Monitoring planktivorous seabird populations: validating surface counts of crevice-nesting auklets using mark–resight techniques

Lisa M. Sheffield, Adrian E. Gall, Daniel D. Roby, David B. Irons, and Katie M. Dugger

Abstract: Least Auklets (*Aethia pusilla* (Pallas, 1811)) are the most abundant species of seabird in the Bering Sea and offer a relatively efficient means of monitoring secondary productivity in the marine environment. Counting auklets on surface plots is the primary method used to track changes in numbers of these crevice-nesters, but counts can be highly variable and may not be representative of the number of nesting individuals. We compared average maximum counts of Least Auklets on surface plots with density estimates based on mark–resight data at a colony on St. Lawrence Island, Alaska, during 2001–2004. Estimates of breeding auklet abundance from mark–resight averaged 8 times greater than those from maximum surface counts. Our results also indicate that average maximum surface counts are poor indicators of breeding auklet abundance and do not vary consistently with auklet nesting density across the breeding colony. Estimates of Least Auklet abundance from mark–resight were sufficiently precise to meet management goals for tracking changes in seabird populations. We recommend establishing multiple permanent banding plots for mark–resight studies on colonies selected for intensive long-term monitoring. Mark–resight is more likely to detect biologically significant changes in size of auklet breeding colonies than traditional surface count techniques.

Résumé : Les stariques minuscules (*Aethia pusilla* (Pallas, 1811)) sont l'espèce la plus abondante d'oiseaux marins dans la mer de Béring et ils peuvent servir de façon relativement efficace à suivre la productivité secondaire dans le milieu marin. La méthode principale consiste à dénombrer les stariques sur des parcelles de surface afin de suivre les changements de densité de ces oiseaux qui nichent dans les crevasses; les dénombrements sont cependant très variables et peuvent ne pas représenter le nombre d'individus en train de nicher. Nous avons comparé les dénombrements maximaux moyens des stariques minuscules sur des parcelles de surface aux estimations de densité basées sur des données de marquage et de signalisation subséquente dans une colonie sur l'île St-Lawrence, Alaska en 2001–2004. Les estimations de l'abondance des stariques minuscules reproducteurs obtenues par le marquage–resignalisation sont en moyenne 8 fois plus élevées que celles faites à partir des dénombrements maximaux en surface. Nos résultats démontrent aussi que les dénombrements maximums moyens sont de mauvais indicateurs de l'abondance des stariques minuscules en reproduction et qu'ils ne varient pas de façon régulière en fonction de la densité de nidification des stariques minuscules dans les différentes parties de la colonie reproductive. Les estimations d'abondance des stariques minuscules obtenues à partir du marquage–resignalisation sont suffisamment précises pour suivre les changements dans les populations d'oiseaux marins. Nous recommandons donc l'établissement de multiples parcelles permanentes de marquage pour les études de marquage–resignalisation dans des colonies sélectionnés pour une surveillance intensive à long terme. La méthode de marquage–resignalisation est vraisemblablement plus apte à détecter les changements d'importance biologique dans la taille des colonies reproductives des stariques minuscules que les méthodes traditionnelles de dénombrement en surface.

[Traduit par la Rédaction]

Introduction

The Bering Sea is one of the most productive marine ecosystems in the world, supporting some of the largest oceanic populations of fish, seabirds, and marine mammals (Loughlin et al. 1999). However, this ecosystem is currently in a state of flux, as a result of climate change (Overland and Stabeno 2004; Grebmeier et al. 2006). Seabirds are a highly visible component of marine ecosystems and, as upper trophic level consumers, can serve as sensitive indicators of change in marine ecosystems (Cairns 1987; Montevecchi 1993; Diamond and Devlin 2003). Seabird diet, productivity, and population trends reveal shifts in marine food webs (Davoren and Montevecchi 2003; Wanless et al. 2005). Least

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Auklets (*Aethia pusilla* (Pallas, 1811)) are one of the most abundant planktivorous seabirds in the North Pacific (Piatt et al. 1990*a*) and breeding colonies can number in the millions of individuals (Sowls et al. 1978; Stephensen et al. 1998). Diet, nesting success, and survival of Least Auklets are known to vary among years (Jones et al. 2002; Gall et al. 2006), suggesting that auklet populations may be sensitive to ocean conditions that influence secondary productivity and food availability within foraging distance of breeding colonies.

Recent evidence suggests that a warming trend is threatening populations of diving seabirds in the northern Bering Sea (Grebmeier et al. 2006). To detect trends in seabird populations caused by changing marine ecosystems or commercial activities in the North, repeatable and accurate census techniques are needed. Suitable methods currently exist for monitoring populations of cliff-nesting piscivorous seabirds, such as murres (species of *Uria* Brisson, 1760) and kittiwakes (species of *Rissa* Stephens, 1826), in the Bering Sea and throughout the circumpolar North (Piatt et al. 1988). Consensus has not been reached, however, on appropriate methods for monitoring breeding populations of crevice-nesting planktivorous seabirds such as Least Auklets (Piatt et al. 1988).

