

AN ABSTRACT OF THE THESIS OF

Adrian E. Gall for the degree of Master of Science in Wildlife Science presented on March 22, 2004.

Title: Planktivorous Auklets (*Aethia cristatella* and *A. pusilla*) Nesting on St. Lawrence Island, Alaska as Indicators of Marine Conditions in the Northern Bering Sea.

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Daniel D. Roby



Monitoring reproductive success, prey species composition, and colony size of marine birds has been proposed as a method of assessing changes in marine systems that are otherwise difficult to sample (Cairns 1987). I measured inter-annual and intra-seasonal variability in reproductive parameters, taxonomic composition of the diet, and adult body condition of Crested Auklets (*Aethia cristatella*) and Least Auklets (*A. pusilla*) at 2 colonies near the village of Savoonga, St. Lawrence Island, Alaska during the 2000-2002 breeding seasons to evaluate how reproductive success of planktivorous seabirds is related to diet. I also assessed the utility of two methods of population monitoring (surface counts and mark-resighting) for detecting annual changes in breeding populations of Crested and Least auklets during the 2001 and 2002 breeding seasons on the Kitnik colony.

Average reproductive success was generally high (> 60% of nests) for both auklet species during the 3 years of the study, but differed among years. Median hatching dates for both species were 2 weeks earlier in the year of highest reproductive success (2002), compared to the previous 2 years. In all 3 years, the diet of Crested Auklets was predominantly euphausiids, while the diet of Least Auklets consisted primarily of calanoid copepods, but species composition of the diet

differed among years for both species. Crested and Least auklets consumed more of the large, lipid-rich copepod *Neocalanus cristatus* in 2002 than in the other 2 years of the study. The year of lowest reproductive success (2001) was associated with low prevalence of euphausiids in Crested Auklet diets late in the chick-rearing period and high prevalence of the small, low-lipid copepod *Calanus marshallae* in Least Auklet diets.

I observed an increase in total body mass of Crested Auklets during the 2002 breeding season, whereas total body mass declined through the breeding season in the other 2 years. Seasonal changes in adult body mass of Crested Auklets may, therefore, be a useful indicator of food availability. Average body mass of Least Auklets declined in all 3 years, but was lowest in 2001, suggesting that low adult body mass of Least Auklets may reflect poor foraging conditions. Fat reserves of breeding auklets during egg-laying were not highly variable among or within breeding seasons and therefore were not a sensitive predictor of subsequent breeding success.

Counts of Crested Auklets in plots on the colony surface were highest in areas of large average boulder size; Least Auklet surface counts were not as variable among plots. Maximum counts of both species of auklets in plots did not differ between years. Patterns of colony surface attendance during the breeding season, however, did differ between years. The colony surface attendance of both auklet species after hatching was higher in the year of high reproductive success. Preventing nest initiation by covering plots with tarps did not reduce subsequent colony surface attendance during chick-rearing (after the tarps were removed) for either species, suggesting that reproductive success, independent of differences in food availability, did not cause a difference in colony surface attendance. I estimated

abundance of Least Auklets nesting in two 100-m² plots using mark-resight methods. I concluded that surface counts may provide an indication of among-year differences in colony attendance, but underestimate the number of breeding individuals by a factor of 10. Mark-resighting techniques show more promise for detecting changes in the number of breeding pairs. Reproductive success, adult body mass, and post-hatch colony attendance of Crested and Least auklets appear positively associated with zooplankton availability, particularly the prevalence of *N. cristatus* in the diet. Annual monitoring of these 3 parameters, together with diet composition, are important for understanding how both natural and anthropogenic climate change may affect trophic structure of the northern Bering Sea ecosystem.

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Planktivorous Auklets (*Aethia pusilla* and *A. cristatella*) Nesting on St. Lawrence
Island, Alaska as Indicators of Marine Conditions in the Northern Bering Sea

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Adrian Gall

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TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1: General Introduction.....	1
LITERATURE CITED	6
CHAPTER 2: Interannual variation in diet, reproductive success, and body mass of plankton-feeding auklets on St. Lawrence Island, Alaska.....	8
ABSTRACT	9
INTRODUCTION	10
METHODS.....	13
RESULTS	22
DISCUSSION.....	37
ACKNOWLEDGEMENTS.....	47
LITERATURE CITED	48
CHAPTER 3: Evaluation of body condition indices for Least Auklets (<i>Aethia pusilla</i>) and Crested Auklets (<i>A. cristatella</i>).....	53
ABSTRACT	54
INTRODUCTION	55
METHODS.....	57
RESULTS	62
DISCUSSION.....	70
ACKNOWLEDGEMENTS.....	74
LITERATURE CITED	75
CHAPTER 4: Factors affecting population indices of planktivorous auklets on St. Lawrence Island, Alaska	78
ABSTRACT	79
INTRODUCTION	80

TABLE OF CONTENTS (Continued)

	<u>Page</u>
METHODS.....	83
RESULTS	92
DISCUSSION.....	108
ACKNOWLEDGEMENTS	114
LITERATURE CITED	115
CHAPTER 5: Conclusions.....	117
BIBLIOGRAPHY	123
APPENDIX	131

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1. Map of St. Lawrence Island, Alaska, showing the location of the Kitnik and Myaughee study colonies.....	14
2.2. Taxonomic composition by biomass of diets fed to Least and Crested auklet chicks on St. Lawrence Island, Alaska from late July through August during the 2000-2002 breeding seasons.	29
2.3. Seasonal changes in the taxonomic composition by biomass of diets fed to Least Auklet chicks on St. Lawrence Island, Alaska from late July through August during the 2000-2002 breeding seasons.....	30
2.4. Seasonal changes in the taxonomic composition by biomass of diets fed to Crested Auklet chicks on St. Lawrence Island, Alaska from late July through August during the 2000-2002 breeding seasons	33
2.5. Predicted total body masses for (A) Least Auklets and (B) Crested Auklets during the 2000-2002 breeding seasons on St. Lawrence Island, Alaska.....	35
3.1. Mean fat index (total body fat mass/ lean dry body mass) of (A) Least Auklets and (B) Crested Auklets during egg-laying on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.	63
4.1. The Kitnik auklet colony on the north shore of St. Lawrence Island, Alaska, showing the location of study plots.....	85
4.2. Diurnal colony surface attendance of Least and Crested auklets on the Kitnik colony, St. Lawrence Island, Alaska in (A) early incubation, (B) late incubation, and (C) early chick-rearing during the 2001 breeding season.	93
4.3. Diurnal colony surface attendance of Least and Crested auklets on the Kitnik colony, St. Lawrence Island, Alaska in (A) early incubation, (B) late incubation, and (C) early chick-rearing during the 2002 breeding season.	94
4.4. Average maximum counts of Crested Auklets per plot on 4 areas of the Kitnik colony, St. Lawrence Island, Alaska in (A) 2001 and (B) 2002.....	96
4.5. Average maximum counts of Least Auklets per plot on 4 areas of the Kitnik colony, St. Lawrence Island, Alaska in (A) 2001 and (B) 2002.....	97

LIST OF FIGURES (continued)

<u>Figure</u>		<u>Page</u>
4.6.	Numbers of Crested Auklets (A) and Least Auklets (B) observed on the surface of index plots in 4 areas of the Kitnik colony, St. Lawrence Island, Alaska, 2001 and 2002.....	98
4.7	Least Auklet colony surface counts on control plots and experimental plots (no active nests) during chick-rearing in 3 areas of Kitnik colony, St. Lawrence Island, Alaska in 2001 and 2002	103
4.8.	Crested Auklet colony surface counts on control plots and experimental plots (no active nests) during chick-rearing in 3 areas of Kitnik colony, St. Lawrence Island, Alaska in 2001 and 2002	104
4.9.	Estimates of the number of breeding adult Least Auklets nesting beneath two 100 m ² study plots at the Kitnik colony, St. Lawrence Island, Alaska.....	107

LIST OF TABLES

<u>Table</u>	<u>Page</u>
2.1 Prey types used to sort Least and Crested auklet diet samples collected during the 2000-2002 breeding seasons on St. Lawrence Island, Alaska.....	18
2.2. Nesting chronology of Least and Crested auklets at the Kitnik and Myaughee colonies on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.....	23
2.3. Reproductive success of Least Auklets at 2 breeding colonies on the north shore of St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.....	24
2.4. Reproductive success of Crested Auklets at 2 breeding colonies on the north shore of St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.....	25
2.5. Taxonomic composition of the meals delivered to Least Auklet nestlings during the 2000 – 2002 breeding seasons on St. Lawrence Island, Alaska.....	28
2.6. Taxonomic composition of the meals delivered to Crested Auklet nestlings during the 2000 – 2002 breeding seasons on St. Lawrence Island, Alaska.....	32
2.7. Models explaining variation in total body mass of Least and Crested auklets on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons	36
3.1. Body composition of Least Auklets and Crested Auklets collected during the 2000-2002 breeding seasons on St. Lawrence Island, Alaska.....	65
3.2 Comparison of multiple regression models explaining variation in fat mass (g) of adult Least Auklets nesting on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons	66
3.3. Comparison of multiple regression models explaining variation in fat mass (g) and of adult Crested Auklets nesting on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons	67
3.4. Multiple regression models explaining variation in the principle components body condition index (PCBCI) of Least and Crested auklets on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.	69

LIST OF TABLES (continued)

<u>Table</u>	<u>Page</u>
4.1. Quasi-likelihood regression output for a model of the effects of year, area of colony, date, and interactions between these effects on maximum counts of Crested Auklets ($R^2 = 65.3\%$) and Least Auklets ($R^2 = 59.2\%$) on plots at the Kitnik colony, St. Lawrence Island, Alaska	100

Dedicated
in loving memory of my grandfather,
Dr. Jorge Pradilla Reyes,
for giving a 6-yr old her first lesson
in the evolution of life

Planktivorous Auklets (*Aethia pusilla* and *A. cristatella*) Nesting on St. Lawrence
Island, Alaska as Indicators of Marine Conditions in the Northern Bering Sea

CHAPTER 1

General Introduction

Adrian E. Gall

Saint Lawrence Island, located in the northern Bering Sea, is a nesting area for ca. 3.6 million seabirds of 16 species, comprising over 10% of Alaska's breeding seabirds (Stephensen et al. 1998). These seabird populations are sustained by forage fish and zooplankton found in the highly productive waters surrounding the island and, in particular, the northward flowing Anadyr Current to the west and northwest (Pavlov and Pavlov 1996). St. Lawrence Island is an important monitoring site because of its bountiful fish and wildlife resources and its location at the crossroads of the North American and Eurasian continents, in the midst of a major transportation corridor from Arctic oil fields to the rest of the world. Current and future commercial use (e.g., fisheries, oil and gas development) of the Bering and Chukchi seas carries the potential for adverse pressures on seabird populations. Native Yup'ik communities on the island also have an interest in monitoring seabird populations, because they depend on seabirds for subsistence use and cultural activities. In addition to effects of development-related activities, there is concern that the anticipated changes in air temperature associated with global climate change will have immediate effects on the Bering Sea ecosystem, as well as the populations of arctic and subarctic seabirds that depend on it (Meehan et al. 1999).

The colonies of planktivorous Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) found on St. Lawrence Island are some of the largest in Alaska (Jones 1993a, 1993b). Piscivorous Common and Thick-billed murres (*Uria aalge* and *U. lomvia*) and Black-legged Kittiwakes (*Rissa tridactyla*) also nest on the Island; these three species are used in seabird monitoring programs throughout the state of Alaska. The extensive database on Alaska's piscivorous seabird populations makes them valuable indicator species for monitoring change in the marine environment (Meehan et al. 1999). Murres and kittiwakes, while relatively easy to monitor

because they nest on cliffs, may not reflect changes at the trophic level of herbivorous zooplankton. The physical characteristics of the northern shelf of the Bering Sea create a domain of primary production that supports a well-developed copepod-based food web (Springer and Roseneau 1985). In such a system, planktivorous auklets serve as a better indicator of zooplankton abundance than piscivorous seabirds.

Marine trophic webs in the Bering Sea and northern Gulf of Alaska have recently experienced a regime shift similar in magnitude to the shift that occurred in the late 1970's (Miller and Schneider 2000). These changes, associated with the Pacific Decadal Oscillation (PDO), are likely to have profound effects on secondary productivity (grazing zooplankton such as copepods and euphausiids) and the food supply of Least and Crested auklets. Despite the enormous size of the auklet colonies on St. Lawrence Island and their key role in the food webs of the northern Bering Sea, there have been no long-term studies of seabirds in general, or planktivorous auklets in particular, in the northern Bering Sea. Establishing a long-term seabird monitoring site on St. Lawrence Island can fill the large gap in our ability to detect even major changes in seabird populations of the northern Bering Sea.

While detecting changes in seabird population size are important for conservation of seabird resources, population sizes of these long-lived birds are more likely to respond to environmental factors on the scale of decades, rather than year-to-year (Meehan 1999). The value of long-term monitoring of auklet populations can be enhanced by combining analysis of population trends with studies of reproductive success and feeding ecology, particularly if seabirds are to serve as indicators of the health of the Bering Sea ecosystem. Annual differences in reproductive performance of seabird colonies are closely tied to variation in prey availability; low availability of

prey can cause complete reproductive failure in some years (Ainley et al. 1996). Monitoring diet composition of planktivorous Least and Crested auklets and the relationship of prey species composition with nesting success is critical for interpreting the influence of food supply on annual variation in reproductive success. Due to the complete reliance of these auklet species on zooplankton, changes in diet composition may indicate a shift at lower trophic levels of the marine food web.

Bédard (1969a, 1969b) and Sealy (1968, 1973, 1975) conducted the first studies of breeding biology and foraging ecology of auklets on St. Lawrence Island. Searing (1977) investigated breeding success of cliff-nesting seabirds, collected limited samples of diets, and estimated auklet numbers. Studies of Least and Crested auklets have been infrequent since 1976, and no study has examined the interannual variation in breeding phenology, nesting success, and food habits of Least and Crested auklets on St. Lawrence Island. Monitoring of auklets on St. Lawrence Island is most likely to detect population changes and trends in reproductive success and food habits if annual visits are made to established plots and a standardized protocol is followed. Data generated can then be compared among years and monitoring sites throughout western Alaska to investigate changes in auklet ecology across their breeding range.

I investigated the breeding biology and diet of Least and Crested auklets nesting on St. Lawrence Island as part of an effort to develop methods to detect changes in their reproductive success, diet, and population size. I examined inter-annual and intra-seasonal variability in adult body mass and prey selection to better understand possible relationships between diet composition and reproductive success. By relating diet composition to reproductive parameters and adult body

composition, I tested the hypothesis that low adult mass is indicative of difficulty in finding preferred foods.

I also used two methods of population monitoring recommended in the literature (colony surface counts and mark-resighting on study plots) and compared their utility for detecting annual changes in breeding populations of Least and Crested auklets. Assessing the relationship between auklet breeding ecology and zooplankton availability may provide a method of monitoring changes in zooplankton communities throughout the summer in a region that is otherwise difficult to sample. Results of this study will contribute to development of protocols for monitoring annual variation in auklet colony attendance throughout the Bering Sea.

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CHAPTER 2

Inter-annual variation in diet, reproductive success, and body mass of plankton-feeding auklets on St. Lawrence Island, Alaska

Adrian E. Gall, Daniel D. Roby, and David B. Irons

ABSTRACT

We assessed the relationship of reproductive success to diet in Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) by measuring reproductive parameters, diet composition, and adult body mass at 2 colonies on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Average reproductive success was generally high (> 60%) for both auklet species during the 3 years of the study. Median hatching dates for both species were 2 weeks earlier in the year of highest reproductive success (2002), compared to the previous 2 years. In all 3 years, the diet of Least Auklets consisted primarily of calanoid copepods, while the diet of Crested Auklets was predominantly euphausiids, but the taxonomic composition of the diet differed among years for both species. Least and Crested auklets consumed more of the large, lipid-rich copepod *Neocalanus cristatus* in 2002 than in the other 2 years of the study. In 2001, the year of lowest reproductive success for both auklet species, the small, low-lipid copepod *Calanus marshallae* was most prevalent in the diet of Least Auklets and euphausiids were least prevalent in the diet of Crested Auklets late in chick-rearing. Average body mass of Least Auklets was lowest in 2001, after accounting for a gradual decline in body mass through the breeding season in all 3 years. Total body mass of Crested Auklets increased slightly through the breeding season in the year of highest reproductive success, whereas body mass declined through the breeding season in the other 2 years. These results suggest that adult body mass of both auklet species may reflect foraging conditions. In 2001, reproductive success of both auklet species was lower for nests monitored at the Kitnik colony, where nests were checked twice as frequently, suggesting that there may be an interaction between food availability and the negative effect of investigator disturbance on reproductive success. Monitoring

of reproductive success, adult body mass, and diet composition of plankton-feeding auklets on St. Lawrence Island may aid in understanding the effects of natural and anthropogenic climate change on auklet populations in the northern Bering Sea.

INTRODUCTION

Sea-ice cover, sea-surface temperatures, surface currents, and vertical mixing are all strongly influenced by climate (Hunt et al. 2002). Large changes in these indices of oceanic and atmospheric conditions that occur on decadal time scales or longer, known as regime shifts, cause significant alterations in the physical and biological characteristics of marine systems (Niebauer 1998, Hare and Mantua 2000). Marine trophic webs in the Bering Sea and northern Gulf of Alaska have recently experienced a regime shift similar in magnitude to the shift that occurred in the late 1970's (Miller and Schneider 2000, Macklin et al. 2002). These changes associated with the Pacific Decadal Oscillation (PDO) will likely have profound effects on secondary productivity of grazing zooplankton such as calanoid copepods and euphausiids. Copepods and euphausiids are the main food supply of a variety of planktivorous seabirds, particularly Least and Crested auklets (*Aethia pusilla* and *A. cristatella*).

Remote sensing techniques have been used to measure changes in climactic conditions as indexed by PDO (Miller and Schneider 2000), but they do not measure responses of upper trophic level organisms. It is necessary to understand the mechanisms by which climate and weather affect biological processes if we are to predict ecosystem responses to climate change (Hunt et al. 2002). Research cruises in the northern Bering Sea provide data on physical oceanography, zooplankton abundance and distribution, forage fish stocks, and seabird foraging ecology (Piatt et

al. 1990, Hunt et al. 1998), but their high cost makes it challenging to conduct these cruises annually. Seabird reproductive success, diets, and adult survival may be useful indicators of annual variation in local prey abundance, as well as changes in large-scale oceanographic conditions (Hatch and Hatch 1988, Bertram et al. 2000, Jones et al. 2002, Hedd et al. 2002). Data on nesting seabirds are less expensive to collect than ship-based monitoring programs and can be used to explore the relationship between predators and their marine environments (Cairns 1987).

St. Lawrence Island, located in the northern Bering Sea, is the nesting area for more than 10% of Alaska's estimated 36 million breeding seabirds (Stephensen et al. 1998). These seabird populations are sustained by forage fish and zooplankton found in the highly productive waters surrounding the island and, in particular, the northward flowing Anadyr Current to the west and northwest (Pavlov and Pavlov 1996). Least and Crested auklets are the most abundant planktivorous seabirds nesting on St. Lawrence Island and other islands throughout the Bering Sea (Jones 1993a, Jones 1993b). They nest primarily in talus slopes, where they lay a single egg in a natural crevice beneath the surface. Both Least and Crested auklets exhibit bi-parental care, sharing incubation and chick-rearing duties between the sexes.

The auklet colonies on St. Lawrence Island are some of the largest in Alaska (Jones 1993a, 1993b); about 4 million auklets nest in several colonies along the northern and western coasts of the island (V. Zubakin, pers. comm.). Despite the enormous size of auklet colonies on St. Lawrence Island and their key role in the food web of the northern Bering Sea (Springer and Roseneau 1985), there are no recent, multi-year studies of breeding biology and foraging ecology for monitoring changes in populations of planktivorous seabirds in the northern Bering Sea. Bédard (1969a, 1969b) and Sealy (1968, 1970, 1975) conducted the pioneering studies of breeding

biology and foraging ecology of auklets on St. Lawrence Island. Searing (1977) investigated breeding success of cliff-nesting seabirds, collected limited diet samples, and estimated auklet numbers at a few breeding colonies. Monitoring has been infrequent since 1976, but Piatt et al. (1988) obtained rough estimates of colony size and data on breeding phenology, nesting success, and diet of Least and Crested auklets during the 1987 breeding season.

Zooplankton life histories are reflected in the taxonomic composition of auklet prey throughout the breeding season. Copepods migrate to the epipelagic layer (0-100 m) in summer (July-August) to graze on phytoplankton, and the combined biomass of the largest species (*Neocalanus cristatus*, *N. plumchrus*, and *Eucalanus bungii*) can reach 90% or more of total zooplankton biomass (Coyle et al. 1996). Large herbivorous copepods such as *N. flemingeri* and *N. cristatus* are restricted to oceanic and outer shelf domains (Springer and Roseneau 1985), but strong turbulence through the Anadyr Strait provides a mechanism for physical transport of copepods to or near the surface around St. Lawrence Island (Coyle et al. 1996). Several studies have provided detailed analysis of auklet diet composition (Bédard 1969b, Piatt et al. 1988, Hunt and Harrison 1990, Obst et al. 1995), but there are still few data on seasonal or annual variation in auklet diets in the northern Bering Sea or showing how this variation is related to nesting success.

We studied breeding biology of Least and Crested auklets on St. Lawrence Island, Alaska during 2000-2002 to evaluate their utility as indicators of environmental change in the northern Bering Sea. Our objectives were to (1) assess annual variability in breeding phenology and reproductive success, (2) quantify inter- and intra-annual variation in taxonomic composition of prey and investigate the relationship between diet and reproductive success, (3) determine inter- and intra-

annual variation in adult body mass and evaluate how adult mass is related to nesting success, and (4) evaluate various methodologies for monitoring auklet reproductive success, adult body mass, and diet composition.

METHODS

Study Area

St. Lawrence Island (ca. 63° 30' N, 170° 30' W) is located approximately 200 km west of the Alaskan coast and about 60 km east of the Chukotsk Peninsula, Siberia. This study was conducted at 2 auklet breeding colonies on the north coast of St. Lawrence Island, east of the village of Savoonga (Figure 2.1). The Myaughee colony is located in a level area of boulders interspersed with vegetation ca. 17-20 km east of Savoonga, extending from the Mahok River valley about 3 km eastward to Cape Myaughee. The talus forms a band of nesting habitat 200-400 m wide along the top of 50 m-high coastal cliffs. The Kitnik colony was located west of the mouth of the Kitnik River, approximately 6-8 km east of the village of Savoonga. Auklets at this colony nest among boulders and talus that extend for ca. 1500 m along the coast. The talus and rocks slope upward from the shore/riverbed for 100 m and then level off, extending south for another 300 m. The colony is bounded on the east by the Kitnik River, on the west by sheer sea cliffs, and on the south by open wet sedge tundra. The Kitnik colony experiences more human activity than the Myaughee colony because it is about 10 km closer to Savoonga and located near the main trail that leads east from the village.

