREA AND METHODS

We conducted our study primarily at the Main Talus auklet colony on Buldir Island, western Aleutian Islands, Alaska (52°21'N, 175°56'E). Buldir Island is ~110 km from its nearest neighboring island and is part of the Alaska Maritime National Wildlife Refuge (Fig. 1). The island supports 21 breeding seabird species, 12 of which are alcids (Byrd and Day 1986). Main Talus is a large north-facing volcanic boulder slide consisting of a central portion composed of large bare boulders surrounded by areas of broken rock with a thin covering of soil supporting short grass (*Poa arctica*) and patches of thicker soil supporting beach rye (*Elymus arenarius*) and cow parsnip (*Heracleum lanatum*; Byrd 1984). Byrd et al. (1983) estimated the size of the Whiskered Auklet population at the Main Talus colony in 1976 to be ~1,000 birds, but their daytime count did not include the large nocturnal portion of their breeding population.

Two additional sites were used for monitoring reproductive performance: Northwest Ridge, a north-facing earthen slope dotted with rocky outcrops, and

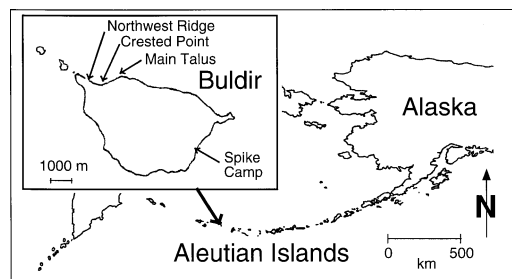


FIG. 1. Location of Buldir Island, Alaska, and study areas. Most islands in the Aleutian Chain, Bering Sea and near the Alaska Peninsula are part of the Alaska Maritime National Wildlife Refuge.

near Spike Camp, an easterly facing slope where birds nested in beach boulders and low cliffs (Fig. 1). Samples of food being delivered to chicks by adult Whiskered Auklets were collected at Crested Point, a dense colony situated in a section of steep cliff rising to ~50 m from a rock and cobble beach (Fig. 1).

We located Whiskered Auklet crevices among and beneath rocks using a small flashlight; crevices typically comprised a nesting chamber with one or more passages leading to the surface. Whiskered Auklets have a "mew" contact call (Byrd and Williams 1993), and many crevices were found by locating adults that responded to our imitations of that call. Crevice entrances were marked with a unique identification code. In some studies, human disturbance has reduced breeding success in Least (*A. pusilla*) and Crested (*A. cristatella*) auklets (Piatt et al. 1990, but see Fraser et al. 1999), so we minimized our visits to the colony, moved quietly around the talus, and avoided approaching study crevices except at the time of checking or catching birds.

Nesting habitat and crevice characteristics.—We investigated whether characteristics of crevices predicted breeding success in 1995 and 1996. Height of nesting chamber and minimum height and width of the entrance passageway was measured to establish whether likely predators or competitors of Whiskered Auklets could enter. We also recorded number of entrances, shape of the nest chamber (round or elongate), substrate type (earth or stone), whether the crevice would accommodate two or more adults, whether the entrance was surrounded by vegetation as a measure of how hidden it was, and whether the crevice consisted partly of rock. Finally, we assessed likelihood of flooding by recording whether crevices were wet or dry after periods of rain and we assigned each crevice to a relative position (high or low) on the talus.

Breeding phenology.—To compare timing of breeding, both among years and to closely related species, we recorded date of hatching from 1995 to 1998 and date of fledging from 1996 to 1998 at a sample of crevices. From 1 June onward, each crevice was checked every three days and its status recorded. Incubating Whiskered Auklets rarely moved from their egg, but were readily displaced from even the smallest chick. Hence, adults were recorded as incubating and were left undisturbed if no movement or presence of broken eggshell revealed a chick. If a chick was present, its date of hatching was estimated on the basis of its appearance: a wet chick was assumed to have hatched that day, a dry but unsteady chick was recorded as having hatched on the previous day, and an alert chick was assumed to have hatched two days previously. When chicks reached 34 days of age, crevices were checked daily to obtain accurate fledging dates. Chicks were assumed to have fledged if they were ≥ 32 days old upon disappearance (i.e. the

breeding attempt was considered to have failed if the chick disappeared at < 32 days old).

Egg size.—We compared egg size among years by measuring eggs from two sources. In 1997 and 1998, eggs were taken from beneath incubating adults, measured, and replaced under the adults. In 1995–1998, any egg found abandoned in a crevice was measured. Length and breadth of each egg was measured to the nearest 0.1 mm with Vernier calipers and the volume index was calculated from the equation $0.512 \times (\text{length} \times 0.1) (\text{breadth} \times 0.1)^2$ (Birkhead and Nettleship 1984).

Chick growth.—Chick growth was quantified in 1996–1998 by measuring samples of chicks every three days from the day they were first found and calculating means of growth rates of individuals per year. Chicks were caught either by hand or with a long wire hook placed above the tarsus. Chick mass was measured to the nearest 1 g with a spring scale, and straight-posterior tarsus and flattened wing length to the nearest 0.1 mm with Vernier calipers. In 1997 and 1998, chicks were weighed and measured every day from 34 days onward to obtain mass and tarsus and wing length at fledging. The majority of chicks were weighed and measured between 1600 and 2000 (AKST) each day to standardize time from feeding and all measurements of chicks and adults (see below) were made by F.M.H.

To compare growth rates among individual chicks and among years, the slopes of simple linear models were used for mass and wing length during the period of linear growth. The period of linear growth was estimated using composite data for each year of the study. Mass and wing length were plotted against age and linear growth was assumed when the resulting regression residuals were randomly distributed around zero. The most conservative estimate for linear-growth period was used; those were from 2 to 22 days for mass and from 7 to 26 days for wing length. Our sample comprised chicks with at least three measurements taken during the linear growth period, and only chicks with known hatch dates were used in this analysis.

Adult measurements.—Mass, tarsus, and wing length of chicks at fledging was compared with the same characteristics in adults. Parents of chicks in our chick-growth sample were taken from their nesting crevice while brooding their young chick during the day. Birds were caught by hand or with a long wire hook around the leg. The first parent was caught when the chick was at least one day old and the second parent was caught the following day. Adults were weighed to the nearest 1 g and the left straight-posterior tarsus was measured to the nearest 0.1 mm. The flattened wings of 10 adults caught in mist nets while bringing food to their chicks was also measured (see below for details). Flattened left wing was measured to the nearest 0.1 mm and

wing length was estimated from the mean of two measurements.