These small alcids nest among rocks on talus slopes (Bédard 1969) that can be up to 5 m deep, with auklets nesting throughout the interstitial spaces (Byrd et al. 1983; Jones 1993*a*, 1993*b*). Obtaining estimates of numbers of breeding pairs at auklet colonies is difficult because nests are concealed beneath the talus surface, and the density of nests is thought to vary considerably both within and among colonies (Stephensen et al. 1998).

Abundance indices for Least Auklets, and the closely-related Crested Auklet (*Aethia cristatella* (Pallas, 1769)), have been measured primarily by counting individuals attending surface plots on breeding colonies (Bédard 1969; Byrd et al. 1983; Piatt et al. 1990*a*). Surface counts may underestimate the number of breeding auklets, however, because an unknown proportion of breeders is either at sea or hidden beneath the talus (Stephensen et al. 1998). Additionally, surface counts are subject to large daily and seasonal fluctuations in colony surface attendance (Piatt et al. 1990*a*; Jones 1992), and may not accurately reflect changes in numbers of breeding birds (Jones 1993*a*, 1993*b*).

More recently, mark–resight techniques have been used to estimate the abundance of crevice- and burrow-nesting seabirds (Jones 1992; Isaksen and Bakken 1995; Kampp et al. 2000; Calvert and Robertson 2002) and other difficult to census wildlife (Neal et al. 1993; Hein and Andelt 1995). Ratios of marked to unmarked birds provide a more reliable estimate of numbers of breeding birds (Gardner and Mangel 1996), but require greater effort than counting birds attending the surface because considerable effort may be required to establish and maintain a marked population.

A previous study by Jones (1992) at St. Paul Island, Alaska, found that estimates of abundance for Least Auklets on a single plot using resighting of color-banded adults were approximately twice the average maximum surface count of individuals on the plot. More studies comparing these two methods are needed to quantify the relationship between auklet nesting density and number of birds attending the surface of breeding colonies.

Our objective was to contribute to the development of methodology for more accurately estimating the size of Least Auklet breeding colonies by measuring the density of nests on multiple plots. Auklet nesting density likely varies both among and within colonies, depending upon nesting substrate and other physical characteristics. We selected a series of study plots that represented the variation in both talus size and relative densities of adult Least Auklets attending the surface (and therefore presumably nest densities) at a breeding colony on St. Lawrence Island, Alaska.

We conducted surface counts and estimated number of breeding adults using mark–resight techniques for Least Auklets on three study plots dispersed across a breeding colony on St. Lawrence Island, Alaska, to (*i*) determine how average maximum surface counts correlate with estimates of abundance for Least Auklets from mark–resight and (*ii*) determine how nesting density varies among different areas within a breeding colony. We also sought to identify how to optimally allocate effort when using mark–resight techniques to monitor numbers of nesting Least Auklets on plots.