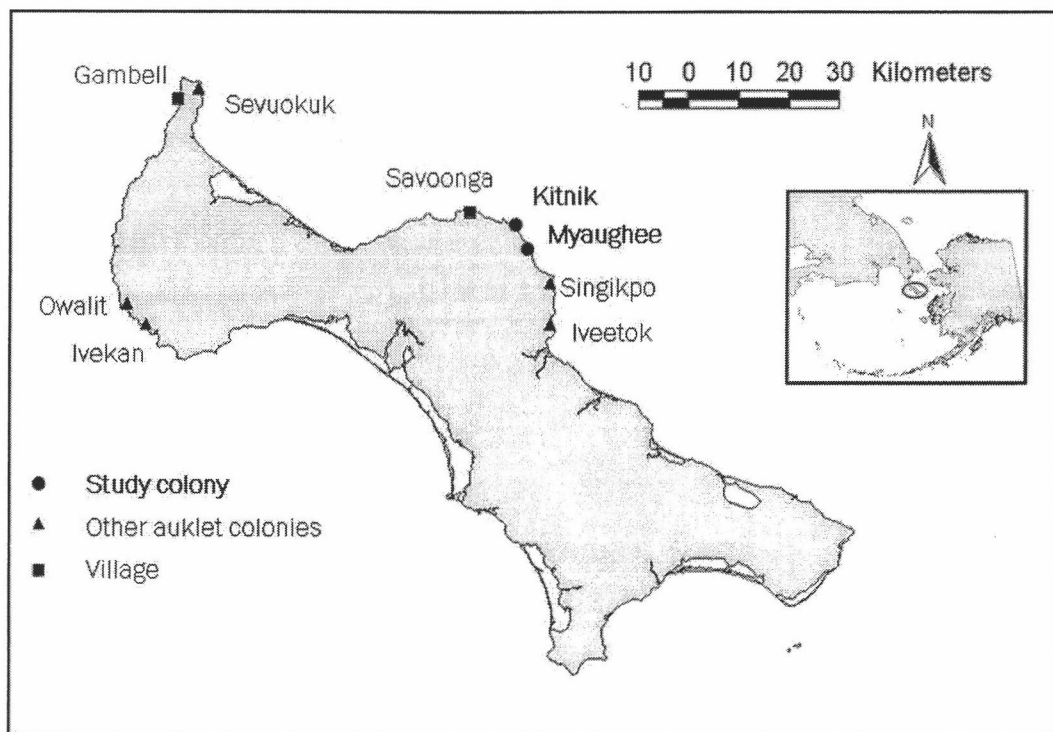


Figure 2.1. Map of St. Lawrence Island, Alaska, showing the location of the Kitnik and Myaughee study colonies.

Reproductive Success

Study plots within each colony were systematically selected to include a variety of talus sizes that provide nesting habitat for both Least and Crested auklets.

Crested Auklets are about 3 times larger than Least Auklets and nest in larger crevices (Bédard 1969a, Byrd et al. 1983, Piatt et al. 1990). Active nest crevices were located at each colony by searching talus and boulder fields using high-powered flashlights during the mid-incubation period. Searching for nests during mid-incubation reduces investigator disturbance during laying and early incubation, which can disrupt incubation activities and reduce hatching success (Piatt et al. 1990).

Crevices containing an adult that was confirmed to be incubating an egg were included in the sample of active nest sites. If we were unable to see the egg, then an adult observed in the same crevice on two consecutive visits was assumed to be incubating an egg. Unattended eggs were touched, if possible, to determine if they were warm and thus being incubated. Cold eggs were monitored, but if no adult was seen attending the egg, it was discarded from the sample, as it might have been from the previous breeding season (Williams et al. 2000).

Nests at the Kitnik colony were checked once every 4 days until 1 week before the expected median hatch date, based on dates provided by previous studies on St. Lawrence Island (Bédard 1969a, Sealy 1975, Piatt et al. 1990). We increased nest check frequency to every other day during the hatching period (approximately 20 July – 15 August) to determine hatching dates more precisely. These dates were used to extrapolate laying dates and expected fledging dates, using the average duration of incubation and nestling periods, respectively, from previous studies (Bédard 1969a, Sealy 1975, Piatt et al. 1990).

After chicks hatched, nests at the Kitnik colony were checked once every 4 days throughout the chick-rearing period to record status. Chicks were recorded as present if they were seen, heard in the crevice, or there was fresh excreta or chick dander (shed down and feather sheaths) in the crevice. When chicks were 22 days old, we increased nest check frequency to every other day to determine fledging date more precisely. Data from nests at the Kitnik colony were used to determine nesting chronology and productivity, and to investigate the frequency of data collection necessary to detect significant change in these parameters. In 2001 and 2002, nests at the Myaughee colony were checked less frequently (once every 8 days) throughout the breeding season to test the hypothesis that the frequency of nest checks affects nesting success.

Breeding success was calculated using the Mayfield (Mayfield 1961, 1975) method because nests were found after the start of incubation and fates of nests could be difficult to determine. This method reduced bias in measuring nesting success by accounting for unsuccessful nests that were less likely to be detected and monitored than successful nests (Johnson and Shaffer 1990). We used chi-squared tests of independence to examine differences in nesting success between species and among years. We re-analyzed the data from nests at the Kitnik colony using data collected every 8 days to test the hypothesis that less frequent nest checks can produce accurate estimates of nesting success.

Diet Composition

Breeding adult auklets carry food in their sublingual throat pouch to provision their chicks until fully grown, and readily regurgitate the food load when captured. Diet samples were collected approximately every 3 days during the chick-rearing

period from late July until late August by capturing adults alive. Adults were captured either by using noose mat traps on display rocks, or by setting up mist nets on the colony. Auklets were trapped on 10 days in 2000, 9 days in 2001, and 15 days in 2002. Contents of the sublingual pouch of each adult were collected in separate plastic bags. In 2000 and 2001, chick meal samples were weighed on an Ohaus scale (± 0.01 g) and preserved by freezing as soon as possible after collection. In 2002, chick meal samples were weighed using Pesola spring scales (± 0.5 g) in the field and preserved in 70% isopropyl alcohol immediately after collection to minimize breakdown of prey items. We weighed all auklets captured for diet composition analysis on Pesola spring scales (± 0.5 g), and measured the flattened wing length (± 1.0 mm) using a flat ruler. We measured tarsus length (± 0.1 mm), culmen length (± 0.1 mm), and bill depth (± 0.1 mm) using calipers. Auklets were released after collection of their chick meal.

Prey items in preserved chick meals were counted and identified to the lowest possible taxonomic group by Kathy Turco (Alaska Spirit Speaks: Sound and Science, Fairbanks, Alaska) with verification from Ken Coyle (Institute of Marine Science, University of Alaska, Fairbanks). Each prey type was further sorted by size (Table 2.1). In cases where individuals could not be identified to species, they were placed in a non-specific genus category. *Thysanoessa raschii* was the only species of euphausiid positively identified in our samples. In some samples, euphausiids could not be sorted by size because they were broken or had parts missing. Broken specimens were assigned to either the *Thysanoessa* spp. prey type or the Euphausiid spp. prey type based on how reliably the remaining parts could be identified.

Table 2.1 Prey types used to sort Least and Crested auklet diet samples collected during the 2000-2002 breeding seasons on St. Lawrence Island, Alaska.

Prey type	Size	Mass ^a
<i>Parathemisto libellula</i>	>12mm	167.0
<i>Parathemisto libellula</i>	<7mm	32.3
<i>Parathemisto</i> spp.	<4mm	3.9
<i>Parathemisto pacifica</i>	<4mm	3.7
<i>Thysanoessa raschii</i>	>12mm	97.9
<i>Thysanoessa raschii</i>	<7mm	30.5
<i>Thysanoessa</i> spp.	>10mm	79.0
Euphausiid spp.	<7mm	22.7
Larval shrimp	<7mm	12.0
<i>Neocalanus cristatus</i>		17.6
<i>Neocalanus flemingeri</i> ^b		3.8
<i>Calanus marshallae</i>		1.8
Copepod spp.		^c
<i>Diastylis bidentata</i>		5.4
<i>Calliopius laevisculus</i>		2.2
<i>Ansiogammarus pugetensis</i>		2.2
<i>Ischyrocerus</i> spp.		2.2
<i>Pontegenia</i> spp.		2.2
<i>Erichthonius hunteri</i>		2.2
Pandalid (shrimp)	>12mm	48.7
Crangonid megalopa (crab)		15.0
Brachyuran zoea (crab)		1.0
Pagurid (larval hermit crab)		1.0
Crangonidae (crab)		5.0
Larval fish	20-30mm	475.0
Pteropod		1.0

^a Mass values represent average mass (mg) of each prey type determined from preserved samples collected from the Bering Sea during 1997-1999 (K. Coyle, Institute of Marine Science, University of Alaska, Fairbanks, unpubl. data).

^b May include *N. plumchrus*, which were not distinguished from *N. flemingeri* in this study.

^c Average mass for this prey type was calculated for each sample proportional to the number of prey items identified as *N. flemingeri* and *C. marshallae* and using the average per item mass for these two prey types.

Calanoid copepods in diet samples belonged to one of two genera: *Neocalanus* or *Calanus*. *N. flemingeri* and *N. plumchrus* are considered two distinct species (Miller 1993), but they are very similar and difficult to distinguish in auklet diet samples. *N. flemingeri* is more common in waters around St. Lawrence Island (K. Coyle, pers. comm.), so we assumed that copepods identified as either *N. flemingeri* or *plumchrus* were *N. flemingeri*. The Copepod spp. prey type included small copepods that could not be identified to species, but were *N. flemingeri*, *N. plumchrus*, or *C. marshallae*. *N. cristatus* individuals were twice the size of the other copepod species, and easily distinguished from the species in the Copepod spp. prey type (K. Turco, pers. comm.). Most of the amphipods in auklet diet samples were identified as *Parathemisto libellula*. Amphipods that could not be positively identified to species were small, similar in size, and placed in the prey type *Parathemisto* spp.

We used the average mass of each prey type from preserved samples collected from the Bering Sea during 1997-1999 (K. Coyle, Institute of Marine Science, unpubl. data) to convert number of items of each prey type to biomass estimates (Table 2.1). The proportion of biomass in the Copepod spp. prey type that was attributable to *N. flemingeri* and *C. marshallae* was calculated for each meal based on the proportions of *N. flemingeri* and *C. marshallae* present in the portion of the sample that could be identified to species. Aggregate percentage of prey biomass (APB) represented by each prey type was calculated to give equal weight to all chick meal samples (Swanson et al. 1974):

$$APB = \sum_{i=1}^N p_i / N * 100$$

where p_i is the biomass proportion of the prey type in the i^{th} sample and N is the total number of samples.

We grouped prey types into the following categories for comparison within and among years: Gammarid amphipods (primarily *Parathemisto libellula*), Euphausiids (primarily *Thysanoessa raschii*), *Neocalanus cristatus*, *N. flemingeri*, *Calanus marshallae*, and other prey (including larval shrimp, fish, crabs, and clams). APB was logit transformed for analysis to normalize the distribution of proportions (Ramsey and Schafer 2002: 541). In order to detect seasonal trends in diet composition within a breeding season, we divided the chick-rearing period into three 8-day periods: early, mid-, and late chick-rearing. We used ANOVAs with Tukey-Kramer procedures for multiple comparisons of means to compare diet composition among years and among stages of chick-rearing within year (Ramsey and Schafer 2002: 161). We established $P = 0.05$ *a priori* as our level of significance for statistical tests

Body Mass of Breeding Adults

Adult auklets were captured throughout the breeding season using noose mat traps on large display rocks. Individuals were weighed and measured (culmen length, bill depth, flattened wing length, and tarsus length), following the methods described above. To establish body size indices (BSI), we performed a principle components analysis (PROC PRINCOMP, SAS Institute 1999) on flattened wing length, tarsus length, culmen length, and bill depth of Crested Auklet adults and flattened wing length, tarsus length, and culmen length of Least Auklets. The principle components analysis generated weighting coefficients that described positive covariance among the linear measurements. These coefficients had consistent loadings across measurements and the first principle component (PC1) accounted for 37-41% of the variance in the original measures. Next, measurements were multiplied by the coefficients of PC1 and summed to produce a PCA factor

score, or body size index (BSI). We evaluated the effects of year and Julian date on adult body mass directly using ANCOVA models. The fit of the global model for each species was assessed using a likelihood ratio test (Burnham and Anderson 2002). We developed a suite of 6 models (Appendix), including a null model and a global model, and conducted separate analyses for Least Auklets and Crested Auklets. We included the PC1-derived BSI in all models for Least Auklets as a covariate to account for differences in body size. For Crested Auklets, we examined the effect of sex by replacing BSI with an indicator for sex in the best model selected to assess whether it would improve the fit of the model. We did not include sex and body size in the same model because they are correlated.

Candidate models in each set were ranked by their fit to the data using Akaike's Information Criterion corrected for small sample sizes (AIC_c), which utilizes the likelihood of each model to select the best approximating model, given the data:

$$AIC_c = -2\ln(L) + 2k + \frac{2k(k+1)}{n-k-1}$$

where L is the likelihood of a model under consideration, k is the number of parameters in the model, and n is the sample size (Burnham and Anderson 2002). AIC_c allows comparison of competing models that are fit to a common data set, but are not nested subsets. Models were weighted based on the difference between each model's AIC_c value and that of the lowest ranked model, and the weights were normalized to sum to 1 over all models considered (Burnham and Anderson 2002). Model weights were interpreted as the probability a given model was the best approximation to the relationship between body mass and year, date, species, and body size. The model with the lowest AIC_c value was selected as the best approximating model given the data, and models within 2 AIC_c units of the top-ranked

model were considered the set of competing models (Burnham and Anderson 2002). Means are reported as ± 1 SE unless otherwise stated. All methods and procedures involving live auklets followed a protocol approved by the Institutional Animal Care and Use Committee (IACUC) at Oregon State University.

RESULTS

Nesting Chronology and Success

Median hatch dates for Least Auklets were similar in 2000 and 2001 at both the Kitnik and Myaughee colonies (Table 2.2). The median hatch dates for Least Auklets at both colonies in 2002 were 6-10 days earlier compared to the previous 2 years. Median hatch dates for Crested Auklets were similar to those of Least Auklets, and exhibited the same among-year pattern. There was no difference in median hatch dates of Crested Auklets between 2000 and 2001 at either colony (Table 2.2), but median hatch dates were 7-15 days earlier in 2002 than in the previous two years.

Average reproductive success was generally high ($> 60\%$ of monitored nests fledged young) for both auklet species during the 3-year study. Reproductive success of Least Auklets was higher than that of Crested Auklets at both colonies in most years, primarily because of higher hatching success (Tables 2.3 and 2.4). Least Auklet reproductive success was higher at the Kitnik colony in 2002 compared to 2000 and 2001 ($X^2 = 44.0$, $df = 2$, $P < 0.01$), primarily because of higher nestling survival ($P < 0.01$, Table 2.3). The reproductive success of Least Auklets nesting at the Myaughee colony was also higher in 2002, but this difference was not significant ($X^2 = 2.07$, $P = 0.35$). As with Least Auklets, average reproductive success of

Table 2.2. Nesting chronology of Least and Crested auklets at the Kitnik and Myaughee colonies on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Values in parentheses are the number of nest sites used to calculate averages.

	KITNIK			MYAUGHEE		
	2000	2001	2002	2000	2001	2002
<u>Least Auklets</u>						
Median laying date ^a	30 June (30)	29 June (41)	23 June (62)	30 June (33)	3 July (37)	23 June (27)
Median hatching date	2 Aug (30)	29 July (41)	23 July (62)	2 Aug (33)	2 Aug (37)	23 July (27)
Median fledging date ^b	n/a	29 Aug (23)	21 Aug (55)	n/a	26 Aug (31)	16 Aug (24)
Chick-rearing period ^c	n/a	29.3 ± 0.74	27.5 ± 0.39	n/a	27.3 ± 0.76	26.8 ± 0.74
<u>Crested Auklets</u>						
Median laying date ^a	30 June (25)	27 June (31)	20 June (55)	4 July (42)	29 June (44)	20 June (37)
Median hatching date	6 Aug (25)	30 July (31)	23 July (55)	7 Aug (42)	2 Aug (44)	23 July (37)
Median fledging date ^b	n/a	29 Aug (24)	30 Aug (51)	n/a	2 Sept (36)	28 Aug (36)
Chick-rearing period ^c	n/a	31.8 ± 0.74	32.1 ± 0.35	n/a	31.0 ± 0.41	31.2 ± 0.60

^a median laying date calculated using Piatt et al.'s (1990) mean incubation period of 33.8 days for Crested Auklets and 30.1 days for Least Auklets

^b chicks present at last nest check assumed to fledge (Piatt et al. 1990)

^c mean number of days from hatching to fledging ± 1 SE.

Table 2.3. Reproductive success of Least Auklets at 2 breeding colonies on the north shore of St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Data used to calculate results for 8-day intervals at the Kitnik colony are a subset of the data collected at 4-day intervals.

	KITNIK (4-day interval)			KITNIK (8-day interval)			MYAUGHEE		
	2000	2001	2002	2000	2001	2002	2000	2001	2002
# eggs	30	63	62	30	63	62	33	41	27
# chicks hatched	29	41	60	26	38	59	28	37	26
# chicks fledged ^a	23	23	55	19	20	58	26	31	24
Egg Daily Survival Rate ^b	0.9985	0.9819	0.9980	0.9934	0.9784	0.9952	0.9924	0.9952	0.9950
Mayfield hatching success ^c	0.96	0.58	0.95	0.82	0.52	0.87	0.77	0.86	0.87
Chick Daily Survival Rate ^d	0.9897	0.9791	0.997	0.9883	0.9822	0.9994	0.9964	0.9943	1.000
Mayfield fledging success ^e	0.74	0.54	0.93	0.71	0.59	0.98	0.89	0.85	0.986
Mayfield reproductive success ^f	0.71	0.31	0.88	0.58	0.31	0.85	0.69	0.73	0.85

^a chicks present at last nest check assumed to fledge (Piatt et al. 1990)

^b 1 - (# eggs lost/# egg days)

^c (Egg DSR)³⁰, mean incubation period (Piatt et al. 1990)

^d 1 - (# chicks lost/# chick days)

^e (Chick DSR)²⁹, mean chick-rearing period (Piatt et al. 1990)

^f (Mayfield hatching success)*(Mayfield fledging success)

Table 2.4. Reproductive success of Crested Auklets at 2 breeding colonies on the north shore of St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Data used to calculate results for 8-day intervals at the Kitnik colony are a subset of the data collected at 4-day intervals.

	KITNIK (4-day interval)			KITNIK (8-day interval)			MYAUGHEE		
	2000	2001	2002	2000	2001	2002	2000	2001	2002
# eggs	33	49	65	33	49	65	54	50	40
# chicks hatched	25	31	55	25	27	55	42	44	37
# chicks fledged ^a	23	24	51	22	21	52	38	36	36
Egg Daily Survival Rate ^b	0.9906	0.9818	0.9930	0.9900	0.9789	0.9933	0.9904	0.9917	0.9930
Mayfield hatching success ^c	0.73	0.53	0.78	0.71	0.48	0.80	0.72	0.75	0.79
Chick Daily Survival Rate ^d	0.9957	0.9916	0.999	0.9940	0.9911	0.9983	0.9942	0.9974	0.999
Mayfield fledging success ^e	0.87	0.76	0.97	0.85	0.75	0.95	0.83	0.92	0.97
Mayfield reproductive success ^f	0.63	0.40	0.76	0.60	0.36	0.75	0.60	0.69	0.76

^a chicks present at last nest check assumed to fledge (Piatt et al. 1990)

^b $1 - (\# \text{ eggs lost} / \# \text{ egg days})$

^c (Egg DSR)³⁴, mean incubation period (Piatt et al. 1990)

^d $1 - (\# \text{ chicks lost} / \# \text{ chick days})$

^e (Chick DSR)³³, mean chick-rearing period (Piatt et al. 1990)

^f (Mayfield hatching success)*(Mayfield fledging success)

Crested Auklets was higher in 2002 than in 2000 or 2001 at the Kitnik colony ($X^2 = 14.17$, $P < 0.001$, Table 2.4).

There were no significant differences in reproductive success between the Kitnik and Myaughee colonies for either auklet species in 2000 or 2002 (Crested Auklets: $X^2 = 4.72$, $P = 0.19$; Least Auklets: $X^2 = 7.52$, $P = 0.06$). Average reproductive success was different, however, between the Kitnik and Myaughee colonies for both species in 2001; nesting success was much lower at Kitnik than at Myaughee, the lowest recorded for either species during the 3-year study. For Least Auklets in 2001, hatching success was 28 percentage points lower (95% CI: 10 – 46 percentage points) and fledging success was 31 percentage points lower (95% CI: 12 – 50 percentage points) at Kitnik than at Myaughee. For Crested Auklets in 2001, hatching success was 22 percentage points lower (95% CI: 4 – 40 percentage points) and fledging success was 16 percentage points lower (95% CI: -1 – 33 percentage points) at Kitnik than at Myaughee.

For Least Auklets, estimates of hatching success were 9.3 percentage points lower (95% CI: 4.6 – 14.0 percentage points) from nest observations collected at 8-day intervals rather than estimates using all the available data (4-day intervals). Estimates of fledging success were 5 percentage points higher, however, in both 2001 and 2002 from data collected at 8-day intervals (Table 2.3). For Crested Auklets, estimates of hatching, fledging, and overall reproductive success at the Kitnik colony were 2.4 percentage points lower (95% CI: 0.9 – 4.0 percentage points) from nest observations collected at 8-day intervals rather than estimates using all the available data (4-day intervals; Table 2.4). Differences between 4-day interval estimates of overall reproductive success and 8-day interval estimates were not significant for either species ($P > 0.1$ for all comparisons).

Diet Composition

Least Auklet diets consisted mostly of calanoid copepods, based on aggregate percent biomass (APB), in each year of the study (Table 2.5). The oceanic copepod *Neocalanus flemingeri* was the single most prevalent prey type in all three years of the study (38 – 62% APB), but the relative proportions of this and other prey categories differed among years (Figure 2.2). Amphipods comprised 28.5% of Least Auklet diets in 2000, but only 4.5% in 2001 and 2.0% in 2002 (Table 2.5). In 2001, there were more euphausiids ($F_{2,190} = 6.31$, $P = 0.002$) and the small, neritic copepod *Calanus marshallae* ($F_{2,190} = 13.52$, $P < 0.001$) in the diet than in 2000, whereas in 2002, there were more of the oceanic copepods *N. cristatus* ($F_{2,190} = 5.72$, $P = 0.002$) and *N. flemingeri* ($F_{2,190} = 15.12$, $P < 0.001$) than in the previous two years. Perhaps most striking was the complete absence of *C. marshallae* in Least Auklet chick diets collected in 2002, despite the very high prevalence of calanoid copepods in the diet that year (Table 2.5). The prevalence of miscellaneous larval prey types was collectively lower in 2002 than in the other two years.

In addition to large differences in taxonomic composition among years, Least Auklet diets varied with stage of the chick-rearing period (Figure 2.3). In 2000, there was a seasonal increase in the prevalence of amphipods in the diet ($F_{1,74} = 10.94$, $P = 0.001$). In 2001, there was a seasonal increase in the prevalence of both of the small copepods *N. flemingeri* ($F_{2,67} = 4.38$, $P = 0.016$) and *C. marshallae* ($F_{2,68} = 4.05$, $P = 0.022$).

Table 2.5. Taxonomic composition of the meals delivered to Least Auklet nestlings during the 2000 – 2002 breeding seasons on St. Lawrence Island, Alaska. Data are expressed as aggregate percent biomass and 95% confidence intervals are in parentheses.

Prey Category	2000 (n = 77)	2001 (n = 71)	2002 (n = 45)
Amphipods ^a	28.5 (± 5.9)	4.5 (± 2.7)	1.9 (± 1.6)
Euphausiids ^b	1.5 (± 1.8)	13.3 (± 5.2)	5.9 (± 4.3)
Calanoid copepods ^c	55.3 (± 5.5)	65.4 (± 7.5)	83.2 (± 5.2)
<i>Neocalanus cristatus</i>	9.8 (± 4.1)	7.9 (± 2.6)	21.3 (± 9.1)
<i>Neocalanus flemingeri</i> ^d	41.0 (± 5.5)	37.6 (± 6.9)	61.8 (± 8.9)
<i>Calanus marshallae</i>	4.5 (± 2.8)	20.1 (± 6.1)	0.0
Other prey types ^e	14.7 (± 3.8)	16.7 (± 5.3)	8.8 (± 3.4)

^a primarily *Parathemisto libellula*

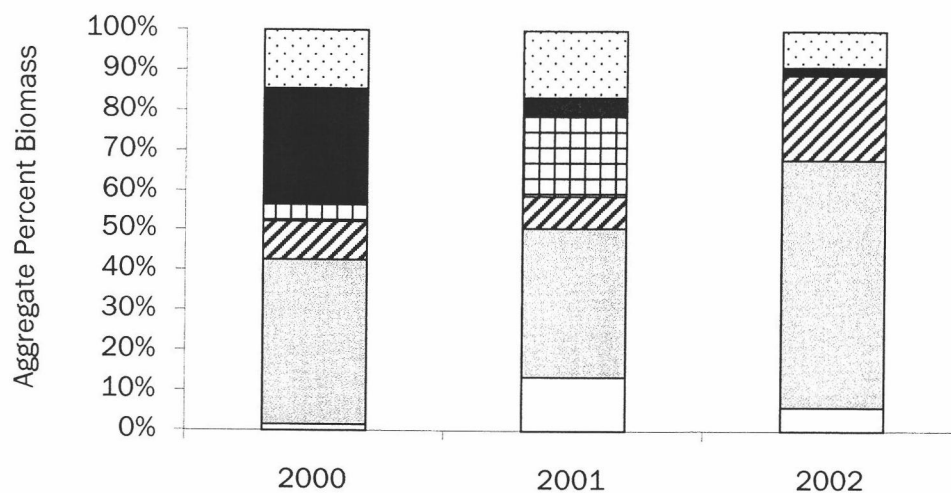
^b primarily *Thysanoessa raschii*

^c includes *Neocalanus cristatus*, *N. flemingeri*, *Calanus marshallae*, and Copepod spp. prey types.