Chick diet.—To examine variation in food type and amounts of food brought to chicks through the season and in different years, food samples were collected during three periods: early, middle, and late chick-rearing from 1993 to 1997. At Crested Point, adults were caught in mist nets placed at different locations each night to avoid catching individual birds more than once. Nets were positioned over large sheets of plastic. In most cases, the birds regurgitated food from their throat pouch as they flew into the net; any food remaining in the pouch was regurgitated after gentle stroking of the throat with the bird's head held down to avoid inhalation. The food samples from the plastic sheeting were collected and placed in whirl-packs, weighed to the nearest 0.1 g with a spring scale, and preserved in 70% ethanol containing 2% glycerin. Prey items were later identified to the lowest practical taxonomic group using reference collections.

Reproductive performance and chick mortality.—Reproductive performance and variation in fledging success (chicks fledged as a proportion of chicks hatched) was quantified among years, and whether fledging success was related to timing of breeding or crevice characteristics was investigated by recording presence or absence of chicks in our growth-rate crevices at three-day intervals. If a chick was apparently absent on one visit the crevice was checked again three days later. Chicks were recorded as disappeared if they were absent on two consecutive visits to the crevice, if there were no signs of activity (fresh feces, feather sheath debris), and if there was no response to our imitated contact calls. Any chick in our chick-growth sample that was found dead was weighed, measured, and examined for signs of injury. Chicks were assumed to have fledged if they reached 32 days of age (see above). This method of measuring reproductive performance was termed the "high-intensity" method.

To assess variation in reproductive performance over a larger number of years and to assess the accuracy of a low-intensity monitoring method, the presence or absence of eggs and chicks in a second sample of crevices was recorded at four to nine day intervals throughout the breeding season from 1990 to 1998. That work was done primarily by U.S. Fish and Wildlife Service personnel, some of whom had little previous experience with seabird work. For that part of the study crevices at Main Talus, Northwest Ridge, and Spike Camp were used and chicks were recorded as being present only if they were seen. Hatching success (eggs hatched as a proportion of eggs laid) was measured only by the low-intensity method and may be overestimated because we arrived at the colony after the onset of laying, therefore missing early season egg loss. To estimate dates of hatching and fledging the mid-point between crevice

checks was used or, if there was an even number of days between checks, the even Julian date was used.

RESULTS

Nesting habitat and crevice characteristics.—Whiskered Auklets nested in five types of habitat on Buldir: unvegetated talus slopes, overgrown talus with rock outcrops, grassy slopes with rock outcrops, cliffs, and cobble-boulder beaches. A detailed analysis of Main Talus, which comprises a mixture of both overgrown and unvegetated talus, revealed crevices that consisted of one or more entry passages of variable length leading to a nesting chamber. Most crevices had one entrance (69.1%, $n = 55$), but crevices with up to four entrances were found (2 entrances 23.6%; 3 entrances 5.5%; 4 entrances 1.8%; $n = 55$). The main entrance had a median height of 61 mm (range 32–179, $n = 52$) and a median width of 64.5 mm (range 39–406, $n = 38$), far too small to allow the passage of a Glaucous-winged Gull (*Larus glaucescens*), the main predator of auklets on Main Talus. Most Whiskered Auklet nesting chambers had an earth floor (92.6%, $n = 54$), although four (7.4%, $n = 54$) crevices on the lower margins of the talus adjacent to the shore had nesting chambers with floors composed of small pebbles. Chambers were either round (75.9%, $n = 54$) or elongate (24.1%, $n = 54$) and had a median ceiling height of 108 mm (range 60–237, $n = 54$; Hunter and Jones 1999). Most crevices (94.4%, $n = 54$) were adjacent to, surrounded by, or (most frequently) underneath rocks, often in the space between the contact points of one large rock resting on others. The remaining three crevices (5.6%, $n = 54$) were not associated with rocks and could be described more accurately as burrows. Indeed they originally may have been made by either Fork-tailed (*Oceanodroma furcata*) or Leach's (*O. leucorhoa*) storm-petrels. On two occasions we found Fork-tailed Storm-petrels in abandoned Whiskered Auklet crevices. Whiskered Auklets showed no preference for vegetative cover in the vicinity of their crevices (long grass 17.0%; short grass 37.7%; no grass 45.3%; $n = 53$). Comparing crevices from which one or more chicks had failed to fledge with crevices that were only ever successful, no character was found that was related to crevice success (Table 1). Many unoccupied holes among the rocks of

TABLE 1. Comparison of characteristics of nesting crevices of Whiskered Auklets based on nesting success. Fisher's exact test was used to test for differences between groups.

| Characteristic | Groups | Fisher's exact probability (P) | n |
|---------------------------------------|------------------------------------|--------------------------------|----|
| Number of entrances | 1/>1 | 0.3 | 48 |
| Size of main entrance | 1 bird width/>1 bird width | 0.2 | 35 |
| Chamber shape | Round/elongate | 1.0 | 48 |
| Chamber size | <2 bird width/ \geq 2 bird width | 0.2 | 35 |
| Substrate type | Earth/stones | 1.0 | 48 |
| Substrate dampness | Wet/dry | 0.6 | 20 |
| Presence of rock around crevice | Yes/no | 1.0 | 48 |
| Presence of long grass around crevice | Yes/no | 0.3 | 47 |
| Position on talus | High/low | 1.0 | 55 |

the talus had characteristics consistent with occupied crevices and some crevices were occupied by breeding Whiskered Auklets in some years but empty in others.

Breeding phenology.—For all eggs and years combined, the mean hatching date was 20 June (± 6.8 days, range 8 June–15 July, $n = 183$), the mean chick-rearing period was 38.8 (± 2.04 days, range 35–46, $n = 98$) and the mean fledging date was 28 July (± 5.41 days, range 20 July–12 August, $n = 104$). The number of days over which hatching occurred did not differ from the number of days over which fledging occurred, so hatching and fledging were similarly asynchronous (Variance ratio test: $F = 0.72$, $df = 104$ and 125 , $P = 0.1$). Hatching dates did not differ between chicks that fledged successfully and those that did not ($t = 0.84$, $n = 103$, 12 , $P = 0.4$).