Methods

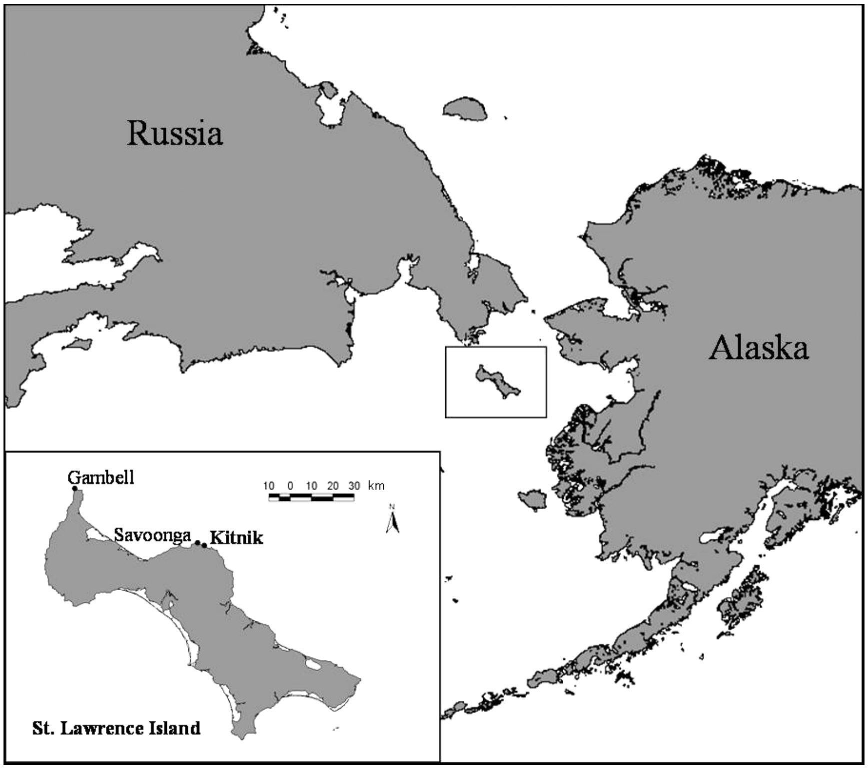
Study area

St. Lawrence Island, Alaska (ca. 63°30′N, 170°30′W), is located in the northern Bering Sea, approximately 200 km southwest of Nome, Alaska, and 60 km southeast of the Chukotsk Peninsula, Siberia. On St. Lawrence Island, Least Auklets nest in volcanic talus on coastal slopes along the western and north-central shores of the island. This research was conducted on the north side of St. Lawrence Island, east of the village of Savoonga (Fig. 1), from mid-June through early September during 2001–2004. Our study plots were located on the Kitnik auklet colony, approximately 3 km east of Savoonga.

Abundance estimation

Three square study plots, each 10 m × 10 m, were selected to represent three distinct areas of the Kitnik colony. Corners of each plot were marked with permanent re-bar stakes and locations were recorded using a global positioning systems (GPS) receiver. The perimeter of each plot was marked with white parachute cord strung between stakes, which was removed at the end of each season. Based on counts of auklets on the colony surface collected during the 2000–2002 breeding seasons (Gall 2004), we selected plots that were intended to represent one each of low, moderate, and high relative nesting density for Least Auklets. We also chose plots that would represent the variation in nesting substrate at the Kitnik colony (Sheffield 2005). Study plot A, which was established in 2000, was located in the lowland section of the colony near the beach with medium-sized nesting substrate, where surface counts of Least Auklets were relatively high. Study plot B, which was established in 2001, was located on the upland flat area of the colony that extends inland toward the mountains with small-sized nesting substrate. Based on surface counts, we expected nesting density within this plot to be relatively moderate. Study plot C, which was established in 2003, was located on the crest of the steeply sloped part of the colony with

Fig. 1. Location of the Kitnik auklet colony on St. Lawrence Island (ca. 63°30′N, 170°30′W) in the northern Bering Sea.



large-sized nesting substrate, where surface counts of Least Auklets were relatively low.

Least Auklets were captured within each study plot during the incubation period using monofilament nooses attached to hardware cloth or cargo net and placed on display rocks (large rocks where auklets tend to congregate for courtship displays). In 2003, auklets were also captured and banded during the early- and mid-chick-rearing periods on plot C to mark a sufficient number of individuals on this newly established plot.

Captured birds were banded with a combination of one stainless steel numbered USGS leg band and a unique color combination of one Darvic plastic band on the left leg and two on the right leg. Captured yearling subadults, distinguished by plumage (Bédard and Sealy 1984), were banded with one each stainless steel USGS band and Darvic plastic band on the left leg to indicate year of capture. An adult bird with a brood patch that was ≥50% de-feathered when banded during incubation or that was seen delivering a chick meal during the chick-rearing period was classified as a breeder during that breeding season. Adult auklets that do not attempt breeding in the current year often attend the colony surface to prospect for mates and nest crevices (Jones 1993*a*, 1993*b*). An adult bird that had a brood patch that was ≤50% de-feathered when banded during incubation (i.e., did not attempt breeding) was classified as a nonbreeder during that season. Least Auklets are highly synchronous breeders; therefore, it is unlikely that any late breeders would have been incorrectly classified as nonbreeders. Breeding auklets carry zooplankton prey to their chicks in a sublingual pouch that is separate from the digestive tract. To further validate breeding status, all captured individuals were examined for presence of a sublingual pouch following the methods of Speich and Manuwal (1974). Depth of the pouch was measured (±1 mm) by gently inserting a blunt-tipped, stainless steel probe through the sublingual pouch opening until resistance was met at the base of the pouch. An adult Least Auklet with a sublingual pouch <10 mm deep was classified as a nonbreeder during that season. Nests were not monitored within study plots because disturbing nesting auklets has been shown to negatively affect hatching and fledging success (Piatt et al. 1990*b*), and may increase the vulnerability of chicks to mammalian predators (Fraser et al. 1999).

We conducted surface counts of Least Auklets every 4 days throughout the breeding season on each of the three study plots. Counts were made during 4 h blocks timed to coincide with the daily period of peak surface attendance. All-day counts were conducted at 3-week intervals in each year to track the shifting period of peak surface attendance (approximately 1000–1600 Alaska Daylight Time). Plots were scanned at 15 min intervals during the 4 h blocks and total numbers of Least Auklets on the colony surface within the plot boundaries were recorded after each scan. We then calculated the mean of the five highest counts recorded during the period from mid-incubation to mid-chick-rearing (stage of the nesting cycle when surface counts are least variable), following the methods of Williams et al. (2000). We tested for differences in maximum surface counts among years and study plots using mixed-model analysis of variance (ANOVA) with Tukey–Kramer procedures for multiple comparisons of means, with year and plot as fixed and random effects, respectively.