^d may also include *N. plumchrus*

^e includes *Diastylis bidentata*, *Calliopus laevisculus*, *Ansiogammarus pugetensis*, *Ischyrocerus* spp., *Pontegenia* spp., *Ericthonius hunteri*, pandalid shrimp, crangonid megalopa, brachyuran zoea, pagurid crab, crangonid crab, larval fish, and pteropods

A. Least Auklets



B. Crested Auklets

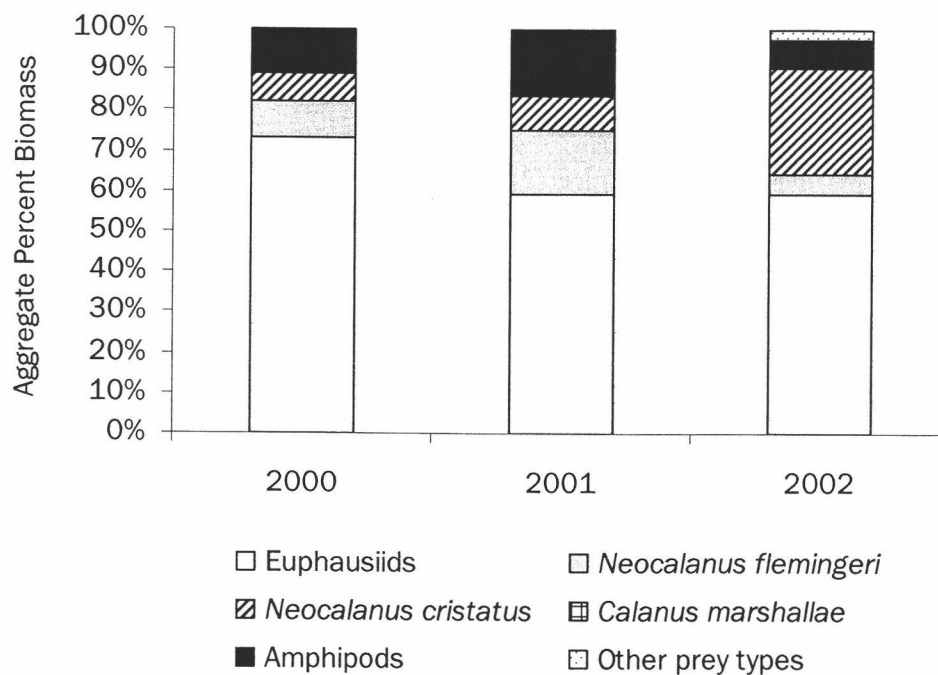
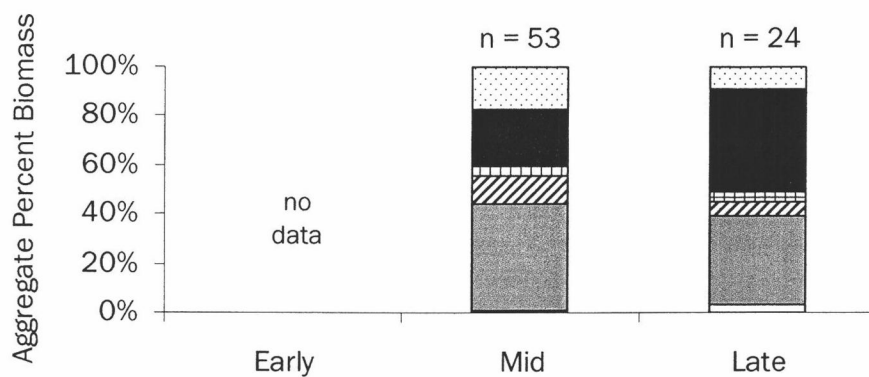
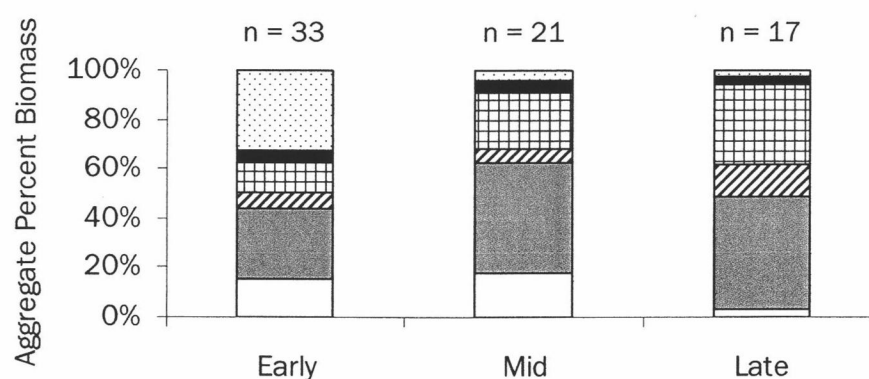


Figure 2.2. Taxonomic composition by biomass of diets fed to Least and Crested auklet chicks on St. Lawrence Island, Alaska from late July through August during the 2000-2002 breeding seasons.

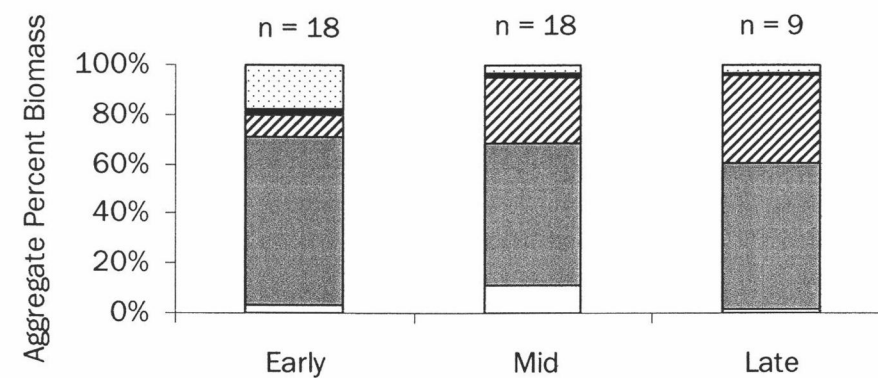
A. 2000



B. 2001



C. 2002



■ Amphipods □ Euphausiids ▨ *Neocalanus cristatus*
 ■ *Neocalanus flemingeri* ▩ *Calanus marshallae* ▤ Other

Figure 2.3. Seasonal changes in the taxonomic composition by biomass of diets fed to Least Auklet chicks on St. Lawrence Island, Alaska from late July through August during the 2000-2002 breeding seasons. The chick-rearing period was divided into three 8-day periods starting on the day the first chick hatched.

In 2002, there was a seasonal increase in the prevalence of the large copepod *N. cristatus* and a decline in the prevalence of *N. flemingeri*, but this trend was not significant ($F_{2,42} = 2.24$, $P = 0.12$). In all three years, prey types in the "Other" category were more prevalent in the diet during early chick-rearing than during mid or late chick-rearing (2000: $F_{1,74} = 8.29$, $P = 0.005$; 2001: $F_{2,68} = 14.23$, $P < 0.001$; 2002: $F_{2,42} = 10.89$, $P < 0.001$).

Crested Auklet diets consisted mostly of euphausiids (primarily *Thysanoessa raschii*) in all three years of the study, contributing 59-74% APB (Table 2.6, Figure 2.2). The relative importance of euphausiids did not differ significantly among the three years of the study ($F_{2,112} = 1.85$, $P = 0.16$). Copepods were the next most prevalent prey category in the diet of Crested Auklets (Table 2.6). While the prevalence of copepods in Crested Auklet diets did not differ significantly among years ($P = 0.16$), the species composition of the copepod portion of the diet did differ among years. *N. cristatus* was more prevalent in the diet in 2002 than in 2000 or 2001 ($P < 0.001$), the same pattern as in Least Auklet diets. In contrast, the smaller copepod *N. flemingeri* was more prevalent in 2001 than in 2002 ($P < 0.001$) or 2000, although the difference between 2001 and 2000 was not statistically significant ($P = 0.08$). In 2000, a year of proportionally less calanoid copepods in the diet, the small neritic copepod *C. marshallae* was more prevalent than in the two subsequent years ($P < 0.001$).

The proportion of euphausiids in Crested Auklet diets did not vary significantly with stage of the chick-rearing period (Figure 2.4). Although amphipods were not significantly more prevalent in the diet in 2001 ($P = 0.28$), there was a significant increase in prevalence of amphipods in the diet late in chick-rearing during 2001 ($F_{2,36} = 7.23$, $P = 0.002$). Other prey types identified in the diet of Crested Auklets

were pandalid shrimp, larval shrimp, *Calliopus laevisculus*, pagurid crabs, and larval fish but collectively these other prey types accounted for less than 3% of the diet by APB. We found no differences between the sexes in taxonomic composition of Crested Auklet chick meals in any year of the study ($P > 0.1$ for all years), suggesting no gender differences in diet composition.

Table 2.6. Taxonomic composition of the meals delivered to Crested Auklet nestlings during the 2000 – 2002 breeding seasons on St. Lawrence Island, Alaska. Data are expressed as aggregate percent biomass and 95% confidence intervals are in parentheses.

Prey Category	2000 (n=29)	2001 (n=42)	2002 (n=44)
Amphipods ^a	9.9 (± 8.7)	16.2 (± 8.6)	7.2 (± 6.0)
Euphausiids ^b	73.5 (± 11.9)	59.5 (± 11.9)	59.4 (± 12.0)
Calanoid copepods ^c	15.9 (± 5.8)	24.1 (± 9.5)	31.0 (± 9.7)
<i>Neocalanus cristatus</i>	7.0 (± 2.7)	8.2 (± 4.5)	26.3 (± 9.4)
<i>Neocalanus flemingeri</i> ^d	8.6 (± 4.6)	16.0 (± 7.0)	4.7 (± 3.8)
<i>Calanus marshallae</i>	0.2 (± 0.2)	0.0	0.0
Other prey types ^e	0.7 (± 1.3)	0.2 (± 0.2)	2.4 (± 1.9)

^a primarily *Parathemisto libellula*

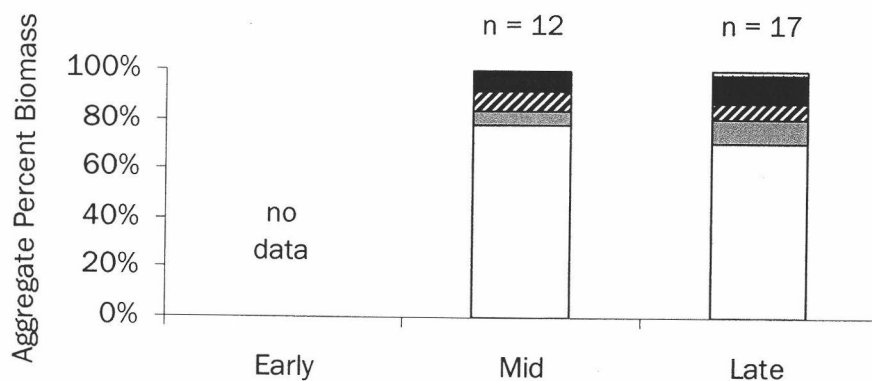
^b primarily *Thysanoessa raschii*

^c includes *Neocalanus cristatus*, *N. flemingeri*, *Calanus marshallae*, and Copepod spp. prey types

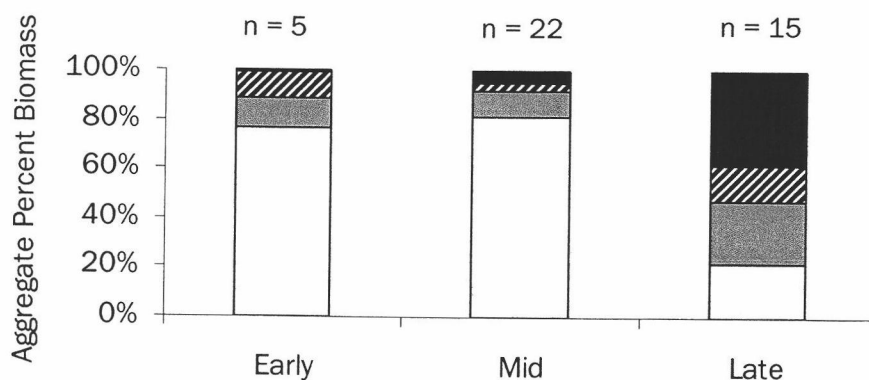
^d may also include *N. plumchrus*

^e includes *Diastylis bidentata*, *Calliopus laevisculus*, *Ansiogammarus pugetensis*, pandalid shrimp, and larval fish

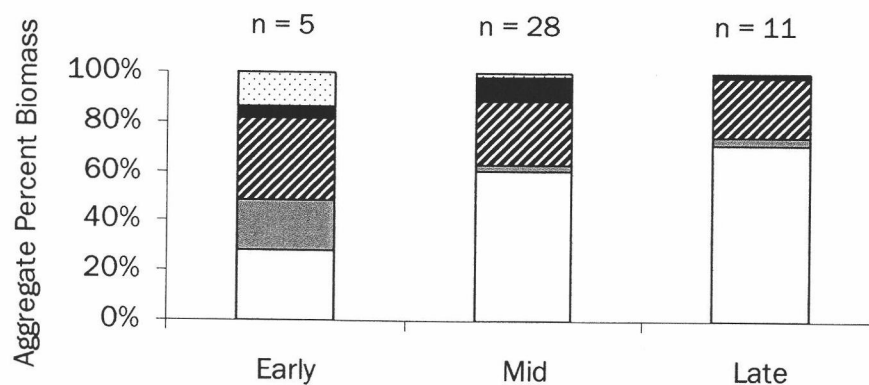
A. 2000



B. 2001



C. 2002



□ Euphausiids ■ *Neocalanus flemingeri* ▨ *Neocalanus cristatus*
 ▩ *Calanus marshallae* ■ Amphipods □ Other

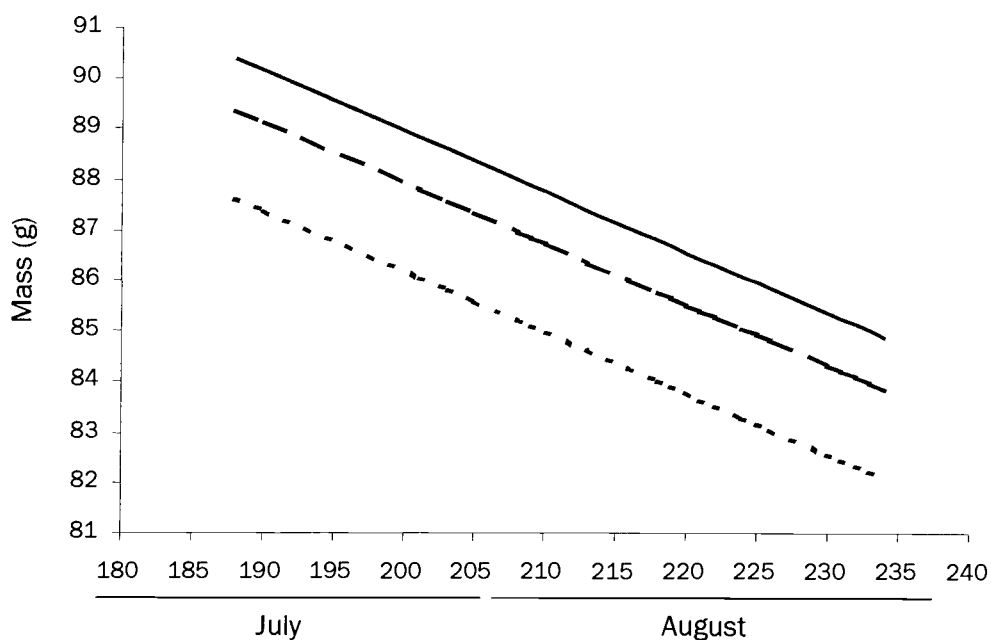
Figure 2.4 Seasonal changes in the taxonomic composition by biomass of diets fed to Crested Auklet chicks on St. Lawrence Island, Alaska from late July through August during the 2000-2002 breeding seasons. The chick-rearing period was divided into three 8-day periods starting on the day the first chick hatched.

Body Mass of Breeding Adults

Total body mass of adult Least Auklets differed among years and declined during the breeding season in all three years of the study, after accounting for differences in body size (Figure 2.5). Average body mass of Least Auklets was lower in 2001 (85.4 ± 0.5 g) than in 2000 (88.6 ± 0.8 g) or in 2002 (89.1 ± 0.4 g). The model that included effects of year, date, and body size on adult body mass was 3.2 times more likely than the global model to be the best approximating model given the data, providing strong evidence of annual and seasonal differences in body condition (Table 2.7). The confidence interval for the estimate of the interaction between year and Julian date overlapped zero, providing little evidence of a difference in trend of loss in body mass among years. Least Auklets are sexually monomorphic, so we were not able to test for differences between the sexes.

Average size-adjusted body mass of Crested Auklets declined through the breeding season in both 2000 and 2001, but showed a slight increase during the breeding season in 2002 (Figure 2.5). Year had a strong effect on total body mass of Crested Auklets (Table 2.7). The only model selected for explaining the variation in body mass of Crested Auklets included interactions between year and Julian date, indicating the different seasonal trend in body mass among breeding seasons. The top model that included sex was not a competitive model ($\Delta AIC_c = 42.82$), suggesting that the seasonal changes in body mass were similar for males and females.

A. Least Auklets



B. Crested Auklets

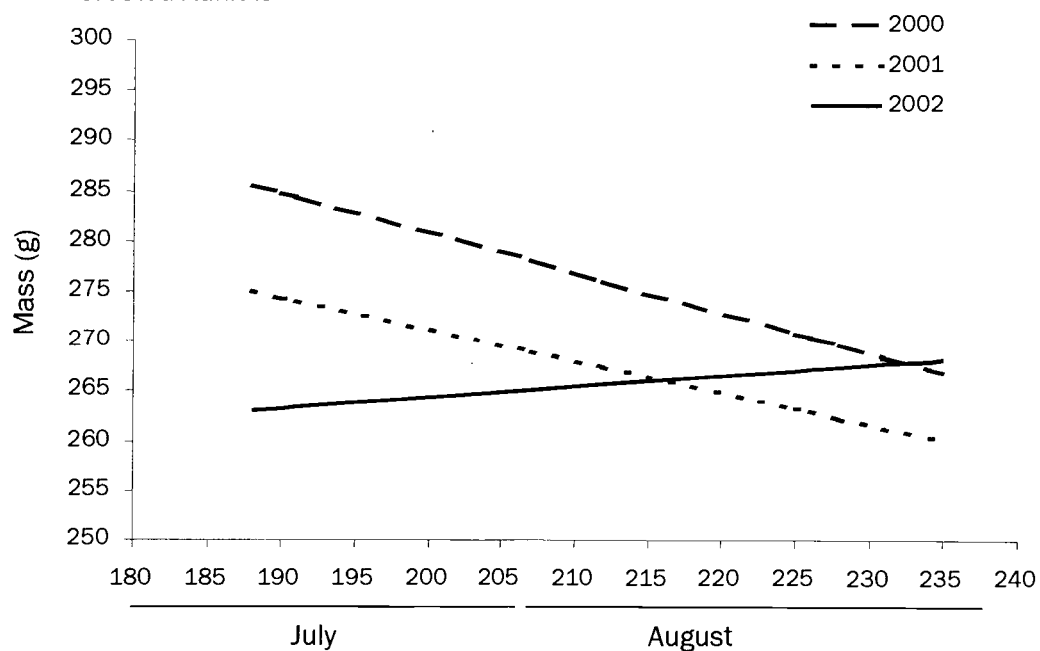


Figure 2.5. Predicted total body masses for (A) Least Auklets and (B) Crested Auklets during the 2000-2002 breeding seasons on St. Lawrence Island, Alaska. Mass was calculated using the multiple regression equation from the best model for mass, given the data (see Table 2.7).

Table 2.7. Models explaining variation in total body mass of Least and Crested auklets on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Model selection results are presented in subsets by species. Competing models ($\Delta AIC_c < 2.0$) are presented in bold type.

Species	Model ^a	Parameters	AIC _c	ΔAIC_c	AIC _c Weight	R ²
Least Auklets	Y + J + B	4	3576.64	0.00	0.76	0.24
	Y + J + B + Y*J	6	3579.00	2.36	0.24	0.24
	J + B	2	3594.46	17.82	0.00	0.21
	Y + B	3	3628.23	51.59	0.00	0.16
	B	1	3656.61	79.97	0.00	0.11
	null	0	3718.78	142.14	0.00	--
Crested Auklets	Y + J + B + Y*J	6	2558.84	0.00	0.998	0.32
	Y + J + B	4	2572.35	13.51	0.001	0.28
	Y + B	3	2573.77	14.94	0.00	0.27
	J + B	2	2584.83	25.99	0.00	0.24
	B	1	2585.66	26.82	0.00	0.23
	Y + J + S + Y*J	6	2601.65	42.82	0.00	0.21
	null	0	2661.31	102.47	0.00	--

^a Y = Year, J = Julian date, B = Body size (PC1), S = Sex

DISCUSSION

Nesting Chronology and Success

There was close synchrony in nesting chronology between the Kitnik and Myaughee colonies for both auklet species, with no significant differences between colonies in hatching or fledging dates in any of the three years of the study. Both Least and Crested auklets were highly synchronous nesters, with most nests hatching within a 10-day period and fledging within an 8-day period in each year of the study. Median hatch dates were 8 days earlier for both species in 2002, however, and this was the year of highest reproductive success for both species at both colonies. The early initiation of nesting in 2002 was similar to that observed at Sevuokuk Mountain, St. Lawrence Island in 1967, a year of early snow melt (Sealy 1975). Less snow was present on the Kitnik colony on our first visit in 2002 compared to either 2000 or 2001, supporting Sealy's (1975) hypothesis that snow cover is a major proximate factor influencing timing of egg-laying in auklets.

Fraser et al. (1999) suggested that a relationship exists between nesting success and the timing of breeding. Nesting chronology of Crested Auklets varied among the 8 years of their study in the western Aleutian Islands, at the southern limit of the breeding range of Least and Crested auklets. Years of earlier median hatching dates, which varied by 9 days among years, were associated with higher reproductive success (Fraser et al. 1999). In our study, we also observed that early median hatching dates for both Least and Crested auklets (23 July) in 2002 were associated with higher nesting success.

Previous studies and our data indicate that the magnitude of annual variation in nesting chronology on St. Lawrence Island has been similar to that in the Aleutian

Islands (Piatt et al. 1990), but auklets in the northern Bering Sea typically nest one month later than auklets in the Aleutian Islands. St. Lawrence Island is located approximately 1700 km north of the Aleutian Islands, and is surrounded by pack ice during the winter, which restricts the breeding season more stringently compared to lower latitudes (Sealy 1970). Changes in nesting chronology could be especially significant in light of evidence for global warming, and these changes are more likely to be detected at the Kitnik and Myaughee colonies, near the northern edge of the auklets' breeding range.