Breeding phenology varied significantly among years, with an 11 day difference in mean hatching dates among seasons (ANOVA, $F = 17.57$, $df = 4$ and 182 , $P = 0.0001$, Table 2). The Scheffé F -test showed that at the 95% confidence level hatching was significantly earlier in 1994 than in 1995 and 1997, and was significantly later in 1995 than in all other years. Nei-

ther the length of the chick-rearing period nor the date of fledging differed among years (chick rearing, $F = 2.07$, $df = 2$ and 97 , $P = 0.1$; fledging date: $F = 2.15$, $df = 2$ and 104 , $P = 0.1$). A lack of any difference in hatching dates among the years 1996 to 1998 ($F = 1.16$, $df = 4$ and 125 , $P = 0.3$), along with the finding that 1994 was an "early" year and 1995 was a "late" year, suggests that the lack of variation among years in the length of the chick-rearing period and the date of fledging may result from low power caused by the limited number of years available for analysis ($n = 3$).

Egg size.—Whiskered Auklets lay a single white oval egg. For all eggs and years combined, Whiskered Auklet eggs averaged 44.1 ± 1.56 mm in length (range 40.5–46.8, $n = 65$), 31.1 ± 1.14 mm width (range 28.7–33.3, $n = 65$), and had a mean volume index of 21.9 ± 2.10 mm³ (range 17.8–25.9, $n = 65$). In 1995, 1997, and 1998, egg volume differed significantly among years (ANOVA: $F = 3.54$, $df = 2$ and 63 , $P = 0.04$, Table 3). The Scheffé F -test showed that at the 95% level of confidence 1995 eggs were significantly larger than 1997 eggs, and 1998 eggs were intermediate and not different from those of either of the other two

TABLE 2. Breeding phenology of Whiskered Auklets at Buldir Island, Alaska, 1994–1998.

| Year | Hatching date | | | n | Chick-rearing period (days) | | | | n | Fledging date | | | | n |
|------|---------------|-----|-----------------|----|-----------------------------|-----|-------|----|---------|---------------|-------------------|-------|---|---|
| | Mean | SD | Range | | Mean | SD | Range | n | | Mean | SD | Range | n | |
| 1994 | 16 June | 6.4 | 8 June–2 July | 28 | | | | | | | | | | |
| 1995 | 27 June | 6.5 | 20 June–15 July | 29 | | | | | | | | | | |
| 1996 | 21 June | 8.4 | 10 June–13 July | 32 | 39.5 | 2.3 | 36–46 | 28 | 29 July | 7.6 | 20 July–22 August | 33 | | |
| 1997 | 20 June | 4.4 | 14 June–5 July | 46 | 38.6 | 2.0 | 35–43 | 34 | 29 July | 4.3 | 20 July–12 August | 35 | | |
| 1998 | 18 June | 4.2 | 10 June–29 June | 48 | 38.5 | 1.8 | 35–43 | 36 | 27 July | 3.5 | 20 July–5 August | 36 | | |

TABLE 3. Dimensions of Whiskered Auklet eggs on Buldir Island, Alaska, 1995–1998.

| Year | n | Length (mm) | | | Width (mm) | | | Volume index (mm ³) | | |
|------|----|-------------|-----|-----------|------------|-----|-----------|---------------------------------|-----|-----------|
| | | Mean | SD | Range | Mean | SD | Range | Mean | SD | Range |
| 1995 | 7 | 45.1 | 0.8 | 44.0–46.4 | 31.9 | 0.6 | 31.1–32.8 | 23.5 | 1.0 | 22.2–25.1 |
| 1996 | 1 | 43.7 | — | — | 29.3 | — | — | 19.2 | — | — |
| 1997 | 27 | 43.9 | 1.7 | 40.5–46.8 | 30.8 | 1.2 | 28.8–33.2 | 21.3 | 2.2 | 17.9–25.7 |
| 1998 | 30 | 44.0 | 1.5 | 40.6–46.8 | 31.3 | 1.1 | 28.7–33.3 | 22.1 | 2.0 | 17.8–25.9 |

years. Egg length did not differ among years but egg width did (length: $F = 1.77$, $df = 2$ and 63 , $P = 0.2$; width: $F = 3.75$, $df = 2$ and 63 , $P = 0.03$, Table 3). Again, the Scheffé F -test showed that at the 95% confidence level 1995

eggs were significantly wider than 1997 eggs, and 1998 eggs were not different from those of either of the other two years.

Chick growth and adult measurements.—Whiskered Auklet chicks on Buldir weighed 17.4 ± 2.4 g ($n = 58$; 15.6% of adult mass) within two days of hatching and gained weight at 3.8 ± 0.9 g day⁻¹ (range -0.74 – $+5.31$, $n = 119$), and wing length at 3.2 ± 0.3 mm day⁻¹ (range 2.17–3.82, $n = 85$) during the period of linear growth (Fig. 2A). Chicks fledged at 101.3 ± 11.3 g (range 69–122, $n = 69$, Fig. 2A), with a wing length of 102.2 ± 4.3 mm (range 90.0–110.7, $n = 65$, Fig. 2B) and tarsus length of 21.8 ± 0.6 mm (range 20.0–23.5, $n = 106$, Fig. 2C). Chick mass declined prior to fledging by a mean of 8.9% (range 0–21.9, $n = 75$), and the chicks finally fledged at 90.5% of adult mass, 93.5% of adult wing length, and 100% of adult tarsus length. Breeding adult Whiskered Auklets captured in crevices had a mass of 111.9 ± 7.3 g (range 92–132, $n = 230$), wing length 109.3 ± 2.4 mm (range 104.2–113.2, $n = 10$), and tarsus length 21.8 ± 0.7 mm (range 20.0–24.0, $n = 229$).

Two chicks, one in 1996 and one in 1997, showed signs of a growth deformity in the joint between the tibia and tarsus. The joint became swollen, and the tarsus twisted upwards and backwards, until the chick was walking directly on its upper tarsal joint. One leg was affected in one chick and both legs in the other. Each chick survived to fledging, although their fledging masses and the wing length of one chick were low (1996 chick: mass 4 days before fledging = 57 g; 1997 chick: fledging mass = 76 g, fledging wing length = 90.0 mm).