We estimated numbers of nesting Least Auklets on study plots using mark–resight techniques. We resighted banded birds on each of the three plots in 4 h blocks during periods of peak surface attendance, every 4 days throughout the breeding season. We resighted marked adults throughout the breeding season to identify those individuals that composed the marked population in each plot in each year. Plots were scanned for marked birds from a distance of approximately 50 m using zoom spotting scopes (20×–60×) to minimize disturbance. Total counts of marked and unmarked birds, along with individual color combinations for each marked bird, were recorded at 15 min intervals during the 4 h peak of colony surface activity. Counts on each of the three study plots were conducted concurrently by three different observers and the observers rotated among the three study plots throughout the season. Marked birds were considered part of the marked population within a study plot for the current breeding season if they were resighted at least once within the plot during that year. Birds that were banded but never resighted in the study area were not included in the marked population. Only resighting events that occurred after completion of banding efforts were used to estimate abundance for each plot. Subadult birds were not included in density estimates from mark–resight because they were not banded with a unique color combination of plastic leg bands. Nonbreeders were marked as part of this study beginning in 2003 and 2004. We began banding nonbreeders with unique color combinations because an unknown proportion of the unmarked population consisted of nonbreeders, and marking nonbreeders allowed us to incorporate the resighting heterogeneity of this group into our estimates.

As part of a separate objective, we conducted three all-day observations of chick meal deliveries in 2003 and 2004 during mid-chick-rearing on plot B (8–9, 12–13, and 18 August 2003, and 9–10, 11–12, and 16 August 2004). We used these observations to estimate abundance from mark–resight data on plot B in 2003 and 2004 based solely upon Least Auklets delivering chick meals following the methods of Jones (1992) to determine (*i*) how estimates of abundance differ between mark–resight of auklets attending the colony surface and mark–resight of auklets delivering meals to chicks and (*ii*) whether ratios of mark–resight estimates during chick-rearing to average maximum surface counts were similar between St. Lawrence Island and a comparable study on St. Paul Island during 1987–1989 (Jones 1992).

Resighting histories were created for each marked auklet to account for resighting heterogeneity. We then used the Bowden's estimator (Bowden and Kufeld 1995) in the program NOREMARK (White 1996*a*) to estimate population abundance for Least Auklets in each plot and year. The Bowden's estimator is robust to resighting heterogeneity because it uses resighting frequencies of marked individuals to estimate population size. Confidence intervals (CIs) are computed based on the variance of the resighting frequencies of the marked individuals. A closed population was assumed because observations were made only during the breeding season and we assumed that losses owing to death were small (Calvert and Robertson 2002). Auklet density was then estimated by dividing the population abundance estimate by the area of the plot. CIs for density estimates were calculated using the Delta method (Williams et al. 2002). The unbiased Bowden's estimator of population size is

$$\hat{N} = \frac{\left[\frac{(u+m)}{\bar{f}} + \frac{s_f^2}{\bar{f}^2}\right]}{\left[1 + \frac{s_f^2}{T\bar{f}^2}\right]^2}$$

with variance

$$\widehat{\mathrm{Var}}(\hat{N}) = \frac{\hat{N}^2\left[\frac{1}{T} - \frac{1}{\hat{N}}\right]\frac{s_f^2}{\bar{f}^2}}{\left[1 + \frac{s_f^2}{T\bar{f}^2}\right]^2}$$

where $\hat{N}$ is the population estimate, T is the number of marked animals in the population, u is the total number of unmarked animal sightings, m is the total number of marked animal sightings, $\bar{f}$ is the mean resighting frequency of marked animals, and s_f^2 is the variance of the resighting frequencies of the marked animals. We tested for differences among years and study plots by comparing 95% CIs for abundance estimates derived from Bowden's estimator (Hein and Andelt 1995). When CIs overlapped, we used two-sample t tests to determine significance at $\alpha \leq 0.05$.

A recommended goal for detection of population change in seabirds is 20% per year at a level of significance of $P \leq 0.1$ (USFWS 1992; Hatch 2003). Although a decline or increase of 20% per year is quite large, this goal reflects the high annual variability in breeding seabird population estimates that is not due to actual changes in population size (Hatch 2003). An alternative goal for long-term monitoring of seabird populations proposed by Hatch (2003) is detection of an annual rate of decline of 6.7% sustained over 10 years (i.e., 50% decline). However, while these objectives relate directly to the ultimate goal of detecting trends in seabird abundance, the initial concern to meet this goal must be estimation and precision of annual abundance estimates. For field studies, estimates of abundance with coefficients of variation (CVs) <20% are generally considered adequate for making inference, but what level of precision is required to meet the above objectives? We used the program TRENDS (software by T. Gerrodette; Gerrodette 1987) to investigate the level of precision in annual abundance estimates (measured as CV) required to detect an annual rate of decline of 6.7% over 10 years, with $\alpha = 0.05$ and power = 0.90. We followed Hatch (2003) and assumed a linear trend with constant CV over time. We found that CVs on abundance estimates ≤24% would meet the above objective.