Our estimates of Least Auklet reproductive success in 2000, 2002, and at the Myaughee colony in 2001 were higher than those reported for St. Lawrence Island in 1987 (Piatt et al. 1990) but within the range of estimated reproductive success for other colonies elsewhere in the Bering Sea (Byrd et al. 1983, Roby and Brink 1986). Likewise, our estimates of Crested Auklet reproductive success were higher than previous estimates for St. Lawrence Island (Piatt et al. 1990). The average reproductive success for all years and both colonies in the present study (69%) was similar to the average reproductive success reported for Crested Auklets on Buldir Island during the 1990's (Fraser et al. 1999).

Unlike the other 2 years of our study, reproductive success for both Least and Crested auklets at the Kitnik colony in 2001 was the lowest recorded for either species in any previously published study (Jones 1993a, 1993b). Pioneering studies of auklet breeding biology (Bédard 1969a, Searing 1977, Roby and Brink 1986) acknowledged the negative effect of nest checks on auklet breeding success. Piatt et al. (1990) controlled investigator disturbance and recorded higher overall reproductive success for Least Auklets on control plots (50-66%) than on disturbed plots (38%) on St. Lawrence Island in 1987. They concluded that increasing the

frequency of nest checks may have resulted in higher rates of adult desertion and chick mortality (Piatt et al. 1990).

The daily survival rate of Crested Auklet eggs was lower than that of Least Auklets in all years and at both colonies, suggesting that Crested Auklets may be more sensitive to nest disturbance during incubation than Least Auklets. Fledging success of Crested Auklets, however, may be less sensitive to nest disturbance than hatching success. Fraser et al. (1999) found that investigator disturbance had no significant effect on fledging success of Crested Auklets on Buldir Island. There were no differences in our estimates of fledging success between the two colonies in 2000 or 2002. In 2001, however, chick daily survival rates of Crested Auklets were lower at Kitnik compared to Myaughee. Estimates of fledging success for Least Auklets were lower at Kitnik compared to Myaughee in all 3 years, lending support to Piatt et al.'s (1990) hypothesis that frequent nest checks result in higher chick mortality. Lower reproductive success of both species at Kitnik in 2001 may have reflected an interaction between lower food availability and higher nest disturbance frequency at the Kitnik colony (i.e., more researcher disturbance and other human activity). Previous studies found that less frequent nest checks may reduce the negative effects of investigator disturbance on nesting success, but result in negatively biased estimates of fledging success (Piatt et al. 1990, Hunter et al. 2002). Contrary to these previous studies, we had no more difficulty re-locating chicks late in chick-rearing at the colony where we checked nests less frequently.

Diet Composition

Previous studies reported that calanoid copepods, particularly *N. flemingeri/plumchrus*, are the main food delivered to Least Auklet chicks on St.

Lawrence Island, but they did not investigate variation in proportions of prevalent prey types among years (Bédard 1969b, Searing 1977, Springer and Roseneau 1985, Piatt et al. 1988, Hunt et al. 1990, Obst et al. 1995). Similarly, both Bédard (1969b) and Piatt et al. (1988) found diets brought to Crested Auklet chicks were dominated by the euphausiid *Thysanoessa* spp. (56% and 80.3%, respectively), but there was little effort to measure among-year differences in proportions of primary prey types in the diet.

While the general taxonomic composition of auklet diets described in this study was similar to those reported by Bédard (1969b) and Piatt (1988), we found significant variation among years in proportions of prey types delivered to chicks. There was variation among years in all major prey categories for Least Auklets, including the prevalence of copepods, the mainstay of the diet for this species (Jones 1993b). For example, in 2000, amphipods made up nearly a third of the diet by percent biomass, but in 2001 and 2002, they comprised less than 5% of biomass. In 2001, the year of lowest reproductive success, the oceanic copepod *N. flemingeri* was less prevalent in the diet than in the other two years of the study. Instead, Least Auklets consumed higher proportions of the neritic copepod *C. marshallae*, which are smaller and have lower lipid content than *N. plumchrus/flemingeri* (S. Smith, personal communication in Hunt and Harrison [1990]) and other non-copepod prey. In 2002, the year of highest nesting success, high-lipid oceanic *Neocalanus* spp. copepods predominated in Least Auklet chick meals and no *C. marshallae* were found in any of our samples. The proportion of *N. cristatus* was highest in the year of highest nesting success, but *N. flemingeri* dominated Least Auklet diets in all three years and was also highest in 2002, suggesting that availability of oceanic

Neocalanus spp. copepods was positively associated with reproductive success of Least Auklets.

Crested Auklets consumed primarily euphausiids in each year of the study, but the proportion of the large, oceanic, high-lipid copepod *N. cristatus* varied significantly among years and was highest in 2002, the year of highest recorded reproductive success. This observation is consistent with other studies, which found that diets high in *N. cristatus* were associated with high reproductive success in both Crested Auklets (Fraser et al. 2002) and Cassin's Auklets (*Ptycoramphus aleuticus*; Hedd et al. 2002). In 2001, the year of lowest reproductive success, the hyperiid amphipod *Parathemisto libellula*, which has smaller lipid reserves and more refractory chitin than oceanic copepods (Bédard 1969b), was more prevalent in the diet than *N. cristatus*. When *N. cristatus* is readily accessible, Crested Auklets may become more selective and include more large, high-lipid copepods in the diet, thereby influencing their reproductive success.

In addition to the inter-annual differences we observed in diet composition of Least and Crested auklets, Least Auklets also exhibited a seasonal shift in diet composition during the chick-rearing period. Early in chick-rearing, non-copepod prey items, such as larval crab and shrimp, comprised as much as 50% of some chick meals. As the breeding season progressed, however, the prevalence of deep-water copepods and euphausiids in Least Auklet diets increased and other prey types decreased. Bédard (1969b) attributed the diet shift to predominantly copepods after hatching to the blooms of grazing zooplankton that occurred in late July and August. The Anadyr Current, which forces water northward through the Bering Strait, is seasonal in its intensity. Transport during August-September is 3 times greater than in February-March, creating a shallow, stable water column structure off the northern

coast of St. Lawrence Island and concentrating plankton near the surface where they are accessible to avian predators (Pavlov and Pavlov 1996). The taxonomic composition of Least Auklet diets was more diverse and more variable than that of Crested Auklets in the 3 years of our study, but smaller sample sizes of chick meals may have limited the power to detect seasonal differences in diet composition of Crested Auklets.

The annual and seasonal variability in auklet diets reflects the influence of hydrographic structure and prey accessibility on auklet foraging. At-sea surveys located Least Auklets foraging over strong, shallow thermoclines and simultaneous acoustic surveys revealed *Neocalanus* spp. copepods concentrated above the thermocline (Hunt et al. 1990, Haney 1991, Hunt et al. 1998). Least Auklets have lower body mass, higher buoyancy, and poorer diving abilities compared to Crested Auklets (Hunt and Harrison 1990), making them especially sensitive to changes in water column structure that might affect prey availability near the surface. Least Auklet reproductive success was positively associated with the prevalence of *N. flemingeri* and *N. cristatus* in the diet. If *Neocalanus* copepods are less accessible, Least Auklets may forage on other zooplankters that occur within 15 m of the surface (e.g., *C. marshallae*, crab larvae, pandalid shrimp). Given the greater variability in their diets, Least Auklets appear to be more generalist foragers than Crested Auklets, possibly in response to their poorer diving abilities. The reproductive success of Least Auklets was also more variable than that of Crested Auklets, being lowest in 2001 at the Kitnik colony, when we hypothesized that auklets were most food-limited. Changes in auklet diet composition and reproductive success may, therefore, signal changes in the availability of *Neocalanus* copepod biomass, and allow tracking

of the influence of oceanographic factors on trophic structure and function in the northern Bering Sea (Barrett 2002).

Hydrographic structure may also affect diet composition among individuals within a species. Crested Auklets in the Aleutians rely on tidal currents flowing through passes to upwell zooplankton (Hunt et al. 1998), whereas Crested Auklets at St. Lawrence Island forage in relatively stable water columns (Haney and Schauer 1994). Fraser et al. (2002) found sexual differences in the proportion of prey types delivered to young by Crested Auklet adults on Buldir Island in years when food availability was suspected to be higher. The results of our study were consistent with Bédard's (1969b) findings of no gender differences in prey composition among Crested Auklets. The taxonomic composition of Crested Auklet diets were similar between our study site and Buldir Island (Fraser et al. 2002), so the sexual differences in Crested Auklet diets observed at Buldir may be related to physiographic features that influence foraging behavior of Crested Auklets, rather than differences in food availability between the two sites.

Body Mass of Breeding Adults

Piatt et al. (1988) found that body mass of adult auklets on St. Lawrence Island were generally lower than those observed by Bédard (1969a) over the entire breeding season, and suggested that the lower adult body mass reflected a long-term decline in average body mass of nesting auklets. We speculated that these differences in mass could be related to differences in prey availability or other inter-annual fluctuations, rather than changes in overall morphology. By comparing taxonomic composition of the diet and reproductive success to adult body

composition, we sought to test the hypothesis that low adult mass was indicative of poor body condition and lower availability of preferred prey.

Total adult body mass of Crested Auklets increased during the breeding season in 2002, a year of high reproductive success. In the other 2 years of the study, however, average adult body mass declined during the breeding season and reproductive success was lower, particularly in 2001. Although body mass of Least Auklets declined during the breeding season in all 3 years of the study, average body mass was lowest in 2001, the year of lowest reproductive success. These differences in average adult body mass, coupled with lower reproductive success at the Kitnik colony, suggest poorer foraging conditions for both auklet species in 2001, compared to 2000 and 2002.

Studies of pelagic seabirds have found that poor body condition early in the breeding season influences the decision to breed (Drent and Daan 1980, Chastel et al. 1995a, Barbraud and Chastel 1999). In neritic and coastal species, however, adults tend to initiate nests and abandon them later in the breeding season if food availability does not improve (Chastel et al. 1995b, Monaghan et al. 1996). Many of the crevices we monitored were active at the beginning of the breeding season in all 3 years of the study (A. Gall, pers. obs.), suggesting that auklets initiated nests, as predicted for neritic species. Auklet reproductive success may, therefore, be more dependent on foraging conditions during incubation and chick-rearing, as they influence egg abandonment and chick provisioning rates, than on adult body condition early in the breeding season.

Implications for Monitoring

Nesting chronology, reproductive success, diet composition, and adult body mass of seabirds have been suggested as useful indicators of change in the marine environment, if monitored on an annual basis (Cairns 1987, Monaghan et al. 1996), but there is limited understanding of how these parameters may be related. Long-term studies of seabird populations need to acquire the most useful information to determine trends and test hypotheses about ecosystem function with minimal cost and effort. We propose that Least and Crested auklets on St. Lawrence Island can provide valuable information on secondary productivity of the northern Bering Sea.

Reproductive success of Least and Crested auklets was positively correlated and appeared to be directly related to zooplankton availability. Reproductive success was practical to measure, but was apparently sensitive to investigator disturbance, particularly in a year of poorer foraging conditions. Given the sensitivity of auklets to disturbance during incubation, we recommend checking auklet nests every 8 days to reduce the effects of investigator disturbance on reproductive success. Estimates of nesting success derived using the Mayfield method can be biased if nests are checked infrequently, but results are not significantly different from those derived using maximum likelihood methods that assume the date of nest failure is unknown (Johnson 1979). By sub-sampling the nest check data from the Kitnik colony, where nests were checked more frequently, we determined that checking nests only every 8 days could negatively bias estimates of reproductive success by 1-3 percentage points, but these differences were not significant in our study. Alternatively, if there is concern about the bias of the Mayfield method for calculating nest success, daily nest survival rates could be modeled using known fate models and maximum likelihood methods available in program MARK to examine directly the effects of food

availability, environmental variables, and parental quality on nest and hatchling survival (Dinsmore et al. 2002).

There is evidence of a trend towards decreased sea-ice cover and earlier sea ice retreat in the late 1990's compared to the 1970's, and these trends affect the timing and magnitude of zooplankton production in the Bering Sea (Hunt et al. 2002). Concerns about global climate change and its effects on high-latitude ecosystems highlight the importance of monitoring auklet nesting chronology, in addition to reproductive success. We suggest conducting nest checks every 2-4 days on a subset of nests to determine hatching and fledging dates, thus minimizing investigator disturbance while still collecting crucial information on nesting chronology.

Collection of diet data is critical to understanding the complex interactions between food availability and auklet breeding ecology. We recommend collecting diet samples every 3 days during chick-rearing for a total of at least 50 chick meals per season to obtain a measure of prey types utilized by auklets. Adult body mass of Least and Crested auklets is easily measured while capturing birds for diet sample collection during the breeding season, and may be a practical indicator of the effects of food availability on adult body condition. Variation in auklet diets among and within years was associated with differences in reproductive success, adult body mass, and colony attendance (see Chapter 4). Annual monitoring of reproductive success, adult body mass, and diet of planktivorous auklets will contribute to understanding how both natural and anthropogenic climate change may affect the trophic structure of the northern Bering Sea ecosystem.

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CHAPTER 3

Evaluation of body condition indices for Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*)

Adrian E. Gall, Daniel D. Roby, and David B. Irons

ABSTRACT

Body condition indices have been used to assess the health of seabird populations, but the relationship between condition indices and body composition is rarely validated. We determined whether or not body condition indices based on size-adjusted body mass predicted fat reserves of Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) nesting on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Fat reserves of breeding Crested Auklets during egg-laying were highest in 2001, the year of lowest reproductive success. Fat reserves of breeding Least Auklets during egg-laying did not differ among the 3 breeding seasons. There was no evidence of a difference in fat reserves between genders for either auklet species in any year. Fat reserves during egg-laying were < 10% of total body mass and exhibited little variability within or among breeding seasons. Fat reserves may not, therefore, be a sensitive predictor of subsequent breeding success for either Least or Crested auklets. Residual condition indices explained only 15-17% of the variation in fat reserves, and were strongly positively correlated with water mass as a proportion of lean mass. While variation in total body mass of nesting Least and Crested auklets may be a useful indicator of food availability, this variation apparently reflects variation in both fat reserves and hydration of lean tissue, providing low precision for estimates of fat reserves in these two seabird species.

INTRODUCTION

Measurement of body composition has been proposed as a valuable tool for examining processes in avian ecology, energetics, and behavior (Perdeck 1985, Conway et al. 1994), but few studies have directly investigated the relationship between body composition and nesting success (Drent and Daan 1980). Fat is the primary form of energy storage in birds and it is mobilized first during periods of food shortage (Walsberg 1988, Blem 1990). Fat reserves are therefore assumed to be a good indicator of nutritional status or health of avian populations (Perdeck 1985, Mainguy et al. 2002). Lean body mass has also been identified as an important component of nutrient reserves for breeding birds of some species (Lindström and Piersma 1993, Bolton et al. 1995), and may contribute to differences in adult body condition. Birds with larger fat reserves are assumed to be more fit because they are better prepared for the energetic demands of the breeding season, including territory defense, acquiring or retaining a mate, egg production, incubation, and provisioning young (Blem 1990, Esler et al. 2001).

Body condition indices (i.e., body mass adjusted by a measure of body size) have been used to indicate differences in fat reserves and, indirectly, food availability (Aebischer et al. 1990, Sæther et al. 1997). Several studies have related body condition indices to various reproductive and life history parameters of seabirds (Chastel et al. 1995, Golet et al. 1998, Golet and Irons 1999, Vleck and Vleck 2002), but have not addressed the relative contributions of fat reserves and lean body mass to variation in body condition indices. Lipid extraction as part of proximate composition analysis is a technique commonly used for measuring fat reserves, but it is expensive, time-consuming, and requires sacrificing individuals (Conway et al. 1994, Golet and Irons 1999). Alternatively, measurements of body mass and

morphology have been used as a non-invasive technique to assess fat reserves in birds (Conway et al. 1994). Body mass is an attractive index to nutritional state because it is relatively easy to measure in the field, and allows for repeated measures on the same individual over time (Johnson et al. 1985). Using body mass alone, however, does not take into account variation in structural size among individuals (Johnson et al. 1985, Chastel et al. 1995a, Golet and Irons 1999). Residual body condition indices have been used to adjust mass for variation in structural size among individuals (Piersma 1984, Conway et al. 1994, Jakob et al. 1996). Residual body condition indices are calculated as the difference between an observed measure of mass and the measure of mass predicted by a regression equation. Residual indices offer advantages over other condition indices because they are not correlated with the measure of linear size (Jakob et al. 1996, Hayes and Shonkwiler 2001) and normalize the distribution of the data for analysis (Jakob et al. 1996).

Residual indices are controversial, however, because the use of residuals as responses in subsequent analyses may lead to erroneous inferences if the residuals are inter-correlated (van der Meer and Piersma 1994, Hayes and Shonkwiler 2001). An alternative approach for estimating body condition is to analyze the effects of mass and body size directly on measures of fat reserves, rather than constructing indices to summarize the relationship between mass and body size (Conway et al. 1994, Hayes and Shonkwiler 2001). Regardless of which technique is used, the relationship between morphometrics and body composition is species-specific and must be validated (Skagen et al. 1993, Golet and Irons 1999, Hayes and Shonkwiler 2001).

In this study, we measured body composition of Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*), two abundant species of planktivorous seabirds, during the nesting season on St. Lawrence Island, Alaska to examine the relationship between body composition at egg-laying and subsequent reproductive success. Least Auklets (*Aethia pusilla*) are small (85 g), pursuit-diving seabirds that nest on islands throughout the Bering Sea and the sexes cannot be distinguished in the field. Crested Auklets (*A. cristatella*) are about 3 times larger than Least Auklets (265 g) and are sexually dimorphic. We collected breeding adults during the egg-laying period to quantify interannual variation in adult fat reserves. We also compared body condition indices and fat reserves to determine whether or not body condition indices based on morphometrics can be used as a non-destructive estimator of fat reserves in adult Least and Crested auklets.

METHODS

Study Area

St. Lawrence Island (ca. 63° 30' N, 170° 30' W) is located approximately 200 km west of the Alaskan coast and about 60 km east of the Chukotsk Peninsula, Siberia. Adult auklets were captured at 2 auklet breeding colonies on the north coast of St. Lawrence Island, east of the village of Savoonga. The Myaughee colony is located ca. 17-20 km east of Savoonga and the Kitnik colony is located west of the mouth of the Kitnik River, ca. 6-8 km east of Savoonga (see Chapter 2 for details).

Body Composition

We collected a total of 66 adult Crested Auklets and 65 adult Least Auklets during the egg-laying period in 2000 (6-9 July), 2001 (1-8 July), and 2002 (24-27

June). We analyzed the carcasses of these birds to assess among-year variation in body composition, fat reserves, and body condition early in the breeding season. Adult Least and Crested auklets develop bilateral brood patches prior to egg-laying, so this characteristic was used to identify adults that were presumed to be breeding. Least Auklets have distinctive adult breeding plumage and are not sexually dimorphic (Jones 1993b). For Least Auklets, we collected 17 adults in 2000, 24 adults in 2001, and 24 adults in 2002 that met the above criteria.

The sexes are also similar in Crested Auklets, but males generally have larger, more strongly hooked bills and longer crests than females (Jones 1993a). We used these characteristics to attempt to identify gender and collect equal numbers of male and female Crested Auklets in each year of the study. There is, however, some overlap in secondary sexual characteristics between the sexes, and experience in handling birds of known sex increased the accuracy of sexing individuals in the field. Consequently, we misidentified 5 males in 2000, 3 males in 2001, and 1 male in 2002 as females in the field, resulting in 41 males and 25 females in the sample of collected Crested Auklets.

Captured auklets were euthanized by cervical dislocation, according to a protocol approved by the Institutional Animal Care and Use Committee (IACUC) at Oregon State University (OSU). After collection, auklet carcasses were placed in plastic bags, frozen, and transported to OSU for proximate composition analysis in the laboratory.

Auklet carcasses were weighed, partially thawed to facilitate processing, plucked, and the feathers weighed (± 0.01 g) to determine feather mass. Contents of the esophagus, proventriculus, and gizzard were removed for analysis of diet composition. The remainder of the carcass was weighed (± 0.01 g) and placed in an

aluminum pan in a forced convection drying oven at 60° C. Carcasses were weighed on a Mettler analytical balance after 5 days, and then every 24 hours until mass was constant (± 0.02 g). We used sample dry mass to calculate percent water content of each carcass by subtraction.

Once dried and weighed, each carcass was ground thoroughly using a meat grinder and mortar and pestle to homogenize the sample. The feathers were discarded after obtaining a dry mass and were not included in further analyses. We used petroleum ether with a Soxhlet apparatus to extract lipids from aliquots of the dried, homogenized carcass. Petroleum ether extracts triacylglycerols, which are the main neutral storage lipid used by vertebrates for energy reserves (Dobush et al. 1985). We extracted three 4-g aliquots of homogenized tissue from each carcass. Samples were refluxed in the Soxhlet apparatus for 12 hours. Percent fat of each aliquot was calculated as:

$$\% \text{ fat} = \frac{(\text{dry mass before extraction}) - (\text{dry mass after extraction})}{(\text{dry mass before extraction})} \times 100$$

We multiplied the total dry carcass mass of each auklet by the average percent fat of the 3 aliquots to calculate the total body fat mass. Total lean dry mass of each auklet was calculated as total dry body mass minus total body fat mass. The fat index of each auklet was calculated as total body fat mass divided by total lean dry mass. We used ANOVAs with Tukey-Kramer procedures for multiple comparisons of means to compare the fat index among years and set $\alpha = 0.05$ (Ramsey and Schafer 2002: 161). We also regressed the fat index of each collected auklet on 3 body condition indices for Least Auklets and 2 body condition indices for Crested Auklets to evaluate the use of non-destructive measures to estimate fat reserves in breeding auklets (Hayes and Shonkwiler 2001).

Body Condition Indices

We used measurements of 547 adult Least Auklets and 299 adult Crested Auklets captured and released from early July to late August 2000-2002 to develop predictive equations relating body mass to body size. Adults were captured using mist nets stretched above the surface of the colony and noose mat traps on large display rocks. We weighed all auklets captured on Pesola spring scales (± 0.5 g), and measured flattened wing length (± 1.0 mm) using a flat ruler. We measured tarsus length (± 0.1 mm), culmen length (± 0.1 mm), and bill depth (± 0.1 mm) using calipers. Measurements of the smaller sample of collected birds were analyzed to generate body condition indices for each individual based on the residual about the regression for the large sample of captured and released adults. The residual body condition index for each collected auklet was then compared to its body composition, as determined by proximate composition analysis in the laboratory.

The body condition indices for both auklet species were based on residuals of the regression of body mass on body size. We quantified variation in body size using 3 measures: (1) a principle components score, (2) flattened wing length, and (3) tarsus length to determine which index of auklet body size would be most useful in predicting fat reserves of breeding auklets.

To establish body size indices for each auklet species, we performed a principle components analysis (PROC PRINCOMP, SAS Institute 1999) on flattened wing length, tarsus length, culmen length, and bill depth of Crested Auklet adults and flattened wing length, tarsus length, and culmen length of Least Auklets. The principle components analysis (PCA) generated weighting coefficients that described positive covariance among the linear measurements. These coefficients had consistent loadings across measurements and the first principle component (PC1)

accounted for 37-41% of the variance in the original measures. Next, measurements were multiplied by the coefficients of PC1 and summed to produce a PCA factor score, or body size index (BSI). We regressed mass on the BSI to develop a least-squares regression that we used to predict the mass of a bird given its body size. Finally, we calculated the body condition index of adults collected for proximate composition analysis by subtracting the predicted mass of each bird (based on the regression equation) from its actual mass, dividing this difference by the predicted mass, and then multiplying the quotient by 100 to produce a principle components body condition index (PCBCI).

We compared the predictive power of the PCBCI to a second body condition index calculated using residuals from a least-squares regression of mass on flattened wing length (WBCI). Measurements of flattened wing length represent proportionally greater differences in structural size than tarsus length, culmen length, or bill depth. Jones (1992) found that measurements of tarsus length were repeatable on Least Auklets between years, and recommended using this measure as an index to body size. We regressed mass of Least Auklets on tarsus length and used the residuals as the third body condition index (TBCI). These 3 residual body condition indices control for variation among individuals in body size and are not correlated with the measure of linear size ($R^2 < 0.01$ for all indices; Jakob et al. 1996, Hayes and Shonkwiler 2001).