We found no difference among years in chick mass at hatching (ANOVA: $F = 0.05$, $df = 2$ and 57 , $P = 1.0$, Table 4) or wing length at hatching ($t = -0.61$, $n = 12$, 26 , $P = 0.5$, Table 4). There was, however, significant variation among years in the rate of linear growth for mass ($F =$

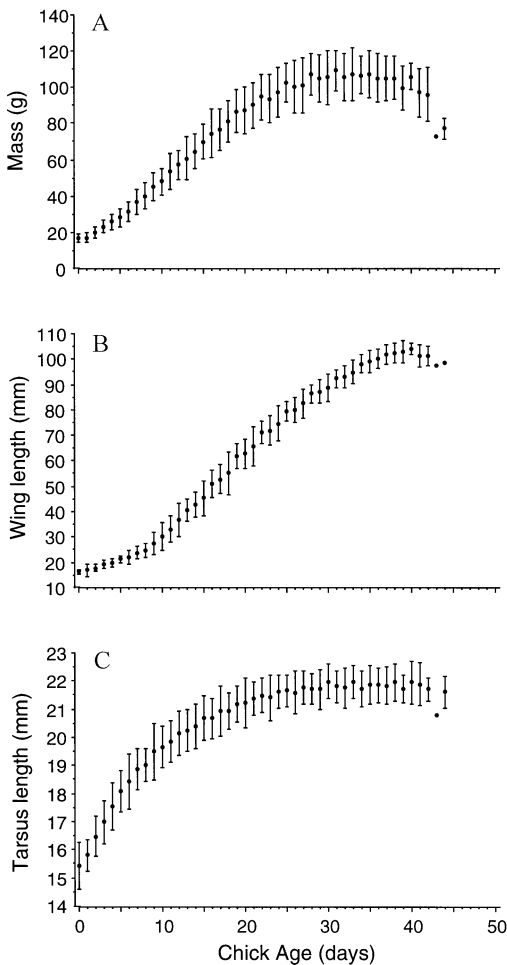


FIG. 2. Growth of Whiskered Auklet chicks at Buldir Island, Alaska: changes in (a) body mass, (b) wing length, and (c) tarsus length. Values are mean \pm 1 SD.

TABLE 4. Chick measurements and growth of Whiskered Auklets on Buldir Island, Alaska, 1996–1998.

| Parameter | 1996 | | | 1997 | | | 1998 | | |
|-------------------------------------|-------|------|----|-------|------|----|-------|-----|----|
| | Mean | SD | n | Mean | SD | n | Mean | SD | n |
| Hatching mass (g) | 17.6 | 2.6 | 19 | 17.5 | 2.2 | 12 | 17.3 | 2.5 | 27 |
| Linear mass (g day ⁻¹) | 3.3 | 0.8 | 29 | 4.0 | 0.7 | 43 | 3.9 | 0.9 | 47 |
| Peak mass (g) | 101.3 | 12.0 | 33 | 111.6 | 13.0 | 36 | 115.8 | 9.3 | 36 |
| Fledging mass (g) | 90.7 | 9.5 | 10 | 101.6 | 13.6 | 31 | 104.0 | 7.4 | 35 |
| Wing length at hatching (mm) | | | 0 | 17.0 | 1.0 | 12 | 17.3 | 1.1 | 27 |
| Linear wing (mm day ⁻¹) | | | 0 | 3.1 | 0.1 | 41 | 3.2 | 0.2 | 44 |
| Wing length at fledging (mm) | | | 0 | 101.2 | 4.7 | 30 | 103.0 | 3.8 | 35 |
| Tarsus at fledging (mm) | 22.0 | 0.4 | 32 | 21.9 | 0.1 | 38 | 21.7 | 0.6 | 36 |

7.80, $df = 2$ and 118, $P = 0.001$, Table 4), but not for wing length ($t = -1.66$, $n = 41, 44$, $P = 0.1$, Table 4). Mass loss prior to fledging did not vary among years ($F = 2.86$, $df = 2$ and 74, $P = 0.1$). Fledging mass differed significantly among years ($F = 6.19$, $df = 2$ and 75, $P = 0.003$, Table 4), but fledging wing length and tarsus length did not (wing: $t = -1.84$, $n = 30, 35$, $P = 0.1$; tarsus: $F = 2.69$, $df = 2$ and 105, $P = 0.1$; Table 4). There was no seasonal decline in fledging mass in any year (1996: $r = 0.25$, $n = 10$, $P = 0.5$; 1997: $r = 0.20$, $n = 31$, $P = 0.3$; 1998: $r = 0.08$, $n = 35$, $P = 0.6$).

In 1996 and 1998, hatching date varied inversely with fledging age (1996: $r = 0.55$, $n = 28$, $P = 0.003$; 1998: $r = 0.38$, $n = 36$, $P = 0.02$).

Chick diet.—At least 14 species of prey were brought to young in the throat pouches of Whiskered Auklet adults during the chick-rearing period. In all years, the majority (60.9–99.0%) of food comprised three prey types: the copepods *Neocalanus plumchrus/flemingeri* and *N. cristatus*, and euphausiids *Thysanoessa* spp. (Table 5). The relative proportion of each of those prey types varied in different years. For example, in 1994 there was relatively less *N. plumchrus/flemingeri*, but more *N. cristatus* and *Thysanoessa* spp., whereas, in 1997, that pattern was reversed with more *N. plumchrus/flemingeri*, less *N. cristatus*, and almost no *Thysanoessa* spp. There was no consistent pattern in the relative type or abundance of prey at different stages of the chick-rearing period (Table 6). The large variation in prey type and abundance among years appeared to supersede any seasonal effects.

Reproductive performance and chick mortality.—Of all chicks in our high-intensity sample that were handled at least once during the chick-rearing period, 88.7% (± 2.0 , $n = 3$ years) survived to fledging. Fledging success did not differ significantly among years ($\chi^2 = 0.3$, $df = 2$, $P = 0.9$, Table 7).