It may be necessary, in some cases, to improve the precision of population estimates using mark–resight techniques to meet these goals by increasing at least one of the following: (*i*) size of the marked population, (*ii*) number or duration of resighting occasions, or (*iii*) proportion of the population viewed during each resighting occasion (White 1996*b*). To explore the precision and utility of this approach to estimating auklet abundance, we used Monte Carlo simulations of the Bowden's estimator in the program NOREMARK to determine how changing the size of the marked population and number of resighting occasions would improve the precision of the abundance estimates. NOREMARK provides 95% CIs as a measure of the precision of generated estimates, but we also calculated SEs and CVs from these symmetrical confidence limits. The NOREMARK simula-

Table 1. Means of the five maximum surface counts of Least Auklets (*Aethia pusilla*) during 2001–2004 on three study plots at the Kitnik auklet colony on St. Lawrence Island, Alaska.

	2001	2002	2003	2004
Plot A	45.2	46.0	59.4	40.6
95% CI	34.3–56.1	43.1–48.9	48.1–70.7	33.4–47.8
CV (%)	19.4	5.1	15.3	14.3
Plot B	52.2	44.0	46.6	33.0
95% CI	35.2–69.2	38.9–49.1	42.8–50.4	31.2–34.8
CV (%)	26.2	9.4	6.5	4.3
Plot C	na	na	na	28.4
95% CI				27.0–29.8
CV (%)				4.0

Note: na, not available.

tions required input of estimated values for population size, number of resighting occasions, proportion of the population marked, proportion of the population seen during each resighting occasion, and proportion of marked animals seen that were correctly identified on each occasion. A hypothetical population size of 300 Least Auklets per plot was used based on estimates for all plots in all years. We resighted approximately 25% of the marked population (i.e., number of known marked birds resighted in the current year) of Least Auklets per resighting occasion during 2003 and 2004. Based on these results, we used 25% as the proportion of the marked population seen per resighting occasion in our models. We estimated that 90% of marked individuals were correctly identified during resighting occasions; we were not able to read complete color-band combinations for approximately 10% of observed marked birds (this 10% was modeled as marked, but unknown in our estimates of abundance). We simulated estimates with values for the proportion of individuals marked that ranged from 0.05 to 0.9, and for the number of resighting occasions that ranged from 1 to 11 (Appendix Table A1).

Results

Surface counts

Average maximum surface counts of Least Auklets varied among years and plots (mixed-model ANOVA, $F_{[3,36]}$ = 10.3, P = 0.04; Table 1). Average maximum surface counts on both plot A and plot B were lowest during 2004 in our 4-year study (Table 1). In 2004, when we obtained average maximum surface counts for Least Auklets on all three study plots, counts were highest on plot A and lowest on plot C (Table 1). Average maximum counts were similar between plot A and plot B, except during 2004 when surface counts on plot A were greater than surface counts on plot B. Precision of our estimates based on surface counts were generally quite high (Table 1).

Mark–resighting

We estimated abundance of nesting Least Auklets on plots A and B using mark–resight techniques during all 4 years of the study (Table 2). Estimated abundance of Least Auklets on plot A did not change significantly during the 4 years of the study based on overlapping 95% CIs (Table 3, Fig. 2). Estimated abundance on plot B was significantly higher in 2003 than during 2001 or 2002, based on nonoverlapping 95% CIs, but was not higher than during 2004 (two-sample t test, t = 1.41, P = 0.16, 95% CI for the difference between means 73.13 and 435.13; Table 3, Fig. 2). During 2004, we compared abundance estimates for Least Auklets among all three plots. Estimated number of breeding Least Auklets was similar on plots A and B in 2004, but significantly lower on plot C based on nonoverlapping 95% CIs (Table 3, Fig. 2) and in agreement with average maximum surface counts.

We calculated nesting densities in number of pairs per square metre for Least Auklets in all plots (Table 4). Density estimates ranged from 0.9 to 2.7 pairs/m^2 (n = 9 plot/years) with an average of 1.7 pairs/m^2 (SD = 0.53, n = 9 plots). The means for Least Auklets during all 4 years were similar on plot A (1.9 nests/m^2, SD = 0.10) and plot B (1.8 nests/m^2, SD = 0.70).