We regressed PCBCI, WBCI, and TBCI on fat mass for collected individuals to determine which body condition index best predicted fat reserves. We included models of combinations of morphological measurements in each model set and developed a suite of 11 models for Crested Auklets and 12 models for Least Auklets. Candidate models in each set were ranked by their ability to explain the data using

the coefficient of determination (R^2) because the models with the highest R^2 values accounted for the most variation in fat reserves.

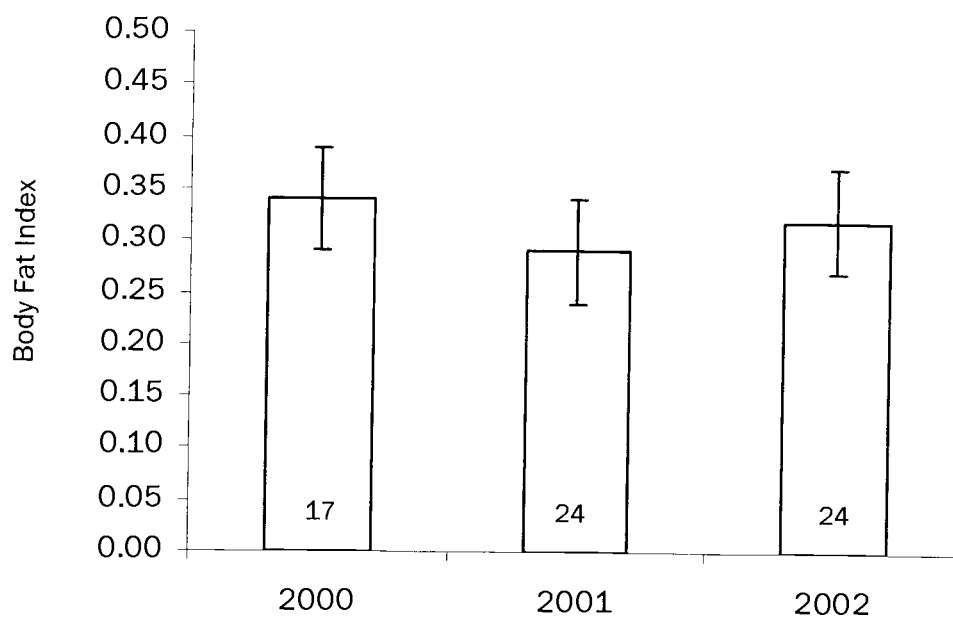
We also developed regression models to determine the amount of variation in the body condition index explained by body composition. For each model, the PCBCI was the response variable. We derived three explanatory variables to represent proportions of fat, lean, and water: fat mass was expressed as a proportion of dry mass, water mass was expressed as a proportion of lean mass, and lean dry mass was expressed as a proportion of total body mass. These proportions accounted for difference in body size among individuals. We built the models using forward selection procedures, including the independent variables that explained the most additional variation in the body condition index and set $\alpha = 0.05$. Means are reported as $\pm 95\%$ CI, unless otherwise stated.

RESULTS

Body Composition During Egg-Laying

Fat reserves of breeding auklets during egg-laying averaged $7.3 \pm 0.6\%$ of total body mass for Least Auklets (range 1.7 – 13.4%, $n = 65$), and $6.6 \pm 0.5\%$ of total body mass for Crested Auklets (range 1.9 – 11.3%, $n = 66$) during the 3 years of the study. There was little variation within years in auklet fat reserves during egg-laying (Figure 3.1). Fat reserves of adult Least Auklets during egg-laying did not differ among the 3 breeding seasons ($F_{2, 61} = 0.98$, $P = 0.38$, Figure 3.1A).

A. Least Auklets



B. Crested Auklets

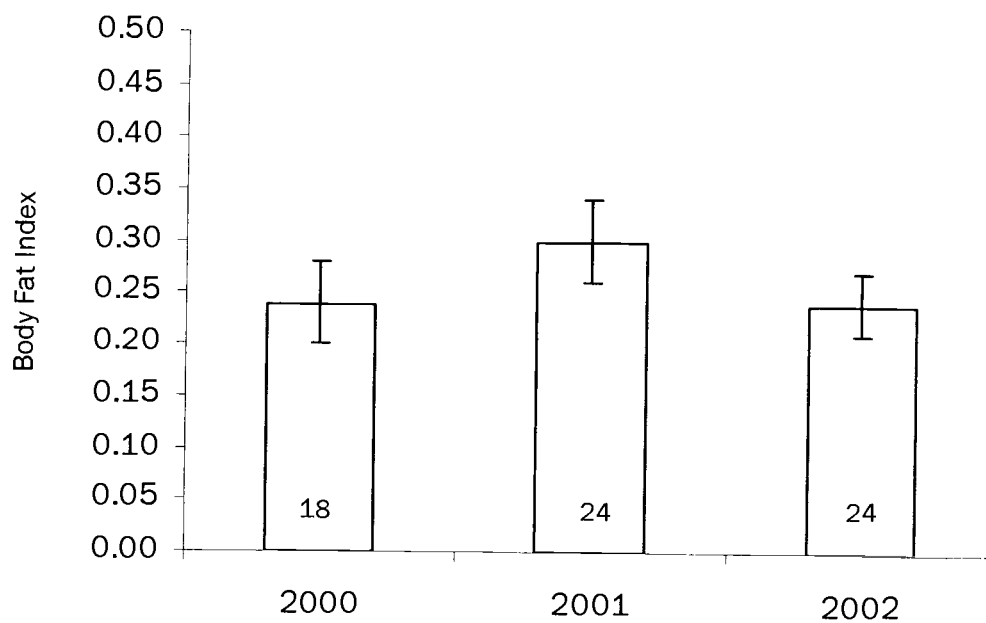


Figure 3.1. Mean fat index (total body fat mass/ lean dry body mass) of (A) Least Auklets and (B) Crested Auklets during egg-laying on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. Error bars represent 95% confidence intervals and numbers on the bars are sample sizes.

There was no evidence of a gender difference in fat reserves of Least Auklets in any year ($F_{1, 61} < 0.01$, $P = 0.98$, Table 3.1). The body composition of adult Crested Auklets during egg-laying, however, differed significantly among the 3 years of the study ($F_{2, 62} = 4.46$, $P = 0.02$, Figure 3.1B). The average fat index was higher in 2001 than in 2000 (difference: 6.3 percentage points, 95% CI: 0.2 to 12.4 percentage points) or 2002 (difference: 6.2 percentage points, 95% CI: 0.6 to 11.9 percentage points, Table 3.1). As with Least Auklets, there were no gender differences in average fat index for Crested Auklets in any year of the study ($F_{1, 62} = 1.20$, $P = 0.28$).

Body Condition Indices

We regressed total body mass on the body size index (BSI) to develop a least-squares regression that we used to predict the mass of a bird given its body size (Least Auklets: $\text{mass} = -6.65 + 1.43 \cdot \text{BSI}$, $n = 547$, $R^2 = 0.11$, $P < 0.001$; Crested Auklets: $\text{mass} = -91.67 + 3.92 \cdot \text{BSI}$, $n = 299$, $R^2 = 0.23$, $P < 0.001$). The regression equation for body mass as a function of flattened wing length for Least Auklets was: $\text{mass} = 10.54 + 0.79 \cdot \text{wing length}$ ($n = 547$, $R^2 = 0.08$, $P = 0.003$); and for Crested Auklets was: $\text{mass} = -52.22 + 2.23 \cdot \text{wing length}$ ($n = 299$, $R^2 = 0.17$, $P < 0.001$). We also regressed mass of Least Auklets on tarsus length ($\text{mass} = 64.17 + 1.21 \cdot \text{tarsus length}$, $n = 547$, $R^2 = 0.03$, $P < 0.001$). We did not, however, find a significant relationship between tarsus length and body mass in Crested Auklets ($P = 0.98$), so a tarsus body condition index (TBCI) was not calculated for Crested Auklets.

Incorporating linear measures of size improved our ability to predict fat reserves of Least Auklets (Table 3.2) and Crested Auklets (Table 3.3) over using body mass alone. The PCBCI was the best residual index predictor of fat reserves for

Table 3.1. Body composition of Least Auklets and Crested Auklets collected during the 2000-2002 breeding seasons on St. Lawrence Island, Alaska. Auklets were collected during the egg-laying period. Fat mass (g) was determined in the laboratory by chemical extraction. Values presented are means (g). Values in parentheses are 95% confidence intervals.

		2000	2001	2002
Least Auklets	<i>n</i>	17	24	24
	Fat Mass	7.4 (± 1.1)	6.2 (± 1.0)	6.9 (± 1.0)
	Lean Dry Mass ^a	21.5 (± 0.6)	21.3 (± 0.8)	21.8 (± 0.6)
	Water Mass ^b	67.0 (± 2.6)	62.1 (± 2.2)	63.3 (± 2.9)
	Fat Index ^c	0.34 (±0.05)	0.29 (± 0.05)	0.32 (± 0.05)
	Total Body Mass	95.9 (± 3.82)	89.5 (± 3.31)	92.0 (± 3.65)
Crested Auklets	<i>n</i>	18	24	24
	Fat Mass	17.3 (± 2.7)	21.1 (3.1)	16.9 (± 2.1)
	Lean Dry Mass	72.8 (± 2.8)	69.4 (± 2.6)	70.2 (± 2.0)
	Water Mass	199.3 (± 8.5)	189.5 (± 6.2)	181.2 (± 5.2)
	Fat Index	0.24 (± 0.04)	0.30 (± 0.04)	0.24 (± 0.03)
Females	<i>n</i>	7	7	11
	Total Body Mass	279 (± 15.8)	265 (± 25.0)	264.6 (± 15.1)
Males	<i>n</i>	11	17	13
	Total Body Mass	296 (± 10.8)	286 (± 11.4)	271 (± 9.9)

^a Lean Dry Mass (g) = dry body mass – fat mass

^b Water mass (g) = total body mass – dry body mass

^c Fat Index = (fat mass/lean dry body mass)

Table 3.2 Comparison of multiple regression models explaining variation in fat mass (g) of adult Least Auklets nesting on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. $P < 0.01$ for all models.

Model ^a	Parameters	R ²
TBM + C	2	0.28
TBM + T + C	3	0.28
TBM + W + C	3	0.28
TBM + W + T + C	4	0.28
PCBCI	1	0.26
TBM + BS	2	0.26
TBM	1	0.25
TBCI	1	0.25
TBM + T	2	0.25
TBM + W	2	0.25
TBM + W + T	3	0.25
WBCI	1	0.24

^a BS = body size (PC1 score), C = culmen, PCBCI = principle component body condition index, T = tarsus, TBCI = tarsus body condition index, TBM = total body mass, W = wing, WBCI = wing body condition index

Table 3.3. Comparison of multiple regression models explaining variation in fat mass (g) and of adult Crested Auklets nesting on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons. $P < 0.01$ for all models.

Model ^a	Parameters	R ²
PCBCI	1	0.30
WBCI	1	0.30
TBM + W + C	3	0.30
TBM + W + T + C	4	0.30
TBM + BS	2	0.29
TBM + W	2	0.29
TBM + W + T	3	0.29
TBM + C	2	0.27
TBM + T	2	0.27
TBM + T + C	3	0.27
TBM	1	0.26

^a BS = body size (PC1 score), C = culmen, PCBCI = principle component body condition index, T = tarsus, TBCI = tarsus body condition index, TBM = total body mass, W = wing, WBCI = wing body condition index

Least Auklets, based on the coefficient of determination ($R^2 = 0.26$), but only marginally so. The PCBCI and WBCI both explained 30% of the variation in fat reserves of Crested Auklets, indicating that body mass scaled by a linear measure of body size was a better predictor of fat reserves for Crested Auklets than body mass alone (Table 3.3).

We used the PCBCI for each species to determine the relationship between the residual body condition index and body composition. For Least Auklets, fat as a proportion of dry mass and water as a proportion of lean mass were both positively associated with the variation in the PCBCI ($F_{2,62} = 23.2$, $P > 0.01$, $R^2 = 0.43$). Fat as a proportion of dry mass and water as a proportion of lean mass were also both positively associated with the variation in the PCBCI of Crested Auklets ($F_{2,63} = 11.2$, $P > 0.01$, $R^2 = 0.26$). Therefore, for both species of auklets, proportions of fat and water were positively associated with the body condition index, providing evidence that auklets with positive body condition index values have both greater fat reserves and greater hydration of lean tissue (Table 3.4). We did not include lean dry mass as a proportion of total body mass in these models because this proportion was negatively correlated with fat as a proportion of dry mass (Least Auklets: $R = -0.58$, $P < 0.01$, Crested Auklets: $R = -0.50$, $P < 0.01$) and with water as a proportion of lean mass (Least Auklets: $R = -0.91$, $P < 0.01$, Crested Auklets: $R = -0.91$, $P < 0.01$). Fat as a proportion of dry mass and water as a proportion of lean mass were not correlated in either species (Least Auklets: $R = 0.20$, Crested Auklets: $R = 0.10$).

Table 3.4. Multiple regression models explaining variation in the principle components body condition index (PCBCI) of Least and Crested auklets on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.

	Explanatory variable	Estimate	SE	P-value	R ²
Least Auklets	Intercept	-243.93	45.14	< 0.01	
	(fat mass/dry mass)	0.44	0.14	< 0.01	0.10
	(water mass/lean mass)	317.9	61.13	< 0.01	0.33
	Total model				0.43
Crested Auklets	Intercept	-141.81	45.30	< 0.01	
	(fat mass/dry mass)	0.48	0.14	< 0.01	0.13
	(water mass/lean mass)	184.82	62.50	< 0.01	0.13
	Total model				0.26

DISCUSSION

Average adult body mass of Crested Auklets on St. Lawrence Island during 1986 was significantly lower than in 1965-1967 (Bédard 1969, Piatt et al. 1988), prompting Piatt et al. (1988) to speculate that body mass had gradually declined in the interim. Without information on body composition and fat reserves, however, it is difficult to determine whether these differences in mass are attributable to changes in overall body size or differences in body condition related to prey availability or other inter-annual fluctuations. We sought to test the hypothesis that low adult mass, adjusted for differences in body size, reflects low lipid stores by comparing adult body composition to body condition indices calculated from measurements of live birds.

Fat reserves exhibited little variability within years for Least Auklets, and there was no difference in fat reserves among years, despite significant interannual differences in reproductive success and diet composition (see Chapter 2). Although the fat reserves of Crested Auklets during egg-laying were highest in the year of lowest reproductive success, the difference represented only 2% of total body mass. Studies of oceanic seabirds have found that poor body condition (low body mass, adjusted for size) early in the breeding season negatively influences the decision to breed (Drent and Daan 1980, Chastel et al. 1995a, Barbraud and Chastel 1999). In many neritic and coastal species, however, adults initiate nests and abandon them later in the breeding season if food availability does not improve (Chastel et al. 1995b, Monaghan et al. 1996). Auklets nesting on St. Lawrence Island generally feed within 56 km of the breeding colony during the breeding season (Obst et al. 1995) and both parents incubate the egg, switching ca. every 24 hours (Roby and Brink 1986, Jones 1993). These incubation shifts are much shorter than the

incubation shifts of several days observed in more oceanic planktivorous seabirds (Chastel et al. 1995b). Our results suggest that auklets are similar to neritic seabirds in not requiring large fat reserves prior to nest initiation. Fat reserves at the beginning of the breeding season may not, therefore, be a sensitive predictor of subsequent breeding success for either Least or Crested auklets.

Can morphological measurements be used as an index to body composition in auklets? Skagen et al. (1993) found models that incorporate morphological measures explained 87% of the variation in fat mass of Semipalmated Sandpipers (*Calidris pusilla*) and 91% in White-rumped Sandpipers (*C. fuscicollis*). Fat mass of these two species represented 17% and 19% of total body mass, respectively (Skagen et al. 1993). In contrast, we found that models that related fat mass to total body mass and linear measurements of body size explained only 28-30% of the variation in fat mass of a sample of Least and Crested auklets. Fat reserves represent only 6-7% of total body mass in auklets, and therefore do not account for much of the variation in total body mass, producing lower coefficients of determination than similar models for shorebirds and waterfowl (see Johnson et al. 1985, Perdeck 1985, Skagen et al. 1993). Predictions of fat reserves based on regression models can have errors that range up to 30%, even when correlations are high, as observed in the validation study conducted on sandpipers (Skagen et al. 1993).

One explanation for the lack of fit when predicting body fat is the imperfect relationship between morphological measurements and body composition (Perdeck 1985). While there is a strong relationship between morphological measurements and body composition, these models assume that variation in body size is perfectly explained by size measurements (van der Meer and Piersma 1994). Including

several measures of linear size in the condition index may not directly address this issue. Coefficients of determination were slightly higher for models that included linear measures of body size, particularly for Crested Auklets. There is little evidence, however, that the residual condition indices provide an advantage over using total body mass alone to predict fat mass based on morphometrics of *Aethia* auklets. Measures of tarsus length, culmen length, and bill depth may be useful for determining the sex of Crested Auklets or answering other research questions, but including these measures of linear size does not appear to improve the predictive power of residual body condition indices.

Another difficulty of predicting body fat mass from live measurements is the confounding factor of water mass. There may be an interaction between an increase in fat mass and the proportion of lean body mass that is attributable to water. In our models, both the water index and the fat index were positively associated with the PCBCI. Lean dry mass as a proportion of total body mass, however, was negatively associated with the PCBCI, suggesting that positive PCBCI's indicate higher proportions of fat and water relative to lean dry body mass (protein).

Fat reserves of individuals have been proposed as an indicator of food availability, and consequently, health of the population (Johnson et al. 1985, Golet and Irons 1999). In shorebirds, the strong relationship between variation in fat mass and variation in total body mass may be attributed to their reliance on endogenous fat reserves to fuel long-distance migration and reproduction (O'Reilly and Wingfield 2003). Least and Crested auklets are pursuit-diving seabirds with short wings and high wing loading, and are not well-adapted to energy-efficient flight compared to shorebirds or surface-feeding seabirds, such as Procellariidae (Pennycuik 1987). Differences in total body mass, which includes mass of muscle and other organs that

respond to the increased energetic demands of chick-rearing, may therefore be a better indicator of adult body condition (Niizuma et al. 2002). While we did not detect any differences in body composition at egg-laying during the 3 years of this study, average body mass of Least Auklets was lowest in 2001, the year of lowest reproductive success, after accounting for a decline in body mass during the breeding season in all 3 years (see Chapter 2). We observed an increase in total body mass of Crested Auklets during the 2002 breeding season, the year of highest reproductive success, whereas total body mass declined through the breeding season in the other 2 years (see Chapter 2). These results suggest that low adult body mass of Least Auklets and seasonal declines in adult body mass of Crested Auklets may reflect low food availability and appear to be more sensitive to foraging conditions than body composition of adults during egg-laying.

Given that fat reserves represent less than 10% of total body mass for nesting Least and Crested auklets, it is unlikely that fat reserves represent a major nutrient resource for breeding adults. Measuring fat reserves may not, therefore, be informative when evaluating the health of nesting auklet populations. While variation in total body mass of nesting Least and Crested auklets may be a useful indicator of food availability, this variation apparently reflects changes in lean body mass more than fat reserves, even after adjusting for body size. Future studies should explore the relationship between patterns of mass change through the breeding season and associated changes in body composition to improve the accuracy of estimating body condition of Least and Crested auklets using non-invasive techniques.

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CHAPTER 4

Factors affecting population indices of planktivorous auklets
on St. Lawrence Island, Alaska

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ABSTRACT

Counts of diurnal crevice-nesting seabirds on the colony surface are highly variable on the scale of days and even hours, but are nonetheless used to monitor the size of breeding populations. We studied colony surface attendance of Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) during the 2001 and 2002 breeding seasons at the Kitnik colony, St. Lawrence Island, Alaska to determine factors affecting variation in surface counts, thereby confounding estimates of population change. Crested Auklets exhibited much more variation in colony surface attendance across the colony than did Least Auklets. Differences in Crested Auklet surface attendance among areas of the colony were consistent between years, with highest counts in areas of large average boulder size. Preventing nest initiation by covering plots with tarps did not reduce subsequent colony surface attendance during chick-rearing for either species, suggesting year-to-year variation in nesting success alone is not likely to affect colony surface attendance. Nevertheless, in the year of lower reproductive success, colony surface attendance of both species declined sharply after the median hatch date, suggesting lower attendance during chick-rearing reflects lower food availability. Maximum counts of auklets on plots did not differ between years, after accounting for differences among areas of the colony. Estimated densities of nesting Least Auklets, based on resighting of marked individuals, differed between 2 plots but not between years. Numbers of nesting adult auklets based on mark-resighting exceeded peak colony surface counts by about an order of magnitude. Based on our comparison, we conclude that surface counts may provide an indication of among-year differences in colony attendance, but mark-resighting techniques show more promise for detecting changes in the number of breeding pairs

within plots. We recommend the use of mark-resighting techniques in conjunction with colony surface counts to assess changes in size of auklet colonies.

INTRODUCTION

Studies of colonial seabirds frequently focus on temporal changes in colony size, asking how and why breeding populations change over time, to assist in making conservation and management decisions (Williams et al. 2000). In the Bering Sea, Native communities also have an interest in monitoring seabird populations because they depend on seabirds for subsistence use and cultural activities. Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) are the two most numerous species of plankton-feeding seabirds that breed on islands in the Bering Sea. These two species nest in crevices in sea-facing talus slopes, cliffs, boulder fields, lava flows, and along rocky beaches where they form large, mixed-species colonies (Jones 1993a, 1993b). Millions of pairs of both species are estimated to nest on St. Lawrence Island in the northern Bering Sea (Stephensen et al. 1998). The numbers of breeding auklets on St. Lawrence Island may have increased during the 1980s (Piatt et al. 1990), but the enormous numbers and concealed nature of their nest sites make it extremely challenging to accurately estimate colony size or detect population changes (Jones 1992).

Methods have been developed for estimating breeding populations of colonial burrow-nesting seabirds, such as Atlantic Puffins (*Fratercula arctica*), by counting occupied burrows (Harris and Rothery 1988, Anker-Nilssen and Røstad 1993). Least and Crested auklets generally nest in rock crevices beneath talus slopes and among boulder piles where few nest sites have discrete entrances, making it difficult to identify and count nest sites in a given area. Auklets attending the surface of the

colony and delivering meals to chicks are the most obvious indication of an active breeding colony.

Early studies of auklet populations on St. Lawrence Island focused mainly on surveys of colony size and location (Fay and Cade 1959, Bédard 1969, Searing 1977, Roseneau et al. 1985). These surveys consisted of counting numbers of auklets in marked surface plots on talus slopes, and extrapolating counts to the estimated area of the colony to estimate population size. Little effort was made to account for the large diurnal and seasonal variation in auklet attendance on the surface of the colony when conducting these counts (Piatt et al. 1990). Colony surveys provide rough estimates of population size relative to other colonies surveyed, but do not provide unbiased estimates of number of breeding pairs and are unlikely to detect even large fluctuations in population size, which is essential for monitoring population responses to environmental change.

Counts of individual auklets on the surface of breeding colonies are simple to perform, minimize disturbance to breeding birds, and can be conducted over a large area (Piatt et al. 1990). These surface counts are difficult to interpret, however, in relation to the size of breeding populations. Several factors are thought to influence colony attendance of seabirds in general, and *Aethia* auklets in particular (Byrd et al. 1983, Hatch and Hatch 1989, Gaston and Nettleship 1992, Jones 1992). Some of these factors can be controlled for through sampling design. The diurnal pattern of auklet attendance on the colony surface is generally bimodal, with the major peak occurring in late morning (Byrd et al. 1983, Piatt et al. 1990, Jones 1992). Consequently, conducting surface counts during this peak in surface attendance can control for the variation among counts due to circadian patterns. Counting under a restricted range of weather conditions (e.g., wind speed, precipitation, fog) can control

for effects of these environmental factors (Jones 1992, Williams et al. 2000). By designing a sampling protocol that controls for known sources of variation, the primary factor of concern, population change, may be detected.