Across years, 11% (14/125) of Whiskered Auklet chicks that were known to have hatched failed to fledge. Of the 14 chicks that failed to fledge, nine (64%) died in their crevices and five (36%) disappeared prior to the age of 32 days, the earliest time at which they could have fledged. Most (7 of 9) of the dead chicks appeared to have died from starvation. They were emaciated and had significantly lower growth rates during the linear-growth period than did

TABLE 5. Relative biomass of prey in food loads delivered to Whiskered Auklet chicks at Buldir Island, Alaska, 1993–1997. Values represent the mass (wet weight) and percent of total mass of each prey species in the combined food samples for each year.

| Prey | 1993 (n = 24) | | 1994 (n = 16) | | 1995 (n = 48) | | 1996 (n = 71) | | 1997 (n = 36) | |
|--------------------------------|------------------|------|------------------|------|------------------|------|------------------|------|------------------|------|
| | Mass (g) | % | Mass (g) | % | Mass (g) | % | Mass (g) | % | Mass (g) | % |
| Gastropoda | | | | | | | | | | |
| <i>Limacina helicina</i> | 0.8 | 1.5 | 0 | 0 | 2.7 | 0.7 | 1.4 | 0.3 | 6.3 | 2.1 |
| Unidentified gastropod | 0 | 0 | 0.2 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Copepoda | | | | | | | | | | |
| <i>Neocalanus cristatus</i> | 9.9 | 18.6 | 34.2 | 36.4 | 101.5 | 26.2 | 102.0 | 21.2 | 33.9 | 11.3 |
| <i>N. plumchrus/flemingeri</i> | 11.6 | 21.8 | 8.4 | 8.9 | 187.2 | 48.3 | 260.9 | 54.2 | 242.9 | 81.0 |
| <i>Calanus pacifica</i> | 0 | 0 | 0 | 0 | 0.4 | 0.1 | 0 | 0 | 0 | 0 |
| Unidentified copepod | 7.4 | 13.8 | 0 | 0 | 3.5 | 0.9 | 0 | 0 | 0 | 0 |
| Amphipoda | | | | | | | | | | |
| Hyperiidia | | | | | | | | | | |
| <i>Hyperoche medusarum</i> | 0 | 0 | 0 | 0 | 6.6 | 1.7 | 2.4 | 0.5 | 0 | 0 |
| <i>Parathemisto pacifica</i> | 2.1 | 3.9 | 0.5 | 0.5 | 0.4 | 0.1 | <0.1 | <0.1 | <0.1 | <0.1 |
| <i>Primno macropa</i> | 0.2 | 0.3 | 7.4 | 7.9 | 0 | 0 | | 0 | 3.9 | 1.3 |
| Gammaridea | | | | | | | | | | |
| Talitridae | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.1 | 0 | 0 |
| Euphausiacea | | | | | | | | | | |
| <i>Thysanoessa</i> spp. | 10.4 | 19.5 | 39.9 | 42.4 | 71.7 | 18.5 | 113.6 | 23.6 | 1.8 | 0.6 |
| Decapoda | | | | | | | | | | |
| Shrimp zoea | 0 | 0 | 3.4 | 3.6 | 13.9 | 3.6 | 0.5 | 0.1 | 4.5 | 1.5 |
| Crab zoea | 0 | 0 | 0 | 0 | 0 | 0 | <0.1 | <0.1 | 1.8 | 0.6 |
| Crab megalopa | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0.1 | 4.8 | 1.6 |
| Fish | | | | | | | | | | |
| <i>Hexagrammos</i> spp. | 11.0 | 20.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 53.4 | | 94.0 | | 387.9 | | 481.3 | | 299.9 | |

chicks that fledged successfully (Mann-Whitney U -test: $z = -2.73$, $n = 3$, 103 , $P = 0.006$; successful chicks: 3.9 ± 0.1 g day⁻¹ ($n = 103$); chicks that died: 0.9 ± 1.2 g day⁻¹ ($n = 3$). The remaining two chicks that we found dead had multiple peck marks around the head and body, some of which had broken the skin, and one chick appeared to have been trampled. Those injuries were consistent with the chicks having been attacked by an adult Crested Auklet (*Aethia cristatella*; Fraser et al. 1999). It is possible that those chicks died of starvation and were pecked by a Crested Auklet after death; however, one of the chicks had gained mass at 3.6 g day⁻¹ during the linear growth period which was near to the average for successful chicks and higher than any of the chicks that were known to have starved. We did not know the exact hatching date of the other chick and

were unable to calculate its growth rate. Further, two otherwise healthy chicks had peck marks consistent with Crested Auklet attacks. In both cases, the injuries healed and the chicks subsequently fledged.

The five chicks that disappeared from their crevices did so between the ages of 13 and 25 days. Growth rates during the linear growth period did not differ significantly between chicks that fledged successfully and those that disappeared (Mann-Whitney U -test: $z = -0.62$, $n = 4$, 103 , $P = 0.5$; successful chicks: 3.9 ± 0.1 g day⁻¹, $n = 103$; chicks that disappeared: 3.5 ± 0.5 g day⁻¹, $n = 4$). The number of chicks that disappeared may be an underestimate because any chick apparently disappearing from a crevice that had a partially or fully hidden nesting chamber was not included in the sample, in case the chick was present but not detectable.

TABLE 6. Biomass of prey in food loads delivered to Whiskered Auklet chicks at different times of the chick-rearing period at Buldir Island, Alaska, 1995–1997. Values represent the mass and percent mass of each prey species in the food samples for all years combined.

| Prey | Early chick-rearing (<i>n</i> = 40) | | Mid chick-rearing (<i>n</i> = 71) | | Late chick-rearing (<i>n</i> = 44) | |
|--------------------------------|---|------|---------------------------------------|------|--|------|
| | Mass (g) | % | Mass (g) | % | Mass (g) | % |
| Gastropoda | | | | | | |
| <i>Limacina helicina</i> | 3.9 | 1.3 | 4.2 | 0.8 | 2.1 | 0.6 |
| Copepoda | | | | | | |
| <i>Neocalanus cristatus</i> | 101.6 | 34.2 | 55.9 | 10.7 | 79.3 | 22.8 |
| <i>N. plumchrus/flemingeri</i> | 147.1 | 49.5 | 327.1 | 62.6 | 216.2 | 62.0 |
| <i>Calanus pacifica</i> | 0 | 0 | 0.5 | 0.1 | 0 | 0 |
| Unidentified copepod | 0 | 0 | 3.1 | 0.6 | 0 | 0 |
| Amphipoda | | | | | | |
| Hyperiidea | | | | | | |
| <i>Hyperoche medusarum</i> | 1.5 | 0.5 | 2.6 | 0.5 | 5.2 | 1.5 |
| <i>Parathemisto pacifica</i> | 0 | 0 | 0.5 | 0.1 | 0.3 | 0.1 |
| <i>Primno macropa</i> | 2.1 | 0.7 | 1.6 | 0.3 | 0.3 | 0.1 |
| Gammaridea | | | | | | |
| Talitridae | | | | | | |
| | 0 | 0 | <0.1 | <0.1 | 0 | 0 |
| Euphausiacea | | | | | | |
| <i>Thysanoessa</i> spp. | 31.5 | 10.6 | 118.1 | 22.6 | 37.4 | 10.7 |
| Decapoda | | | | | | |
| Shrimp zoea | 9.2 | 3.1 | 3.1 | 0.6 | 6.6 | 1.9 |
| Crab zoea | <0.1 | <0.1 | 1.0 | 0.2 | 0.7 | 0.2 |
| Crab megalopa | 0.3 | 0.1 | 4.7 | 0.9 | 0.3 | 0.1 |
| Total mass | 297.2 | | 522.4 | | 348.4 | |