Abundance estimates from mark–resight data using the program NOREMARK were, on average, approximately 8 times greater than the average maximum surface counts on all plots and in all years (SD = 2.4, n = 9; Table 5, Fig. 2). There was no significant correlation between average maximum surface counts and mark–resight abundance estimates for Least Auklets (R = 0.29, P = 0.45, n = 9 plot/years). We also examined the data separately for plots A and B during all 4 years, because this ratio could vary among plots. There was no significant correlation between average maximum surface counts and mark–resight abundance estimates for Least Auklets either on plot A (R = –0.26, P = 0.74, n = 4 years) or on plot B (R = –0.13, P = 0.87, n = 4 years).

Estimates of Least Auklet abundance (using Bowden's estimator) from mark–resight of birds delivering meals to chicks on plot B were 263 (95% CI = 233–298; CV = 6.5%) in 2003 and 273 (95% CI = 239 – 313; CV = 7.1%) in 2004, lower than estimates from mark–resight of Least Auklets attending surface plots (Table 3). These estimates were relatively precise and the ratios of estimates from mark–resight of Least Auklets delivering chick meals to average maximum surface counts on plot B were 5.6 in 2003 and 8.3 in 2004.

Model simulations

Increasing the proportion of marked individuals improved the precision of the estimate (i.e., reduced the coefficients of variation) more efficiently than increasing the number of resighting occasions (see Appendix Table A1). Increasing the number of resighting occasions initially improved the precision of estimates, but was subject to diminishing returns after about the fifth resighting occasion. However, increasing the proportion of marked birds on a plot by 10% likely requires a greater investment of time and resources than adding two resighting occasions, depending upon trapping efficiency, retention of marked individuals, and number of recaptures.

An annual rate of decline of 6.7% sustained over 10 years in a Least Auklet population beginning with 300 individuals could be detected with either 10% of the population marked and two resighting occasions (CV = 23%; Appendix Table A1) or 20% of the population marked and one resighting occasion (CV = 21%; Appendix Table A1). A 20% change in abundance between years at a lower level of significance

Table 2. Resighting effort measured by number of 4 h resighting occasions used to develop abundance estimates and number of marked individuals observed on each of three study plots.

	2001	2002	2003	2004
Plot A				
Resighting occasions for estimates	4	9	7	5
Marked Least Auklets (marked nonbreeders)	26 (0)	43 (0)	48 (0)	67 (6)
Proportion marked (%)	7.4	10.9	13.3	19.6
Plot B				
Resighting occasions for estimates	4	2	5	5
Marked Least Auklets (marked nonbreeders)	23 (0)	50 (0)	79 (3)	77 (4)
Proportion marked (%)	9.5	22.4	15.3	22.9
Plot C				
Resighting occasions for estimates	na	na	na	5
Marked Least Auklets (marked nonbreeders)	na	na	na	51 (6)
Proportion marked (%)	na	na	na	30.6

Note: Proportion of the population marked is estimated from the number marked in each plot and year divided by the abundance estimate for each plot and year (see Table 3). na, not available.

Table 3. Estimates of abundance from mark–resight of Least Auklets during 2001–2004 on three study plots at the Kitnik auklet colony on St. Lawrence Island, Alaska.

	2001	2002	2003	2004
Plot A	352	395	361	372
95% CI	248–501	306–510	252–516	278–497
CV (%)	19.6	13.9	20.0	16.1
Plot B	242	223	535	354
95% CI	172–342	171–291	365–787	265–473
CV (%)	19.2	14.3	21.7	15.9
Plot C				186
95% CI	na	na	na	135–257
CV (%)				17.8

Note: na, not available.

($P \leq 0.10$; USFWS 1992; Hatch 2003) would not require such precise estimates; therefore, if CVs for abundance estimate can be kept below 20%–25%, all current objectives for detecting trends in auklet abundance can be met.

Discussion

The estimated numbers of nesting Least Auklets based on mark–resight were consistently greater than the average maximum surface counts. The ratio of estimates of abundance from mark–resight to average maximum surface counts varied over a wide range (4.6–11.5) and was not consistent within plots or within years across plots. Consequently, it is difficult to identify a single conversion factor that would convert average maximum surface counts to numbers of breeding adults. It is not apparent what factors were responsible for the wide range of values for the ratio of mark–resight estimates to average maximum surface counts.

The ratios of our mark–resight estimates of number of auklets to average maximum surface counts were greater than those recorded by Jones (1992) on a plot at St. Paul Island during the breeding seasons of 1987–1989. Estimated nesting densities of Least Auklets on the plot at St. Paul Island ranged from about 0.7–1.1 birds/m^2 during the 3 years, which is similar to the estimate of nesting density for plot C in the present study (0.9 birds/m^2) but less than the nesting densities on plots A and B (1.9 and 1.8 birds/m^2, re-

Fig. 2. Average maximum surface counts and mark–resight abundance estimates for Least Auklets on study plots A and B in 2001–2004, and on study plot C in 2004 at the Kitnik colony on St. Lawrence Island, Alaska. Error bars represent 95% CIs.