Counts of auklets on the colony surface vary widely not just within, but also between breeding seasons. Comparing protocols for surface counts proposed by Piatt (1990), Jones (1992), and Fowler and Irons (1994) would be useful for developing a standard census method that can yield reproducible and comparable counts among years and among colonies. Developing indices that account for within-season variation may also be useful for inferring among-year differences in parameters such as breeding success and food availability.

Measuring nesting densities using marked populations has been proposed as an alternative to surface counts for estimating changes in colony size of *Aethia* auklets (Byrd et al. 1983, Jones 1992). Resighting frequencies of marked individuals within a breeding season can be used to estimate abundance in study plots (White 1996). These estimates can be compared to results from surface counts to potentially validate and calibrate estimates of nesting density from surface counts. Marked populations also provide insight into parameters of interest other than changes in breeding population size (Neal et al. 1993, Manning et al. 1995, Calvert and Robertson 2002). Observations of marked individuals can be used to estimate reproductive success, survival rates, emigration rates, and immigration rates which can significantly influence population trends (Jones 1992).

Studies of banded birds suggest that surface counts may underestimate numbers of breeding adults by as much as an order of magnitude (Jones 1992, Calvert and Robertson 2002). Nevertheless, if there is a direct relationship between the number of auklets attending the surface and the number of active nests beneath

the surface, it may be possible to obtain an index of breeding birds based on that relationship. Due to the enormous temporal variation in surface counts and attendance of non-breeding auklets, however, this relationship has been difficult to define. Comparing surface counts among areas of known nesting density would test the hypothesis that changes in surface counts are indicative of changes in nesting density.

We studied colony surface attendance of Least and Crested auklets on St. Lawrence Island, Alaska in order to: (1) describe diurnal and seasonal patterns in colony surface attendance as a function of species and area of the colony; (2) determine whether or not surface counts reflect the density of nests beneath the surface and between-year variation in colony size; and (3) compare surface count indices with abundance estimates based on mark-resight methods.

METHODS

Study Area

St. Lawrence Island (ca. 63° 30' N, 170° 30' W) is located approximately 200 km west of the Alaskan coast and about 60 km east of the Chukotsk Peninsula, Siberia. Glacially-formed talus slopes and precipitous cliffs along the northern and western coasts of the island provide nesting habitat for over 3 million crevice-nesting and cliff-nesting seabirds (Stephensen et al. 1998). This study was conducted at a colony of more than 400,000 Least and Crested auklets (V. Zubakin, unpubl. data) at the mouth of the Kitnik river on the north shore of St. Lawrence Island, approximately 6-8 km east of the village of Savoonga. Auklets at this colony nest among boulders and talus fields that are bounded on the north by the Bering Sea, on the east by the

Kitnik River, on the west by sheer sea cliffs, and on the south by open wet sedge tundra.

Study Plots

We established a series of 12 monitoring plots (10 m x 10 m) in 2001 that included areas of both high and low auklet surface attendance to serve as population index plots (Figure 3.1). We monitored numbers of auklets on these plots during the 2001 and 2002 breeding seasons. Eight of the plots were established on a steeply sloping section of the colony to enhance visibility of each plot from an observation blind at the base of the slope. Plots were selected to represent three different habitat types on the talus slope. Three plots (102, 105, and 108) were situated along the crest of the slope (hereafter referred to as Slope Crest plots) in an area of large boulders with a high proportion of attending Crested Auklets. Two plots (103 and 106) were situated in the mid-section of the slope (Mid-Slope plots), in an area of medium-sized talus with visible organic substrate between talus boulders. Three more plots (101, 104, and 107) were situated at the base of the slope on flatter terrain (Low Slope plots) with smaller talus and a higher proportion of attending Least Auklets. All 8 plots on the slope were visible from a blind located on the western end of the beach at the mouth of the Kitnik River. Four more plots (201-204) were located on the upland area of the colony above the talus slope (Upland Flats), on the western edge of this habitat type. The observation point for these four plots was about 40 m east of the plots. These 12 plots appeared representative of the range of boulder sizes, slopes, orientations, and surface attendance densities present at the Kitnik auklet colony.

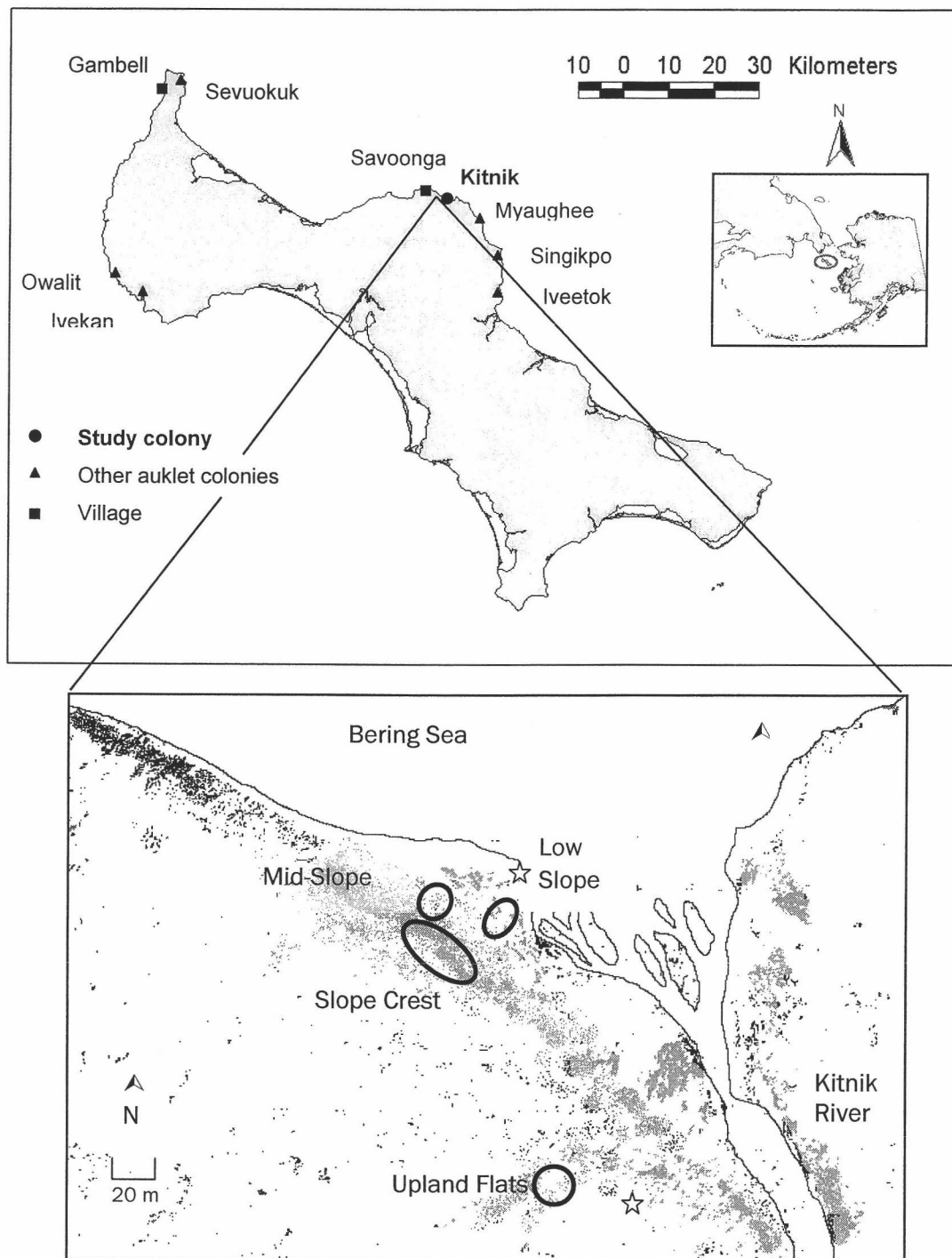


Figure 4.1. The Kitnik auklet colony on the north shore of St. Lawrence Island, Alaska, showing the location of study plots. Stars indicate the location of the observation points. Circles indicate the areas of the colony. Shading represents changes in elevation.

We photographed the 12 study plots, marked the four corners permanently with metal stakes, and delineated the perimeter with white cord, which was removed at the end of each field season. The coordinates of the four corners of each plot were also marked using a Garmin eTrex GPS receiver.

Surface Counts

We counted Least and Crested auklets present on the surface of the colony within the boundaries of the 12 monitoring plots ("surface counts") using both 10x42 binoculars and a Leica 30-60x spotting scope. Counts were conducted at 15-minute intervals during 4-hour monitoring periods timed to coincide with the daily period of peak surface attendance. Surface counts were conducted every 4 days (weather permitting) during 7 July – 26 August 2001 and 25 June – 20 August 2002. An initial all-day count was conducted at the beginning of each field season, on 2 July in 2001 and 21 June in 2002, to confirm the timing of peak surface attendance and determine the timing for 4-hour monitoring periods. For the initial all-day count, auklets on the 8 slope plots (101-108) were counted every 15 minutes during daylight hours (0500-0200 hrs Alaska Daylight Time). All-day counts were conducted every 3 weeks to adjust the timing of counts because the timing of peak surface attendance shifted during the breeding season.

In 2001 and 2002, we conducted nest exclusion experiments to test the assumption that densities of Least and Crested auklets on the colony surface are closely associated with the density of active nests below the surface. One plot from each of 3 main areas of the colony (Low Slope, Slope Crest, and Upland Flats) was used for the nest exclusion experiment. Auklets were excluded from nesting in these plots by covering them completely with plastic tarps, which prevented nesting auklets from accessing nest sites beneath. The tarps were left in place for three weeks from

egg-laying until about one week prior to chick hatching to ensure that no nests were initiated beneath the tarped plots. In two of the areas, pre-existing plots were designated as control plots and were not covered with tarps in either year. In the third area, one plot was randomly selected as the control plot. Of the 2 remaining plots in each area, one plot was randomly selected to be an experimental plot in 2001 and the other plot was used as an experimental plot in 2002. Plots 101, 102, and 201 were covered with tarps in 2001, while plots 104, 105, and 202 were covered in 2002. Surface counts on the three experimental plots during chick-rearing were compared to simultaneous counts on plots that had not been covered with tarps. The maximum daily counts for each control plot were used for comparison of colony surface attendance between treatments, among areas, and between years.

Mark-resighting

One monitoring plot on the Kitnik Colony (Plot 107) was selected in 2000 as a banding plot. This plot was located close to the beach on the western edge of the Kitnik River delta, directly in front of the observation blind. A second banding plot (Plot 204), located in the Upland Flats area, was added in 2001. Banding and resighting continued at both plots through 2002.

Least Auklet adults were captured on banding plots using noose mats during incubation and chick-hatching. On Plot 107, we banded 23 breeding adults in 2000, 17 breeding adults in 2001, and 27 breeding adults in 2002. On Plot 204, we banded 40 breeding adults in 2001 and 41 breeding adults in 2002. Breeding adults were identified by plumage (Jones 1993a, 1993b) and presence of a brood patch. Each individual was banded with a stainless steel band on the distal portion of one leg, and a unique color combination of Darvik plastic bands: one colored band on the proximal portion of the metal-banded leg and 2 colored bands on the other leg.

Resighting observations were conducted on each banding plot at least once every 4 days. During 4-hour monitoring periods timed to coincide with the daily peak in surface attendance, we recorded all resightings of color-banded adults. Any banded bird sighted multiple times within a single 15-minute period was recorded only once. We banded Crested Auklet adults following the same protocol, but sample sizes of banded birds on the 2 plots were too small to estimate abundance using mark-resighting techniques.

Statistical Analysis of Surface Counts

We used 2 metrics to characterize surface counts: maximum daily counts and mean daily high counts. Jones (1992) and Fowler and Irons (1994) used the single highest count of auklets $\text{plot}^{-1} \text{ day}^{-1}$ to estimate day-to-day variability in surface attendance. Williams et al. (2000) used the mean high count (i.e., average of the five highest counts) $\text{plot}^{-1} \text{ day}^{-1}$ to estimate the daily peak in surface attendance. Results were similar regardless of whether means or maximum counts were used. Test statistics reported are from analysis of maximum counts $\text{plot}^{-1} \text{ day}^{-1}$, as in previous studies (Jones 1992, Fowler and Irons 1994).

Surface count analysis was based on Piatt et al.'s (1990) recommendations for censusing auklet colonies. Other studies have found that the period from mid incubation to mid chick-rearing is the stage of the nesting cycle when surface counts are least variable (Piatt et al. 1990, Fowler and Irons 1994). Talus size strongly influences relative densities of Least and Crested auklets on surface plots (Byrd et al. 1983, Piatt et al. 1990), so plots were grouped according to habitat characteristics. We used the maximum daily counts per plot during the mid incubation to mid chick-rearing period (referred to as the Piatt index) to examine differences in surface counts among areas and between years. We analyzed for differences in the number of

auklets per plot among plots and areas of the colony using parametric nested ANOVAs, and we used non-parametric Kruskal-Wallis rank sum procedures in S-Plus (Insightful Corp. 2001) to determine possible differences in colony surface attendance related to area of the colony and year.

We compared results of the recommended methods for analyzing surface counts to an alternative method of modeling surface attendance from laying to late chick-rearing. We used quasi-likelihood, log-linear models to examine the effects of species, plot area, date, and year on colony attendance from laying to late chick-rearing. Quasi-likelihood regression was used because the response variable consisted of integer counts (maximum daily count per plot), and these models account for both Poisson distribution of counts and extra-Poisson variation (Ramsey and Schafer 2002: 656). Maximum attendance per plot was regressed against three variables: year, Julian date, and area of the colony. Least Auklets and Crested Auklets were modeled separately. We also considered interactions and quadratic terms to account for non-linear relationships among variables. We started with two simple models (one for each species) including the main effects (year, date, and area of the colony), and then used step-wise selection to include quadratic and interaction terms. The final model for each species was tested against its corresponding global model (model including interaction terms) for lack of fit using a drop-in-deviance F test (Ramsey and Schafer 2002: 655). Low F-values indicate the reduced model accounts for similar variance as the full model, and provides a fit to the data that is not significantly different from the global model.

Data were tested for serial correlation because the data were collected at regular intervals (every 4 days). There was no evidence of serial correlation in either year for either species in any area of the colony, so we proceeded with the analyses.

The Low Slope plots were chosen as a reference level for this analysis, because this was the area of lowest counts for Crested Auklets. There were no significant differences in Least Auklet counts among areas of the colony (see Results), so we chose the Low Slope plots as the reference level to be consistent with Crested Auklet models. We assessed effects of the other three areas on maximum number of auklets per plot relative to the Low Slope plots. *P*-values reported for relative effects of area, date, and year were derived from Wald's tests for single coefficients and are approximate. *P*-values reported for relative effects of groups of variables were assessed using drop-in-deviance *F* tests. Parameter estimates of quadratic and interaction effects are difficult to interpret (Ramsey and Schafer 2002: 245), so results are presented as a qualitative analysis to determine which factors are useful to develop predictive models for maximum values of colony surface attendance. Results of the nest exclusion experiment were analyzed using two-way ANOVAs, after verifying that the data met the assumptions of normality.

Analysis of Band Resighting

We counted all visible Least Auklets at the beginning of each 15-min period of resighting and recorded status as either: banded and identified, banded but not identified, or unbanded. We used the resighting frequencies y_i of all individuals seen on each plot from the last day of banding to the last day of colony surface activity (27 July – 8 August in 2001 and 25 July – 15 August in 2002) to calculate Bowden's estimate of abundance (Bowden and Kufeld 1995) for each plot in each year using program NOREMARK (White 1996). The parameters included in this estimator were: the total number of unmarked individuals sighted ($u.$), the total number of marked individuals resighted ($m.$), and the total number of marked birds available for

resighting in that year (T). Bowden's estimator is a bootstrap estimator of population size based on the sighting frequency of individuals:

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

where f is the mean resighting frequency of marked individuals and s^2 is the variance of sighting frequencies of the marked individuals. The confidence intervals are computed based on the variance of the resighting frequencies of marked animals:

$$\text{Var}(\hat{N}) = \frac{\hat{N}^2 \left(\frac{1}{T} - \frac{1}{\hat{N}} \right) \frac{s_f^2}{f^2}}{\left(1 + \frac{s_f^2}{T \cdot f^2} \right)^2}$$

Bowden's estimator is robust to heterogeneity of individuals being resighted, provides a closed form estimator of the sampling variance, and procedures for setting confidence intervals (Bowden and Kufeld 1995).

In order to include Least Auklets banded in previous years as well as during both years of the study, we estimated the total current size of the marked population on each plot for each year of the study. We created capture histories for all marked individuals sighted on each banding plot in each year. Individuals seen attending the surface of a banding plot at least twice at any time during the breeding season, or seen delivering a chick meal to a crevice at least once were included in the marked population for that plot in that year. Means are reported ± 1 SE, unless otherwise stated.

RESULTS

Colony Surface Attendance

Timing of daily peak attendance

We conducted three 20-hour counts (all-day counts) during each breeding season to determine the periods of peak colony attendance. In 2001, all-day counts were conducted on 2 July (early incubation), 19 July (late incubation), and 8 August (early chick-rearing). In 2002, all-day counts were conducted on 21 June (early incubation), 11 July (late incubation), and 31 July (early chick-rearing). The peak surface activity periods of Least and Crested auklets occurred during the early morning hours in late June, but shifted through the season to peak in mid-afternoon by August (Figure 4.2, Figure 4.3). The peak activity periods of Least and Crested auklets were from 0630 to 1100 during early incubation, 1130–1600 during late incubation, and 1430–2000 during chick-rearing in both years. Surface counts of Least and Crested auklets during incubation were bi-modal, consisting of a 4–6 hour period of activity in the morning and a 2–3 hour period of activity at dusk. During chick-rearing, peak surface attendance shifted later in the day and the peaks in attendance became less distinct. We used counts conducted during the morning/early afternoon surface attendance period in subsequent analyses of daily colony attendance.

Mid incubation to mid chick-rearing surface counts

Daily maximum counts on plots revealed that colony surface attendance of Least and Crested auklets peaked within two weeks of median hatch date in both 2001 and 2002, but peak attendance occurred prior to the median hatch date in

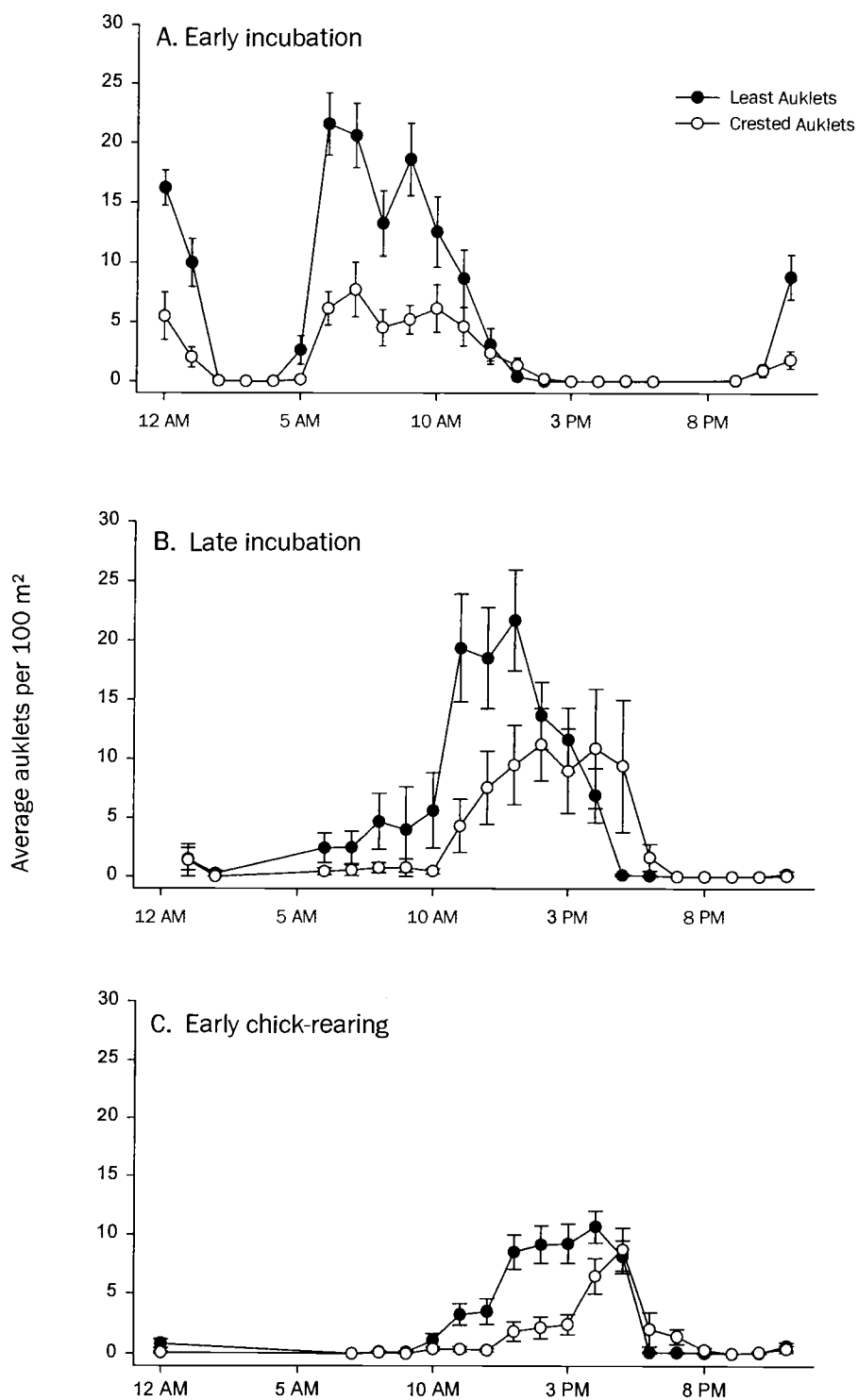


Figure 4.2 Diurnal colony surface attendance of Least and Crested auklets on the Kitnik colony, St. Lawrence Island, Alaska in (A) early incubation, (B) late incubation, and (C) early chick-rearing during the 2001 breeding season.