In the low-intensity monitoring sample, 84.4% (*n* = 11 years) of eggs hatched over the period 1988 to 1998, and 72.7% (*n* = 9 years) of chicks fledged during the period 1990 to 1998 (Table 7). Neither hatching success nor fledging success differed significantly among years (hatching success: $\chi^2 = 17.4$, *df* = 10, *P* = 0.1; fledging success: $\chi^2 = 9.2$, *df* = 8, *P* = 0.3). For Main Talus in 1996–1998, for which we had data for both high-intensity and low-intensity monitoring methods, the low-intensity method gave a significantly lower estimate of fledging success (61.3%) than the high-intensity method (88.8%; $\chi^2 = 19.4$, *df* = 1, *P* = 0.0001). In addition, similar proportions of chicks died ($\chi^2 = 0.1$, *df* = 1, *P* = 0.8), but a higher proportion of chicks disappeared in the low-intensity sample ($\chi^2 = 28.6$, *df* = 1, *P* = 0.0001).

DISCUSSION

Whiskered Auklet ecology relative to other auk species.—Our study clarifies the breeding bio-

logical characteristics of the Whiskered Auklet, allowing at last a meaningful comparative discussion of their biology with four other sympatric auklet species (Least [*Aethia pusilla*], Crested, Parakeet [*Aethia psittacula*], and Cassin's [*Ptychoramphus aleuticus*] auklets) that are the product of a remarkable adaptive radiation of small planktivorous seabirds in the North Pacific (Jones 1999). Whiskered Auklets have a suite of related biological characteristics that likely evolved together in part in relation to competition with other auk species for nest sites. Unlike Least and Crested auklets, Whiskered Auklets generally breed at low densities over a range of habitat types. We believe that this dispersed breeding evolved in relation to competition with other alcids for nest sites (e.g. the inter-specific killing of nestlings by other auklet species observed in our study). Whiskered Auklet adults are subject to breeding site disturbance both by other auklet species and also Horned Puffins (*Fratercula corniculata*; Byrd and Williams 1993) when they choose to

TABLE 7. Reproductive performance of Whiskered Auklets at Buldir Island, Alaska, 1988–1998.

| Parameter ^b | All study plots | | | | | | | | | | | | | | | | | |
|-------------------------------|----------------------------|------|------|------|------|----------------|------|------|------|------|------|------|------|------|------|------|------|------|
| | Low-intensity ^a | | | | | | | | | | | | | | | | | |
| | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 | |
| | Main Talus only | | | | | | | | | | | | | | | | | |
| | Low-intensity | | | | | | | | | | | | | | | | | |
| | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 | 1996 | 1997 | 1998 |
| Number eggs found | 7 | 16 | 9 | 46 | 55 | 54 | 57 | 67 | 57 | 90 | 78 | — | — | — | — | — | — | — |
| Eggs disappeared | 0 | 1 | 1 | 5 | 5 | 8 | 4 | 2 | 1 | 8 | 9 | — | — | — | — | — | — | — |
| Eggs abandoned | 0 | 2 | 0 | 4 | 3 | 4 ^c | 2 | 9 | 3 | 3 | 2 | — | — | — | — | — | — | — |
| Eggs broken | 0 | 2 | 0 | 4 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | — | — | — | — | — | — | — |
| Number eggs hatched | 7 | 11 | 8 | 33 | 47 | 41 | 51 | 56 | 53 | 78 | 66 | 24 | 20 | 18 | 38 | 43 | 44 | 44 |
| Chicks disappeared | — | — | 2 | 7 | 9 | 6 | 6 | 10 | 6 | 17 | 20 | 2 | 7 | 11 | 1 | 0 | 4 | 4 |
| Chicks died | — | — | 1 | 3 | 5 | 4 | 3 | 1 | 7 | 2 | 5 | 3 | 0 | 1 | 4 | 4 | 1 | 1 |
| Number chicks fledged | — | — | 5 | 23 | 33 | 31 | 42 | 45 | 40 | 59 | 41 | 19 | 13 | 6 | 33 | 39 | 39 | 39 |
| Hatching success ^d | 1.00 | 0.69 | 0.89 | 0.72 | 0.85 | 0.76 | 0.89 | 0.84 | 0.93 | 0.87 | 0.85 | — | — | — | — | — | — | — |
| Fledging success ^e | — | — | 0.63 | 0.70 | 0.70 | 0.76 | 0.82 | 0.80 | 0.75 | 0.76 | 0.62 | 0.79 | 0.65 | 0.33 | 0.87 | 0.91 | 0.89 | 0.89 |
| Productivity ^f | — | — | 0.56 | 0.50 | 0.60 | 0.58 | 0.73 | 0.67 | 0.70 | 0.66 | 0.53 | — | — | — | — | — | — | — |

^a Monitoring method.
^b Data are for nest site visit-intervals at hatching and fledging of ≤12 days (usually 4–8 days) for low-intensity method and 3 days for high-intensity method.
^c Adult found dead on egg; injuries consistent with Crested Auklet attack.
^d Proportion of eggs found that hatched.
^e Proportion of chicks hatched that survive to fledging age (32 days before disappearing or 29 days at the time of the last visit).
^f Hatching success × fledging success.