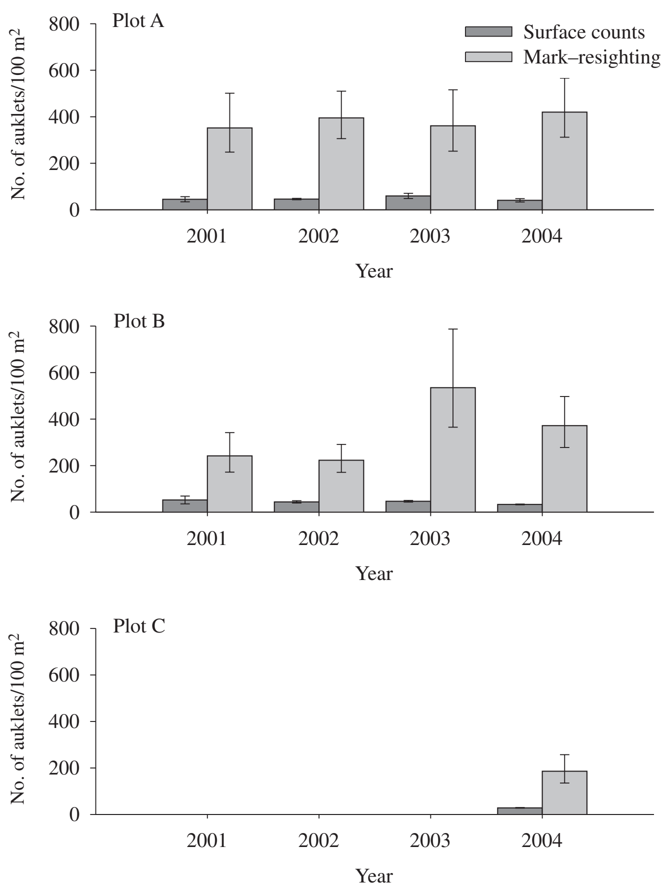


Table 4. Estimated nesting densities (numbers of pairs/m^2) for Least Auklets on three 100 m^2 plots at the Kitnik colony, St. Lawrence Island, Alaska, during 2001–2004.

	2001	2002	2003	2004
Plot A	1.8	2.0	1.8	1.9
95% CI	1.1–5.2	1.4–5.8	1.1–5.3	1.3–5.5
CV (%)	19.6	13.9	20.0	16.1
Plot B	1.2	1.1	2.7	1.8
95% CI	0.8–3.6	0.8–3.3	1.5–7.9	1.2–5.2
CV (%)	19.2	14.3	21.7	15.9
Plot C				0.9
95% CI	na	na	na	0.6–2.8
CV (%)				17.8

Note: na, not available.

Table 5. Ratios of estimates of abundance from mark–resight data to average maximum surface counts for Least Auklets on three study plots at the Kitnik colony on St. Lawrence Island, Alaska, during 2001–2004.

	2001	2002	2003	2004	Mean
Plot A	7.8	8.6	6.1	9.2	7.9
Plot B	4.6	5.1	11.5	10.7	8.0
Plot C	na	na	na	6.55	na

Note: na, not available.

spectively). The mark–resight estimates from the St. Paul Island plot were 2–3 times greater than average maximum surface counts (Jones 1992). We saw much larger differences between mark–resight estimates and average maximum surface counts, at least in part, because we used Bowden's estimator (Bowden and Kufeld 1995) to account for resighting heterogeneity. Failure to account for heterogeneity (i.e., using a Lincoln–Petersen estimator) overestimates the marked proportion of the population and therefore underestimates abundance (White et al. 1982). Additionally, the estimation method used by Jones (1992) only included individuals that were observed delivering chick meals, which excluded breeders that failed during incubation. Our methods included all marked adults that had been resighted in the current year in the banded population regardless of reproductive success.

The precision of our estimates was high enough to meet management objectives in all plots and years. On average, we observed higher CVs in years when estimated marked proportions in our plots were low (i.e., plots A and B in 2001), and lower CVs when marked proportions were higher (i.e., plots A and B in 2004). Our most precise estimate of abundance in all plot/years was for plot A in 2002 (CV = 13.9%), when only 10.9% of birds were marked. Greater resighting effort in this plot/year (9 occasions) resulted in high precision, very near the predicted CV of 11% (Appendix Table A1). Likewise, we observed relatively high precision in plot B in 2002 (14.3% observed CV, 15% predicted CV), when resighting effort was low, but the proportion marked was relatively high (Table 2, Appendix Table A1). However, our data did not always fit this pattern. During 2003 and 2004, precision was lower than predicted based on our simulations (Table 3, Appendix Table A1). This lower precision may be due to the presence of nonbreeders in the marked population in these years. For example, on plot C in 2004, we had high proportions of marked birds (30.1%, Table 2) and 5 resighting occasions, yet our CV of 17.8% was higher than the expected 7.0% (Table 3, Appendix Table A1). This plot had a higher proportion of marked nonbreeders (12%; Table 2) than any other plot/year. Nonbreeding auklets may have more variable surface attendance patterns that may have added to the imprecision of this estimate. More information is needed on the variability in attendance patterns of breeders versus nonbreeders on the colony surface.