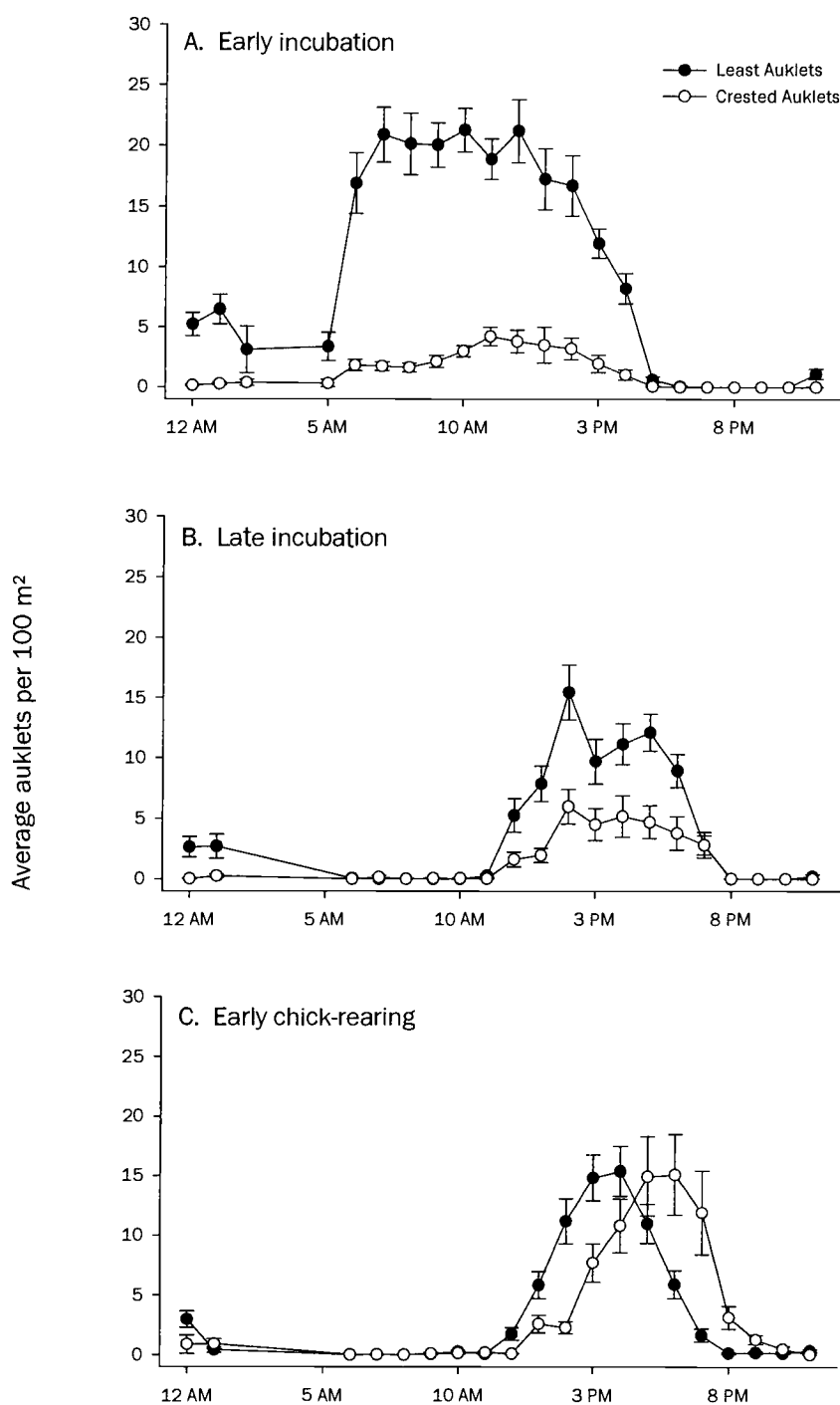


Figure 4.3. Diurnal colony surface attendance of Least and Crested auklets on the Kitnik colony, St. Lawrence Island, Alaska in (A) early incubation, (B) late incubation, and (C) early chick-rearing during the 2002 breeding season.

2001 and after the median hatch date in 2002 for both Crested Auklets (Figure 4.4) and Least Auklets (Figure 4.5). Both species spent little time attending the surface of the colony after mid-August, the latter half of the chick-rearing period.

To compare surface attendance levels among areas and between years (2001 vs. 2002), we compared daily maximum counts for each of nine control plots during the mid incubation to mid chick-rearing period (15 July - 19 August, 2001; 9 July - 14 August, 2002). Area differences in colony surface attendance were consistent between years for Crested Auklets (Figure 4.6A). Surface counts of Crested Auklets from the four areas of the colony were significantly different from each other in 2001 (Kruskal-Wallis, $H_3 = 19.07$, $P < 0.001$) and in 2002 (Kruskal-Wallis, $H_3 = 35.1$, $P < 0.001$). Maximum counts of Crested Auklets were similar among plots within the same area in 2001 (Plot nested within Area: $F_{5, 66} = 0.61$, $P = 0.69$) but differed within area in 2002 (Plot nested within Area: $F_{5, 84} = 4.06$, $P = 0.002$). Surface counts of Crested Auklets were highest on plots in the Slope Crest area of the colony in both 2001 ($\bar{x} = 15.6$ birds, $n = 9$ days sampled) and in 2002 ($\bar{x} = 20.5$ birds, $n = 10$ days sampled). Surface counts of Crested Auklets were lowest in the Low Slope area of the colony in 2001 ($\bar{x} = 1.6$ birds, $n = 9$ days sampled) and 2002 ($\bar{x} = 3.5$ birds, $n = 10$ days sampled). We compared average surface attendance of Crested Auklets between years for each area separately using Mann-Whitney U-tests and found no significant differences between 2001 and 2002 for any of the four colony areas (all P -values > 0.2).

Differences in colony surface attendance among areas of the colony were less pronounced for Least Auklets (Figure 4.6B) compared to Crested Auklets. Surface counts of Least Auklets were not significantly different among the four areas of the

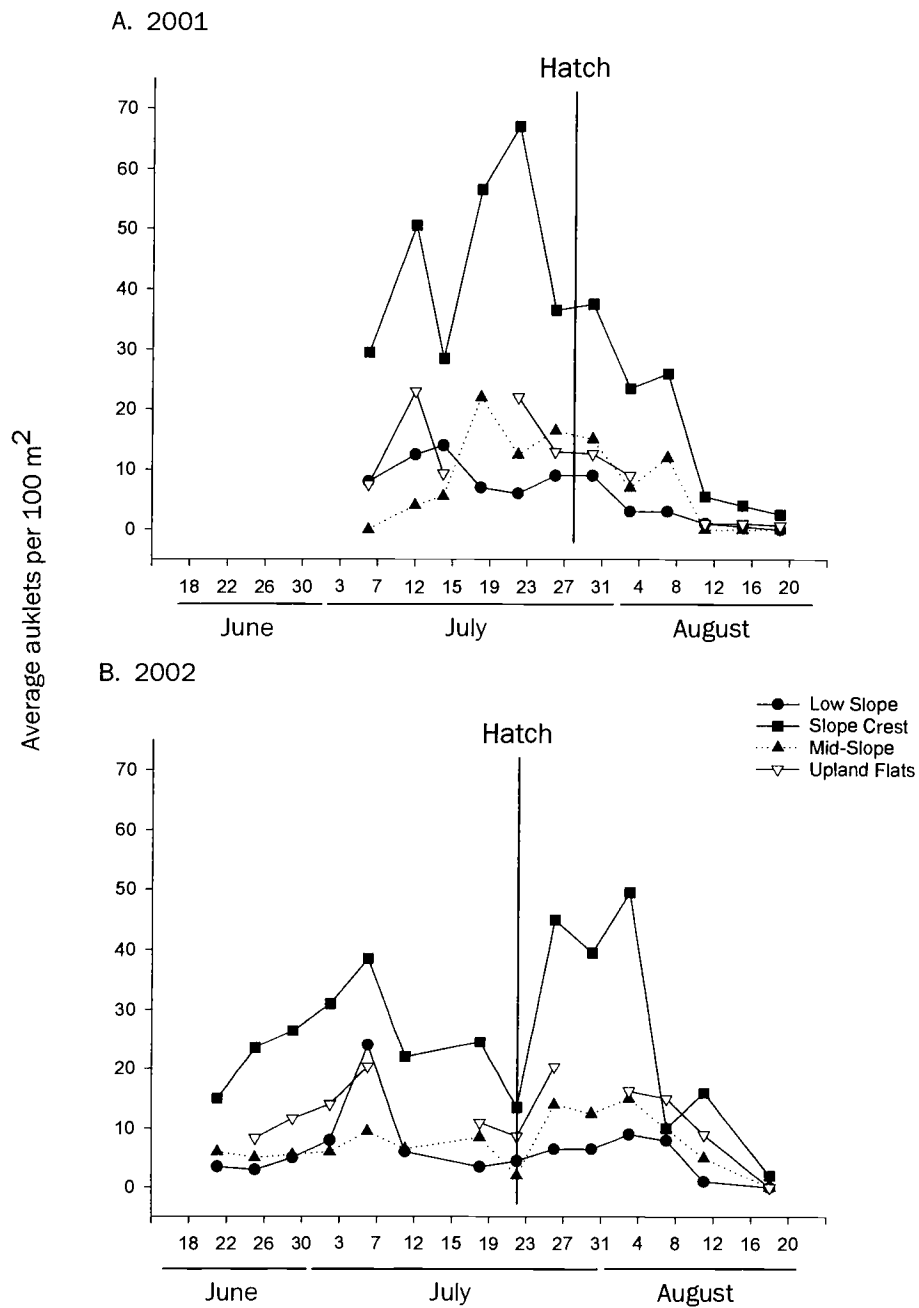


Figure 4.4. Average maximum counts of Crested Auklets per plot on 4 areas of the Kitnik colony, St. Lawrence Island, Alaska in (A) 2001 and (B) 2002.

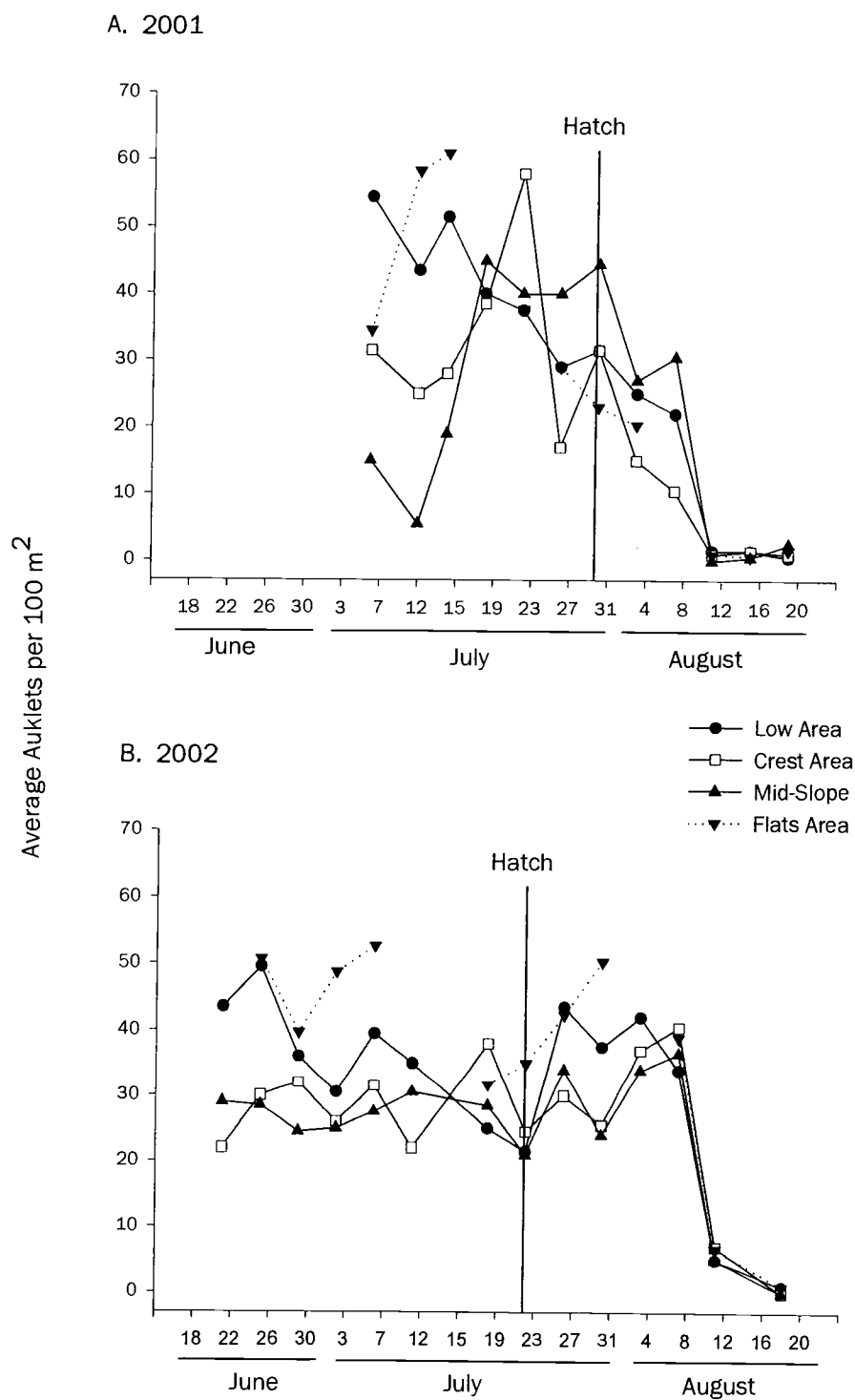


Figure 4.5. Average maximum counts of Least Auklets per plot on 4 areas of the Kitnik colony, St. Lawrence Island, Alaska in (A) 2001 and (B) 2002.

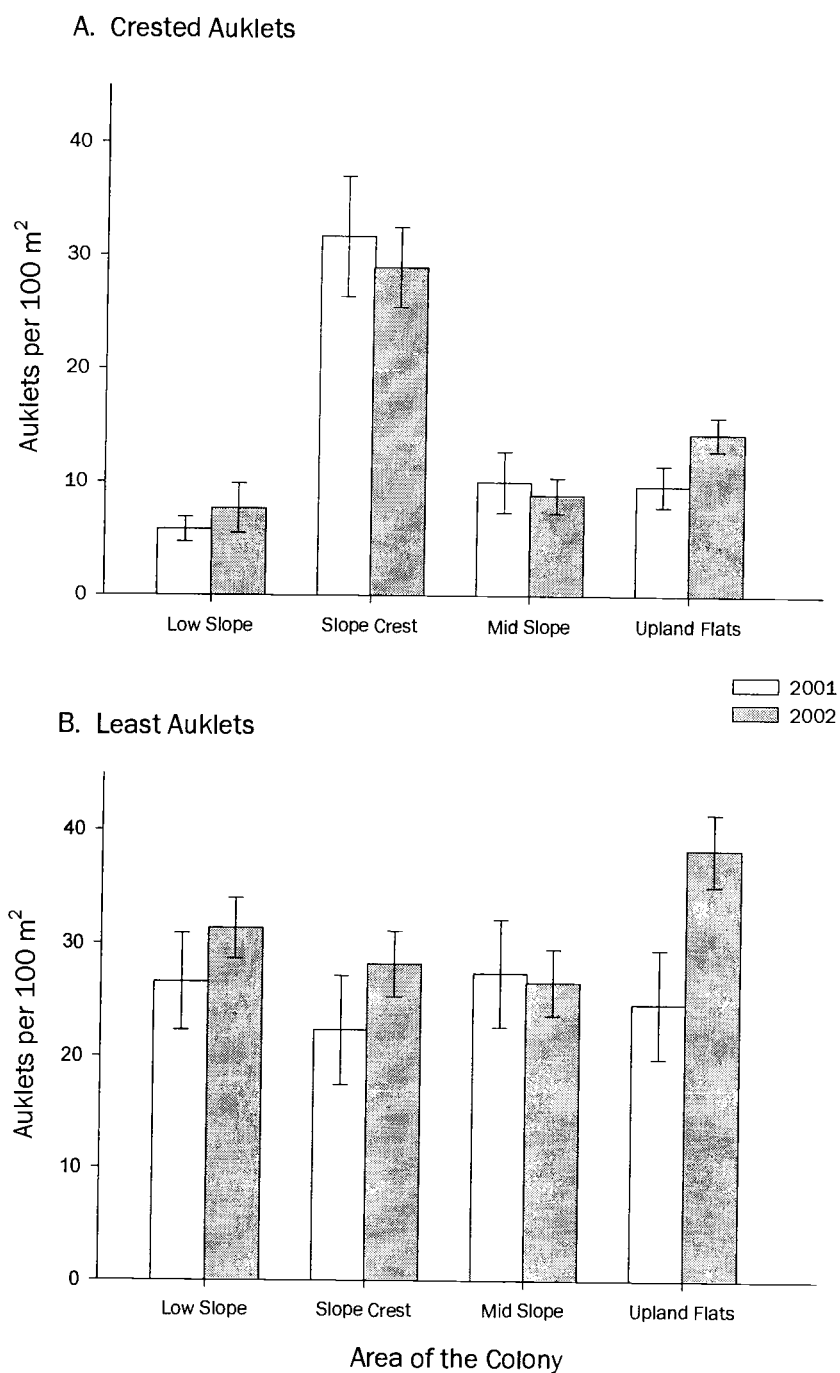


Figure 4.6. Numbers of Crested Auklets (A) and Least Auklets (B) observed on the surface of index plots in 4 areas of the Kitnik colony, St. Lawrence Island, Alaska, 2001 and 2002. Numbers represent means of the maximum counts on each of 9 plots, during the mid-incubation to mid chick-rearing period. Error bars represent one standard error.

colony in 2001 (Kruskal-Wallis, $H_3 = 3.21$, $P = 0.361$), but they were in 2002 (Kruskal-Wallis, $H_3 = 15.2$, d.f. = 3, $P = 0.002$). As with Crested Auklets, maximum counts of Least Auklets differed among plots within the same area in 2002 ($F_{5, 84} = 9.73$, $P < 0.001$), but not in 2001 ($F_{5, 66} = 0.80$, $P = 0.55$). In 2002, surface counts of Least Auklets were lowest on plots in the Slope Crest area ($\bar{x} = 20.0$ birds, $n = 10$ days sampled) and highest on the Upland Flats area. As with Crested Auklets, there were no significant between-year differences in average colony surface attendance for Least Auklets on any of the four colony areas (all P -values > 0.3).

Log-linear regression models

In addition to variation in surface counts among areas of the colony, there was high temporal variability in surface counts across the breeding season. The log-linear regression model for Crested Auklet surface attendance indicated that area differences in surface attendance were consistent between years, after accounting for effects of date (Table 4.1). Counts on the Slope Crest area of the colony were significantly higher than counts on the Low Slope area in both years of the study ($P < 0.001$ from t-test for effect of Slope Crest area) and counts on the Mid-Slope area were significantly higher than counts on the Low Slope ($P < 0.001$). Quadratic terms for date were incorporated into the models to account for non-linear changes in colony attendance through the breeding season. These quadratic terms provided support for the observation that the number of Crested Auklets on a plot increased to a maximum value during late incubation/early chick-rearing and subsequently declined during mid chick-rearing. Including quadratic terms in the inferential model significantly increased the fit of the model ($F_{2, 200} = 38.8$, $P < 0.001$ from a drop-in-deviance F test).

Table 4.1. Quasi-likelihood regression output for a model of the effects of year, area of colony, date, and interactions between these effects on maximum counts of Crested Auklets ($R^2 = 65.3\%$) and Least Auklets ($R^2 = 59.2\%$) on plots at the Kitnik colony, St. Lawrence Island, Alaska. All t-tests are based on the coefficient estimates and the adjusted standard errors.

Coefficients	Crested Auklets				Least Auklets			
	Estimate	Standard Error	t-value	P-value	Estimate	Standard Error	t-value	P-value
Intercept	-90.84	12.92	-7.03	< 0.001	-69.51	9.98	-6.96	< 0.001
Date	64.13	12.92	4.96	< 0.001	58.70	9.98	5.88	< 0.001
Date ²	-0.002	0.000	-7.41	< 0.001	0.74	0.10	7.52	< 0.001
Slope Crest	0.76	0.07	10.58	< 0.001	-0.11	0.05	-2.34	< 0.001
Mid-Slope	0.18	0.05	-3.87	< 0.001	-0.04	0.03	-1.43	0.08
Upland Flats	0.01	0.03	0.41	0.34	0.06	0.02	3.31	< 0.001
Year * Date	-0.64	0.13	-5.02	< 0.001	-0.59	0.10	-5.97	< 0.001
Year * Date ²	0.001	0.00	5.07	< 0.001	0.001	0.000	6.06	< 0.001

There was strong evidence that seasonal patterns of colony surface attendance differed between years, after accounting for differences among areas of the colony ($P < 0.001$, from a test for interaction between year and date²). In 2001, the highest count of Crested Auklets was recorded on plots in the Slope Crest area of the colony 14 days before the median hatch date and colony surface attendance was very low 10 days after the median hatch date (Figure 4.4A). In 2002, the highest count of Crested Auklets was recorded 12 days after the median hatch date, and colony surface attendance persisted until 20 days after the median hatch date (Figure 4.4B). The inferential model explained 65% of the variation in surface counts ($R^2 = 0.653$), and inclusion of more parameters did not significantly improve the fit of this model ($F_{6,200} = 1.50$, $P = 0.82$).

Patterns of surface attendance by Least Auklets also differed between 2001 and 2002. The highest average surface count of Least Auklets in 2001 was recorded in the Upland Flats area 16 days before the median hatch date (Figure 4.5A). Surface attendance remained high during late incubation, and then declined steadily to very low levels 12 days after the median hatch date. In 2002, the highest average counts were again recorded in the Upland Flats area of the colony, but occurred both 16 days before and 8 days after the median hatch date (Figure 4.5B). Contrary to 2001, in 2002 there were 20-50 auklets recorded on each plot in each area of the colony during peak attendance periods until 25 days after the median hatch date, when colony surface attendance sharply declined. There was strong evidence of a quadratic effect of date on surface counts of Least Auklets for all four areas of the colony ($F_{3,203} = 45.9$, $P < 0.001$, from a drop-in-deviance test). As with Crested Auklets, seasonal patterns of Least Auklet colony surface attendance also were different between 2001 and 2002 ($t = 6.1$, $df = 200$, $P < 0.001$ for interaction of year

and date²). The same parameters selected for Crested Auklet colony surface counts provided the best fit to Least Auklet colony surface counts, relative to a global model including interaction terms ($F_{9, 200} = 2.02$, $P = 0.96$). The inferential model explained 59% of the variation in surface counts ($R^2 = 0.592$), suggesting similar factors affected both Least and Crested auklet colony surface attendance (Table 4.1).

Nest Exclusion Experiment

No adults were observed delivering meals to chicks within the experimental plots, providing evidence that there were no active nests within plots that had been covered by tarps. Preventing nest initiation by covering plots with tarps did not reduce subsequent colony surface attendance during chick-rearing (after the tarps were removed) for either species. There was no difference in surface counts of Least Auklets conducted after median chick hatch date between control plots and experimental plots (no active nests) in either 2001 (ANOVA, $F_{2,55} = 0.163$, $P = 0.850$) or 2002 ($F_{2,55} = 0.740$, $P = 0.482$), after accounting for area of the colony (Figure 4.7). There was no difference in surface counts of Crested Auklets conducted after the median hatch date between control and experimental plots in 2001, after accounting for area of the colony ($F_{2, 55} = 0.004$, $P = 0.95$). There were, however, higher Crested Auklet surface counts on experimental plots compared to control plots in 2002 ($F_{2,64} = 15.87$, $P < 0.001$; Figure 4.8).

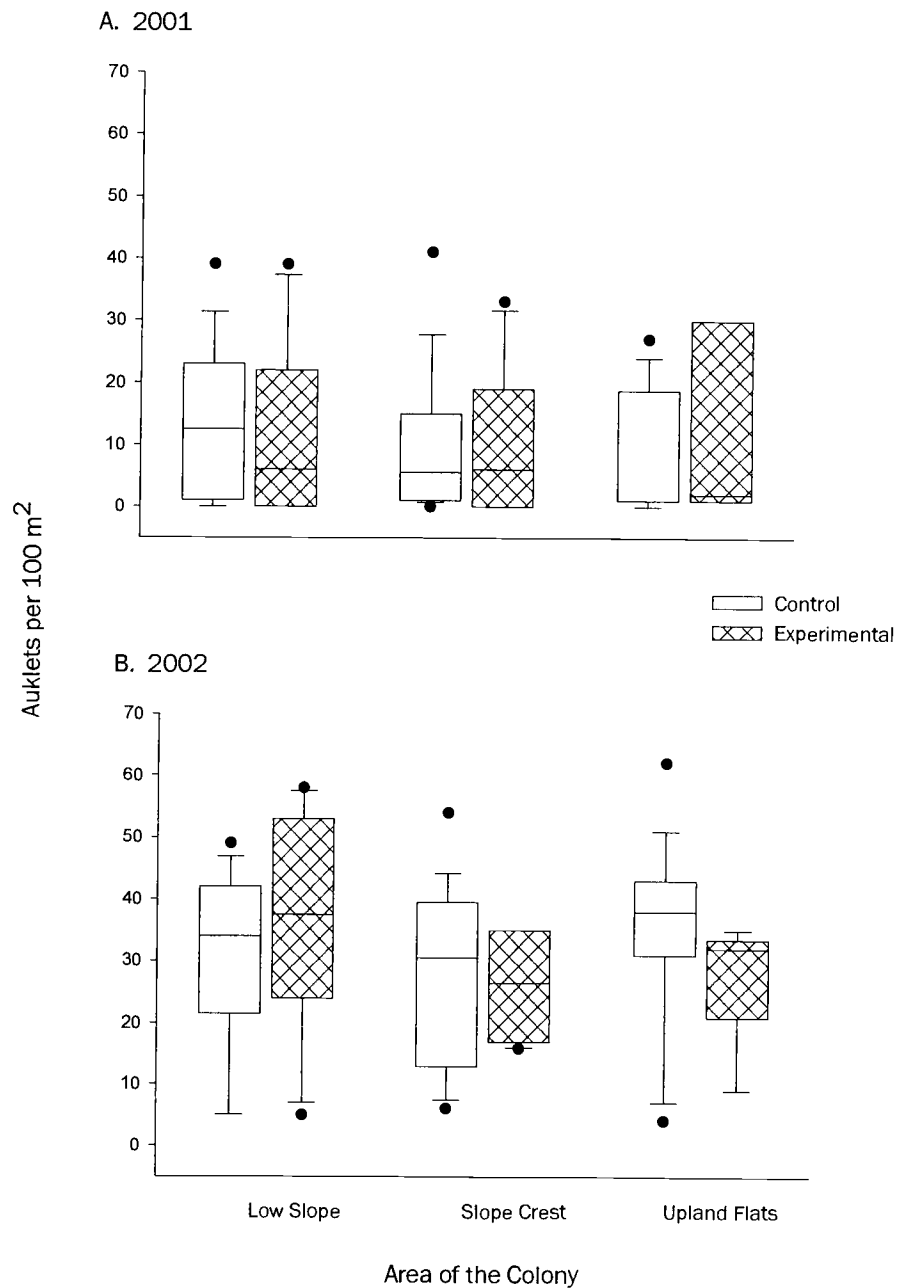


Figure 4.7 Least Auklet colony surface counts on control plots and experimental plots (no active nests) during chick-rearing in 3 areas of Kitnik colony, St. Lawrence Island, Alaska in 2001 and 2002. Whiskers represent 1st and 4th quartiles. Dots represent the range of surface counts.