breed in dense mixed colonies of the other species. Low density breeding exposes small auks to predation by gulls, a threat that the diurnal Least and Crested auklets overcome by nesting in dense colonies. Whiskered Auklets appear to avoid this predation risk by their almost exclusively nocturnal transits between the sea and their breeding sites (Zubakin and Konyukhov 1999). Nocturnality having evolved (assuming Whiskered and other auklets had a diurnal common ancestor; Jones 1999), Whiskered Auklets were free to colonize many islands within their breeding range (Least and Crested auklets together are restricted to only eight of the Aleutian Islands due to their narrow habitat preferences; cf. Gaston and Jones 1998). However, the restriction of breeding site arrivals and departures to hours of darkness reduced parents' opportunities to provision chicks, causing relatively slow chick growth. Whiskered Auklets approach Least Auklets in body mass, but their chicks grow relatively very slowly and age at fledging is closer to the other nocturnal species, the Cassin's Auklet. Whiskered Auklets are also unusual for their foraging closer to their breeding sites in tide rips (Byrd and Williams 1993) and their flexible and possibly more opportunistic prey selection compared to Least and Crested auklets, and their unique terrestrial roosting behavior after the breeding season (Stejneger 1885, Konyukhov and Zubakin 1994, Zubakin and Konyukhov 1999), all traits that may also be linked to their nocturnal activity at colonies. Taken together with previously published information (Byrd and Williams 1993, Jones 1999, Zubakin and Konyukhov 1999), our study reveals the biology of a remarkable relationship among closely coexisting diverse planktivorous seabird species (see below).

Nesting habitat and crevice characteristics.—Whiskered Auklets breed in a range of different habitats that occur on many islands in the Aleutians and in the Okhotsk Sea, yet the literature reports confirmed Whiskered Auklet breeding at few locations (Flint and Golovkin 1990, Kondratiev 1991, Litvinenko and Shibaev 1991, U.S. Fish and Wildlife Service 1999). Most Aleutian islands rarely are visited during the breeding season, and casual exploration of a potential colony during the day would not reveal the presence of Whiskered Auklets because of their secretive crevice nesting habits

and nocturnal activity. Hence Whiskered Auklets probably breed in more locations than have been reported so far. No relationship was found between breeding success and any crevice characteristic, possibly because we did not measure the crucial characteristic or because our measure of productivity was not specific enough. Breeding failure frequently resulted from chick starvation, which was unlikely to be the result of any crevice characteristic. Chicks that either disappeared or were found with mortal injuries may have been more vulnerable because they were in crevices with entrances large enough to admit the bill of a Glaucous-winged Gull or a Crested Auklet (where present). Alternatively, chicks may have been vulnerable to predators when venturing outside very small crevices to exercise their wings and call to their approaching parents at nightfall. However the sample of chicks that disappeared or died of injuries was too small to investigate this question further.

Breeding phenology.—Hatching dates varied significantly among years, likely due to variation among years in environmental conditions (e.g. Jones et al. 2002) and, specifically, food availability early in the season when females were gathering resources to produce their eggs. Hatching dates also varied among individuals within years, suggesting that timing of breeding was dependant on female quality and that some females were ready to breed earlier than others in any year. Hatching dates in all years of our study were considerably earlier than those reported for Whiskered Auklets on Main Talus by Knudtson and Byrd (1982) for the 1976 breeding season and Hipfner and Byrd (1993) for the 1991 season. The 1976 study involved only six nests and the late hatching recorded may have therefore resulted from a sampling bias. However, 1991 appeared to have been a particularly late year being several days later than 1995, our latest year. Interestingly, 1991 chicks hatched later but fledged at a time similar to chicks in our study. Within our study, the three years for which fledging dates were available had the least variable hatching dates and so cannot be used to investigate this idea further. However our finding that in two of the three years later-hatching chicks fledged younger supported that pattern. These findings suggest that fledging date may be constrained. Timing of fledging may have evolved in re-

sponse to some fixed environmental factor such as time available to feed at sea before onset of winter. In contrast, the timing of hatching, which is probably directly related to the timing of laying, is likely to be determined by female readiness to breed which will depend on both early season food availability and female quality (Perrins 1970, Verhulst et al. 1995, Hipfner 1997).

Variation in egg size and chick growth among years.—In addition to hatching dates, egg size, growth rates, and fledging mass all varied among years. Egg size at Buldir was apparently 5–10% smaller than that reported from two populations in Russia (Sakhalin Oblast Island: range 46.0–48.5 mm \times 31.5–32.8 mm, no sample size reported, Gizenko 1955; Mednyi Island: range 45.2–48.0 mm \times 32.0–33.5 mm, no sample size reported, Kozlova 1957). It seems unlikely that variation in measuring techniques among observers could account for such a large difference in egg size (Barrett et al. 1989). It is possible that the difference resulted from interannual differences in egg size because the Russian eggs were measured in the 1950s, and we found variation in egg size among years on Buldir. However, again it seems unlikely that this could account for such a large difference in size. Adult Whiskered Auklets in the Aleutian Islands are smaller than those in Russia (Byrd and Williams 1993). Feinstein (1959) has suggested that two subspecies of Whiskered Auklet exist, one in the Aleutian Islands the other in the Kuril Islands, whereas more recent studies suggest that there is a simple east–west cline in body size within the species (Byrd and Williams 1993). This cline may explain the difference in egg size between the two regions as the trend in body size is in the same direction as the trend in egg size.

In our study, in 1996 both chick-mass increase during the linear growth period and fledging mass were lower than in other years. Although chick survival to fledging was no different in 1996, the fledging weight of chicks may affect their chances of surviving at sea, especially during the first few months after fledging while they learn to forage efficiently (Perrins et al. 1973, Jarvis 1974, Gaston 1997, but see Harris 1982), therefore chicks may be less likely to survive to breed in a season in which fledging mass is low. Interannual variation in chick growth rates and fledging mass suggests that

Whiskered Auklets respond to interannual variation in environmental conditions. Whiskered Auklets feed on zooplankton, which is affected by both natural and anthropogenically induced variation in the marine environment (National Research Council 1996, Jones et al. 2002). Hence, any reduction in plankton availability in traditional feeding sites is likely to have an adverse effect on chick growth and reproductive performance.