Estimates of abundance from ratios of marked to unmarked birds delivering chick meals were lower than the estimates based on all marked and unmarked auklets, as expected, because the estimates only included breeders that had successfully hatched eggs and were raising young. Also, the CVs for these estimates were smaller, 6.5% and 7.1% in 2003 and in 2004, respectively, providing more precise estimates of population size. Estimates based upon birds delivering meals to chicks eliminate the variability inherent in the intermittent colony surface attendance by nonbreeders and failed-breeders, and are clearly superior for estimating abundance of auklets that are successful breeders. Measuring abundance using birds delivering chick meals also offers opportunities to obtain other useful information, such as meal delivery rates that are indicative of food availability. Although mark–resight of birds delivering chick meals estimates abundance of only breeding birds that successfully hatch an egg and begin raising a chick, the increase in the precision and reliability of the population estimate may offset the omission of failed breeders from the population estimate. Additionally, estimates of egg hatching success based on nest monitoring would provide a means to adjust estimates of abundance for the proportion of breeders that failed during incubation.

The ratio of estimates from mark–resight of Least Auklets delivering chick meals to average maximum surface counts on plot B was higher than for the plot on St. Paul Island (Jones 1992). This difference may be due to differing levels of food availability or predation pressure on the two islands. If food availability and foraging efficiency were lower on St. Lawrence Island, auklets may have had less time to attend the colony surface. If disturbance by predators was more intense on St. Lawrence Island, this could have suppressed surface attendance relative to St. Paul Island, because auklets are reluctant to land on the colony surface when predators are present nearby, thus reducing average maximum surface counts.

Estimating abundance with mark–resight techniques can be labor- and time-intensive, but this method provides much more accurate and reliable estimates of abundance compared with other available techniques. It will not be practical to employ mark–resight techniques in all situations, however, especially at colonies where only brief visits are possible or long-term monitoring is not feasible. Average maximum surface counts reflect only a small and variable proportion of breeding auklets, and further investigation is needed into relationships between numbers of birds attending the surface and nesting density. Average maximum surface counts may provide a sufficiently reliable index to population size of Least Auklets at colonies where intensive monitoring is not feasible if factors that affect colony surface attendance without influencing nest density (i.e., seasonal variation in weather, food availability, and disturbance) can be taken into account. Maximum surface counts and colony mapping techniques may be the only means for detecting auklet population change in areas where maintaining a marked population is not possible. Comparison of population estimates from mark–resight with average maximum surface counts in other years and at other colonies may validate surface counts as an index to population size and increase the utility of this method for monitoring changes in colony size, if conversion factors can be developed to account for variability in surface counts. A larger sample of surface counts and mark–resight estimates, with a wider range of counts and population sizes, may reveal relationships between the two methods that were not apparent in this data set.

Further investigation is also needed into the relationship between nesting densities and surface attendance of Crested Auklets, which are subject to similar monitoring difficulties and form mixed breeding colonies with Least Auklets. Preliminary results indicate that average maximum surface counts may also underestimate nesting density of this species by about an order of magnitude (Sheffield 2005).

We recommend that marked populations of Least Auklets should be established wherever long-term intensive monitoring sites for this species are designated. Estimates of auklet nesting densities from mark–resight should be conducted at multiple plots that represent variation in auklet density whenever possible. Estimates of nesting densities, coupled with overall measurements of colony area, will provide a much-needed technique to detect and track biologically significant changes in size of auklet breeding colonies associated with a warming northern Bering Sea. Additionally, these methods may prove valuable for other difficult to census crevice- and burrow-nesting species.

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Appendix A.

Table A1. Coefficients of variation (%) for different proportions of marked Least Auklets (*Aethia pusilla*) and numbers of resighting occasions.

Proportion of population marked	Number of resighting occasions							
	1	2	3	4	5	7	9	11
0.05	44	37	30	25	23	19	16	15
0.10	33	23	19	16	14	12	11	10
0.15	26	18	14	12	11	9	8	7
0.20	21	15	12	10	9	8	7	6
0.25	18	13	10	9	8	7	6	5
0.30	16	11	9	8	7	6	5	5
0.40	13	9	7	6	6	5	4	4
0.50	10	7	6	5	5	4	3	3
0.70	7	5	4	3	3	2	2	2
0.90	3	2	2	2	1	1	1	1

Note: A hypothetical population size of 300 individuals is used based on average estimates for Least Auklets across the three study plots during 2001–2004.