Chick diet.—Whiskered Auklets showed considerable interannual variation in the primary prey species brought to their young. In 1994, 45% of prey were copepods and 43% were euphausiids, whereas 92% of prey were copepods and <1% were euphausiids in 1997. The latter year was similar to 1976, in which 91% of prey were copepods and 0.3% were euphausiids (Day and Byrd 1989). This ability to switch from one prey species to another may account for the lack of annual variation in numbers of chicks surviving to fledging and suggests that Whiskered Auklets may be less susceptible to relative changes in zooplankton abundance than a species that is inflexible in its use of prey. Bédard (1969) found some variation in prey types among years in Least and Crested auklets feeding around St. Lawrence Island, Alaska, during the period 1964 to 1966. Although relative abundance of the different species of zooplankton may not affect breeding success in Whiskered Auklets, a change in absolute abundance or availability probably would have a considerable effect on breeding success.

Productivity and chick mortality.—In our high-intensity sample, 89% of chicks that hatched survived to fledging, with the majority of chick mortality resulting from starvation. Chicks may starve either from problems with food availability or the death or abandonment of one parent, leaving the other parent incapable of feeding the chick sufficient food for survival. We attributed most of the remaining chick mortality to predation by Glaucous-winged Gulls. Older chicks often came to the entrance of their crevices after dark and called, probably in anticipation of their parents arriving to feed them. Glaucous-winged Gulls were seen hopping around the Main Talus colony at dusk cocking their heads to one side apparently listening for calling chicks (F. M. Hunter pers. obs.).

Eighty-nine percent survival is a high level of fledging success for a seabird and probably reflects the absence of mammalian predators on Buldir. Naturally occurring tundra voles (*Microtus oeconomus*) and red-backed voles (*Clethrionomys rutilus*), and introduced Norway rats, Arctic foxes and red foxes (*Vulpes vulpes*) have all been recorded predated auklets on islands in the Bering Sea (Sealy 1982, Roby and Brink 1986, Bailey 1993). However, the lack of mammalian predators cannot fully explain the high fledging success of Whiskered Auklets on Buldir. All three of the *Aethia* auklets, which have similar ecologies and breeding habits, nest on Main Talus, yet Crested Auklets average only 77% fledging success and Least Auklets average 75% fledging success at this site (Knudtson and Byrd 1982, Fraser et al. 1999). We speculate that the nocturnal behavior of the Whiskered Auklet may reduce interference to parents delivering food to chicks, enhancing their chance of raising chicks to fledging. Diurnally hunting Glaucous-winged Gulls and Peregrine Falcons (*Falco peregrinus*) are the primary predators of auklets on Main Talus (Knudtson and Byrd 1982, F. M. Hunter pers. obs.). Of all *Aethia* auklet remains found in Glaucous-winged Gull pellets, only 3% ($n = 33$) were from Whiskered Auklets; similarly, of all *Aethia* auklet remains found in Peregrine aeries in 1976 only 3% ($n = 61$) were from Whiskered Auklets (Knudtson and Byrd 1982). Even when a peregrine nest was located directly above the dense Whiskered Auklet colony at Crested Point in 1991 and 1992, only 11% ($n = 54$) and 8% ($n = 53$) of *Aethia* remains were from Whiskered Auklets (J. C. Williams unpubl. data).

Comparison of high- and low-intensity monitoring methods.—Low-intensity productivity monitoring carried out partly by staff with little experience of seabird work gave significantly lower estimates of fledging success than did high-intensity monitoring carried out solely by experienced workers. More chicks were reported disappeared prior to fledging in the low-intensity sample, likely because of the longer intervals between crevice visits, due to poor selection of crevices for monitoring or from failure to detect the presence of a chick through indirect clues such as chick calls and fresh feces. We believe that there are limitations to the low-intensity method of monitoring breeding success, but that if the aim is to identify large-

scale changes in breeding success in comparison with studies using the same method, it is an acceptable procedure. Furthermore, low-intensity monitoring permits crucial monitoring of breeding performance of seabirds when funding, time, or human resources are limited.

Neither method of monitoring showed variation in fledging success among years, suggesting that there was little variation in the environmental conditions that are important in determining fledging success. Our findings that chick-mass increase during the linear growth period varied among years and that fast-growing chicks fledged with a heavier mass suggests that chick growth is a more sensitive indicator of environmental conditions and breeding performance than breeding success. Chick growth reflects the ability of parents in the population to locate and provide food for their young. Quantifying chick growth in mass during the linear growth period provides a useful measure that can be compared among years. We suggest the use of mass here, because mass increase during the linear growth phase varied among years, whereas increase in wing length did not. In addition, mass is a simple measurement to take whereas measurements of wing or tarsus length are more likely to vary among observers. However some skill is involved in catching and handling chicks, especially when their parents are present, so it may not be appropriate to use chick growth as a performance indicator in all situations.

Evolution of juvenile life history.—Cody (1971) suggested that, in species with high chick survival, there should be no selective pressure on the chick to fledge early and indeed the Whiskered Auklet has a longer chick-rearing period (35–46 days) than most other alcids. Only Rhinoceros Auklet (*Cerorhinca monocerata*) (45–60 days), Tufted Puffin (*Fratercula cirrhata*, 43–51 days), and Atlantic Puffin (*Fratercula arctica*) (34–74 days) have longer chick-rearing periods (Ydenberg 1989). This is particularly striking because the Whiskered Auklet is the second-smallest species of alcid. Successful fledging may be dependant on wing length and muscle development because fledging chicks need to be able to fly strongly from the nest to the sea. Further, Whiskered Auklet fledglings are unique among alcids in that they return to the colony site in the months after fledging (Stejneger 1885, Konyukhov and Zubakin 1994, Zu-

bakin and Konyukhov 1999), and an ability to fly effectively would be of benefit during that period. We found that wing length continued to increase until (and almost certainly beyond) time of fledging. Hence, Whiskered Auklet chicks appear to benefit from staying in their crevices for a long time because they are safe from predation and because, the longer they stay (assuming parental care is sustained), the better their flight performance will be at fledging. However, a prolonged chick-rearing period will result in parents suffering the costs of an increased risk of predation, because they would have to fly from the open ocean to the nesting crevice a greater number of times. This risk is minimized in most populations of Whiskered Auklets by parents coming and going from the colony only in darkness. On Iona Island, in the Okhotsk Sea, there are no mammalian or avian predators and Whiskered Auklets are reported to have a diurnal pattern of activity (Kharitonov 1980). Further research emphasizing patterns of demography and survival of Whiskered Auklets and other auklet species is needed to establish whether nocturnality is a plastic trait that responds to predation pressure.

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