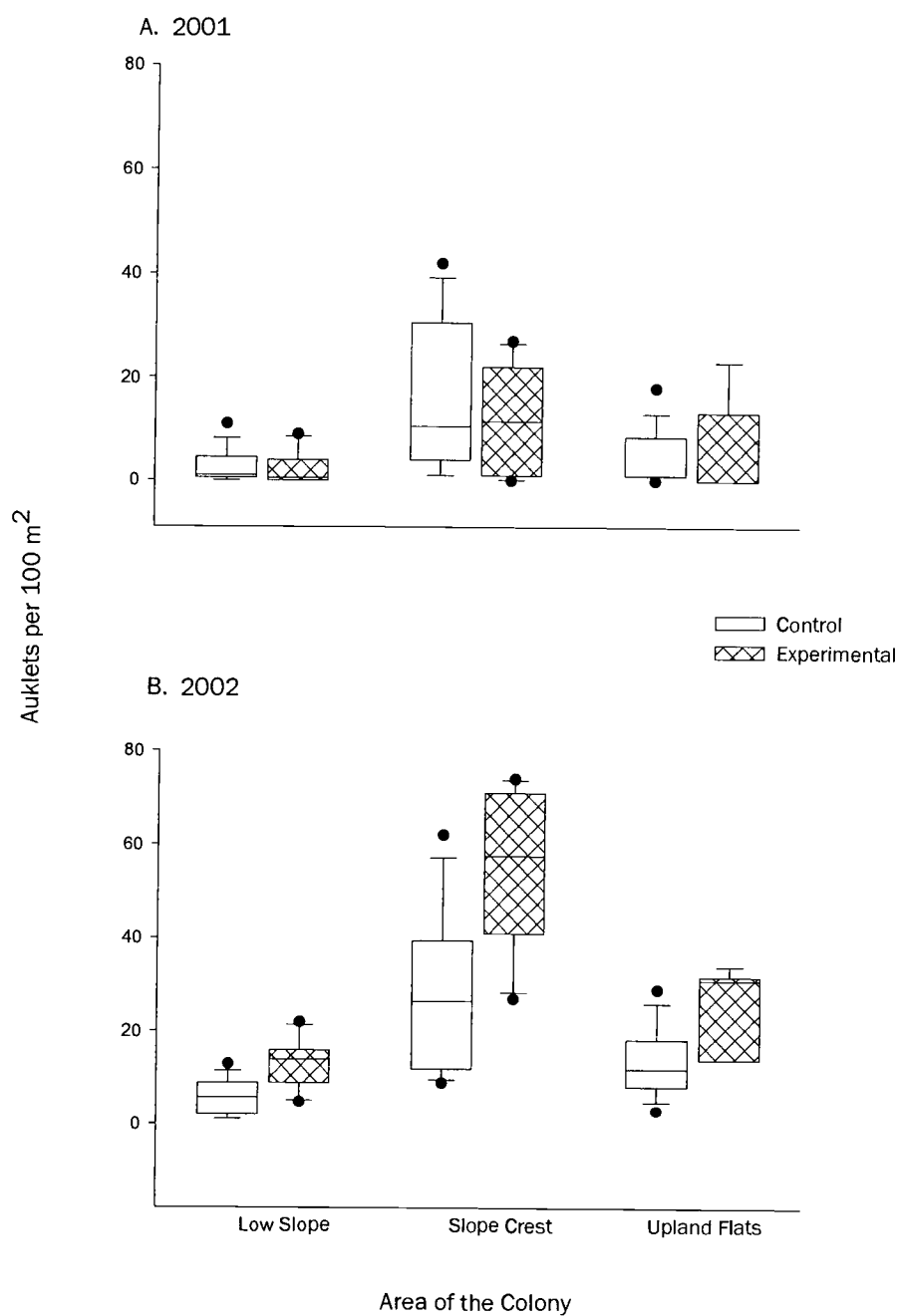


Figure 4.8. Crested Auklet colony surface counts on control plots and experimental plots (no active nests) during chick-rearing in 3 areas of Kitnik colony, St. Lawrence Island, Alaska in 2001 and 2002. Whiskers represent 1st and 4th quartiles. Dots represent the range of surface counts

Estimates of nesting density

Based on 12 days of resighting effort for plot 107 in 2001, 26 color-banded Least Auklet adults were resighted on the surface of the plot at least twice and/or delivering a chick meal at least once and were assumed to be breeding adults during the resighting period. In 2002, 43 banded breeding adults were resighted on plot 107 during 22 days of observation. On plot 204, 23 banded adults were resighted during 13 days of observation in 2001 and 50 banded adults were resighted during 18 days of observation in 2002.

Estimates of the number of breeding adult Least Auklets in Plot 107 in the Low Slope area were 352 (95% CI: 248 to 501) in 2001 and 395 (95% CI: 306 to 510) in 2002. Estimates of the number of breeding adults for Plot 204 in the Upland Flats area were 242 (95% CI: 172 to 342) in 2001 and 223 (95% CI: 171 to 291) in 2002 (Figure 4.7). The similarity in estimated number of breeding adults between years and the large overlap in confidence intervals indicated there was no significant between-year difference in the estimated number of adult Least Auklets nesting in either Plot 107 or Plot 204. Coefficients of variation for estimates of the number of breeding adults were 8% between years on Plot 107 and 6% between years on Plot 204. We divided the estimated number of nesting adults by 2 and calculated Least Auklet nesting densities of 1.8 pairs per m² (95 % CI: 1.2 – 2.5) in 2001 and 2.0 pairs per m² in 2002 on Plot 107. Estimated nesting densities of Least Auklets were lower on plot 204 in both years. In 2001, there were 1.4 nests per m² (95% CI: 0.9 – 1.7) and in 2002, there were 1.1 nests per m² (95% CI: 0.9 – 1.5) on plot 204.

Average counts of Least Auklets attending the surface of the banding plots during the mid incubation to mid chick-rearing period were an order of magnitude

lower than estimates of the number of breeding adults nesting in the plots. On Plot 107, there were 37.2 ± 12.4 Least Auklets attending the surface in 2001 and 38.1 ± 12 Least Auklets attending the surface in 2002. On Plot 204, we counted 42.6 ± 12.4 Least Auklets on the surface in 2001 and 44.2 ± 12.0 Least Auklets on the surface in 2002. Maximum counts did not differ between years or between plots ($F_{3,28} = 0.78, P = 0.52$). In addition, coefficients of variation in surface counts between years were low on both plots (Plot 107: CV = 2%, Plot 107 CV = 3%).

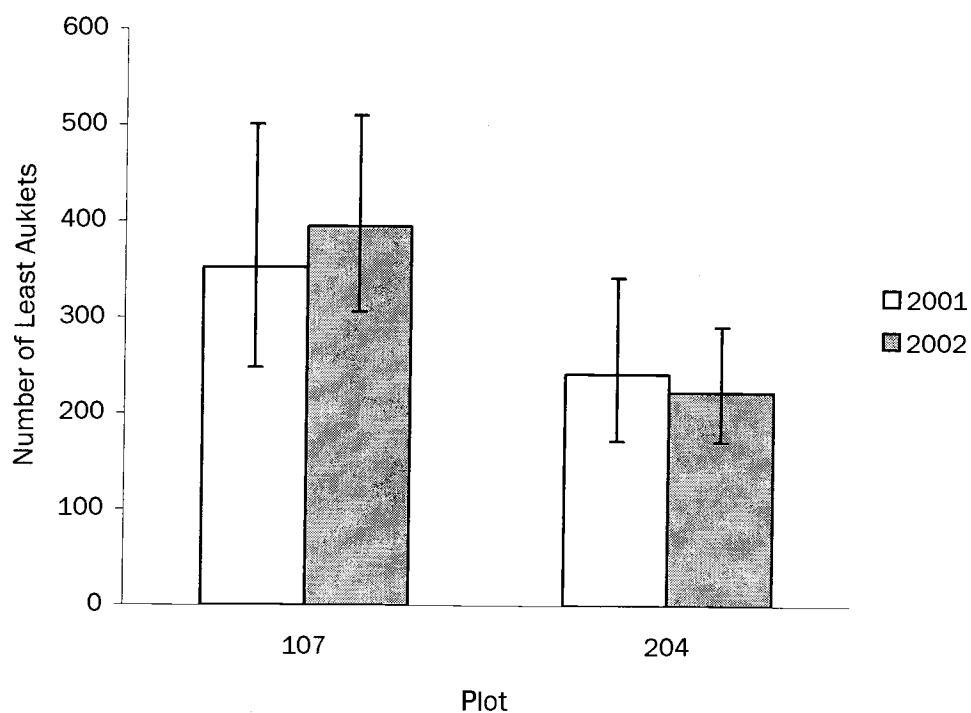


Figure 4.9. Estimates of the number of breeding adult Least Auklets nesting beneath two 100 m² study plots at the Kitnik colony, St. Lawrence Island, Alaska. Estimates were made using the Bowden estimator based on resighting frequencies of color-banded adults. Error bars represent 95% confidence intervals for the estimates.

DISCUSSION

Colony attendance

Crested Auklets may influence the numbers of Least Auklets attending the surface of mixed colonies through aggressive interactions (Bédard 1969, Byrd et al. 1983, Piatt et al. 1990), and these interactions are even more apparent in areas where nesting habitat for Crested Auklets is more limited than habitat for Least Auklets. The Kitnik colony includes steeply sloped sections with large average boulder size and little soil substrate visible between boulders, flat sections with small average boulder size and only one layer of boulders resting on dirt and organic substrate, and many intermediate microhabitat types. While Least Auklets are more abundant at the Kitnik colony than Crested Auklets (V. Zubakin, unpubl. data), there were areas of the colony that were dominated by Crested Auklets. Surface counts of Crested Auklets were highest on plots in the Slope Crest area of the colony, where average talus size was larger and the matrix of boulders was at least 2 m deep with little organic substrate visible from the surface. Crested Auklet counts were lowest on the Low Slope area of the colony, where talus size was smaller and there was more vegetation and soil between boulders. In 2002, surface counts of Least Auklets were highest on the Upland Flats, an area of little slope, smaller average talus size, and soil/vegetation between boulders. Differences in relative abundance of the two species in different areas of the colony highlight the importance of establishing replicate plots across the colony.

Models explaining variation in colony surface attendance contained the same parameters for both Least and Crested auklets. The models identified area of the colony, date, and year as significant factors explaining differences in surface counts. The between-year difference in timing of peak surface attendance was associated

with differences in the pattern of colony surface attendance all season long. In the year of relatively low reproductive success (2001; see Chapter 2), surface attendance peaked well before the median hatch date and declined rapidly after the median hatch date. In the year of relatively high reproductive success (2002; see Chapter 2), colony surface attendance was high during late incubation, but did not peak until after the median hatch date and persisted later into the chick-rearing period.

Counts of Least Auklets on surface plots differed significantly among the three years of a study at St. Paul Island in the southeastern Bering Sea, and were highest in the year of highest reproductive success (Jones 1992). Colony surface attendance also persisted later on St. Paul Island in the year of relatively high reproductive success (Jones 1992). We observed similar patterns of colony surface attendance at the Kitnik colony; colony surface attendance continued later into chick-rearing on Kitnik in 2002, the year of higher nesting success compared to 2001. Higher nesting success in 2002 apparently reflected higher availability of preferred prey (see Chapter 2). High colony surface attendance later in chick-rearing may be an indication of more time available for social interaction and territorial defense at the colony because of high food availability.

The results of the nest exclusion experiment indicate that numbers of auklets on surface plots during chick-rearing were not a reflection of the number of active nests beneath the plot. Auklets exhibit high nest-site fidelity at some colonies (Jones 1992, Fraser et al. 2002), so it is likely that many of the adults on the surface of experimental plots may have been breeders defending nest crevices they had used in previous years. Alternatively, adults on experimental plots during chick-rearing may have been prospecting for unoccupied nest sites. We speculate that the higher

counts of Crested Auklets on the experimental plots in 2002 compared to controls may have been due to prospecting non-breeders attracted by the unoccupied nest sites. These results also suggest that annual variation in reproductive success does not directly affect colony surface attendance per se, but instead low food availability may directly limit colony surface attendance.

Models to explain variation in colony surface attendance were developed using counts conducted throughout incubation and chick-rearing. Counts of both Least and Crested auklets on Mid-Slope plots during early incubation were lower than those in any other area of the colony. This difference was not apparent in the analysis of the Piatt index, which only used counts conducted during late incubation and early chick-rearing. The Mid-Slope area has a steep northern exposure, and so retains snow cover longer than other areas of the colony. If ice and snow linger, nesting crevices in the Mid-Slope area are not accessible to auklets prospecting for nest crevices during the laying period. Delayed accessibility may result in fewer auklets establishing and defending a territory or crevice nest site in this area of the colony. While the nest exclusion experiment indicated that surface attendance during chick-rearing was not a reflection of the number of active nests beneath the surface, limited or delayed access to nest crevices for several seasons may be sufficient to dissuade returning nesters and produce a difference in colony surface attendance, particularly during incubation.

Mark-resighting

A primary concern with using colony surface counts to detect changes in the size of breeding colonies is that changes in counts could be related to changes in behavior associated with prey availability or disturbance at the colony, rather than actual changes in numbers of breeding pairs (Gaston and Nettleship 1982, Jones

1992). Population estimates based on resighting marked individuals have an advantage over surface counts in that they can account for among-individual differences in behavior. Calvert and Robertson (2002) compared 5 techniques (including both counts and resighting estimates) for estimating colony size of Atlantic Puffins and were most confident in the estimate based on the Bowden estimator (Bowden and Kufeld 1995). Our estimates of numbers of breeding adults on plots based on resighting banded birds suggested that the number of breeding adults nesting beneath the plot did not differ between years. While the confidence intervals of each estimate were large, there was little difference in the estimates between years for either plot. Least and Crested auklets generally exhibit high nest-site fidelity and high survivorship (Fraser et al. 2002, Jones et al. 2002), so we expected that the numbers of adults attending the surface of banding plots would not change appreciably between years. These results were consistent with our results based on the Piatt index, which indicated no difference in maximum counts of auklets on the colony surface between 2001 and 2002.

Counts of auklets on the colony surface may provide an indication of among-year differences in colony attendance (Byrd et al. 1983, Jones 1992, Calvert and Robertson 2002), but estimation of the number of breeding pairs on plots based on a sample of marked birds shows more promise for detecting changes in the number of breeding pairs. Our results suggested that nesting density of Least Auklets was higher on Plot 107 than on Plot 204 in both years, whereas the Piatt index based on counts of auklets visible on the surface did not detect a difference between the plots in either year. The Bowden estimator is based on resighting frequencies and is robust to heterogeneity of resighting probabilities among marked individuals (Bowden and Kufeld 1995). Observations of marked birds can account for

individuals that are nesting in the plot but not observed on the surface and therefore provide an estimate of abundance, rather than an index. Resighting of marked individuals can also be used to estimate other parameters that indicate the health of the population, such as adult survival, reproductive success, and chick provisioning rates.

The number of auklets visible on the surface of the colony represents a small proportion of the number of breeding adults that may be nesting in the talus below the surface. In our study, surface counts on Plot 204 represented only 18% of the number of auklets estimated to be breeding in that plot and similarly, of surface counts on Plot 107 were only 10% of the estimate based on marked individuals. The proportion of breeding adults observed on the surface appears to vary across the colony, supporting results from the nest exclusion experiment that suggested there is no clear linear relationship between surface attendance and the number of auklets nesting beneath the surface.

Implications for monitoring

We documented several sources of variation in colony surface counts, thereby improving the sampling protocol so that the periods of highest and least variable colony surface attendance can be targeted. Despite the large variation in counts within 4-hour survey periods, the maximum counts during the mid-incubation to mid chick-rearing period did not differ between years. Relying on surface counts alone to estimate numbers of breeding adults is nevertheless confounded by the presence of non-breeders, and patterns of seasonal attendance that vary between years. These sources of variation in colony surface counts suggest that counts have lower power to detect changes in colony size compared to estimating number of breeding adults based on mark-resighting techniques.

Monitoring a marked sample of birds on plots is time-consuming, however, and can be difficult to apply to a sufficient number of plots across the colony to account for variation among areas of the colony. Individuals must be marked every year to maintain a high proportion of marked individuals in the plot. If a low proportion of individuals are banded, it is difficult or impossible to generate estimates with sufficient precision to detect even large a 50% change in abundance, as was the case with Crested Auklets in our study. Likewise, if nesting densities vary considerably across a large colony, inferences based on estimates of abundance from only a few plots may not be representative of the colony as a whole.

We recommend identifying at least 3 strata of habitat based on surface counts for each species: low, medium and high density. At least one banding plot should be established in a representative area of each stratum. Estimates of abundance and capture rates can be incorporated into simulations using program NOREMARK to explore trade-offs between banding and resighting effort for obtaining more precise estimates of abundance (White 1996). In situations where auklets are difficult to capture, or the range of habitat types (strata) exceeds the number of banding plots that can be monitored annually, we recommend establishing permanent surface count plots as the next best technique for assessing changes in auklet populations.

We recommend conducting surface counts every 4 days for at least 4 weeks (mid incubation to mid chick-rearing) to obtain a measure of the daily maximum number of auklets attending the surface of the study plots (Piatt index). If resources allow, surface counts should be conducted throughout the breeding season to further investigate the relationship between seasonal patterns in surface attendance and differences in reproductive success. These counts, if conducted on an annual basis as part of a long-term study of auklet populations, offer some hope of detecting

major change in colony size. While surface counts are highly variable across a breeding season, our increased understanding of the sources of variability improves our ability to detect the signal of population change. More research is needed to explore daily activity budgets of individual auklets and determine how individual differences in behavior of breeding birds may influence surface counts. Mark-resight studies of adult survival and proportions of breeders attending the colony surface should be used in conjunction with surface counts to validate inferences based on surface counts and to assess changes in density of breeding auklets in plots over time.

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CHAPTER 5

Conclusions

Adrian E. Gall

Seabirds are recommended as indicators of marine conditions (Cairns 1987, Monaghan et al. 1996), but an understanding of their basic life history is required in order to interpret how differences in populations reflect changes in the marine environment. I studied Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) nesting at two colonies on St. Lawrence Island, Alaska to develop a protocol for long-term data collection capable of detecting changes in planktivorous seabird populations, their nesting success, and their food habits. Specifically, I examined how reproductive success of planktivorous seabirds was related to diet. I evaluated the use of morphometrics to estimate body composition of breeding auklets and examined the relationship between body composition of adults at egg-laying and subsequent reproductive success. I also compared two methods of monitoring populations (counts of auklets on the colony surface and mark-resighting) for detecting annual changes in breeding populations of Crested and Least auklets during the 2001 and 2002 breeding seasons on the Kitnik colony.

The results of this 3-year study emphasized the relationship between the breeding ecology of plankton-feeding auklets and the marine environment. Least and Crested auklets nesting on St. Lawrence Island are dependent on prey forced to the surface by the Anadyr current, which carries with it zooplankton species characteristic of deep oceanic waters (Obst et al. 1995). In a year when diets of breeding auklets indicated relatively high availability of large, oceanic copepods, I found that: (1) adult body mass of Least Auklets was relatively high, (2) adult body mass of Crested Auklets increased, rather than decreased, through the breeding season, and (3) reproductive success was relatively high (> 70%) at both colonies monitored. In a year when diets indicated relatively low availability of oceanic copepods, I found that: (1) adult body mass of Least Auklets was relatively low, (2)

adult body mass of Crested Auklets declined through the breeding season, and (3) reproductive success was relatively low (30-40%) at the Kitnik colony. These results suggest that auklet breeding parameters were influenced by the availability of prey resources that are dependent on ocean conditions.

Cairns (1987) suggested that behavior of seabirds (i.e., colony attendance) may be the most sensitive indicator of marine food supply. My study of banded Least Auklets indicated that there were differences in patterns of colony attendance between years, despite no significant between-year difference in estimated nesting densities within the study plots. Colony surface attendance of Least and Crested auklets declined abruptly after the median hatch date in the year of relatively low food availability. I found attendance on the colony surface persisted until late chick-rearing in the year of relatively high food availability, consistent with the hypothesis that auklet colony attendance increases when food is abundant (Jones 1992). Colony surface attendance may, therefore, be useful to assess auklet responses to changes in prey availability around St. Lawrence Island. More research is needed to investigate the daily activity budgets of auklets and quantify differences in prey availability that may affect the behavior of breeding birds.

Mark-resighting techniques may provide more accurate estimates of changes in the breeding population than colony surface counts, and can also be used to estimate annual adult survival. Monitoring a marked sample of birds, however, is time-consuming, and if a small proportion of individuals are banded, it is not possible to generate estimates with sufficient precision to detect even large differences in breeding populations. While surface counts are highly variable across a breeding season, an increased understanding of the sources of this variability will improve our ability to detect population change from surface counts. Further research into how

the behavior of sub-adults and non-breeding adults may influence counts of individuals attending the colony surface would be useful, particularly if surface counts continue to be used for monitoring changes in auklet populations.

In addition to providing an index to marine conditions around St. Lawrence Island, auklet breeding populations are being monitored throughout their range to evaluate their conservation status as species under the trust of the U.S. Fish and Wildlife Service (Dragoo et al. 2003). The protocols developed in this study were based on those used to monitor auklets in the Aleutian Islands, approximately 1700 km south of St. Lawrence Island. It is important to understand the sources of temporal variation at each monitoring site and to standardize the protocols if comparisons are to be made among colonies. Factors such as latitude, nesting habitat, oceanography, and predation pressure can lead to observed differences in breeding and population parameters among auklet colonies in the Bering Sea. For example, auklets on St. Lawrence Island are exposed to native mammalian predators, and those on Kiska Island (in the Aleutian Island chain) are under strong predation pressure from introduced Norway rats (*Rattus norvegicus*; Major and Jones 2003). In contrast, there are no mammalian predators on Buldir Island, a major auklet colony in the Aleutian Islands (Jones 1993a, 1993b). By refining monitoring protocols and identifying sources of variability in breeding parameters at each colony, a comprehensive monitoring program such as the one currently conducted by the Alaska Maritime National Wildlife Refuge can track auklet population changes throughout their range.

Monitoring changes in populations and breeding ecology of Least and Crested auklets in the northern Bering Sea may be especially important given the potential for broad-scale changes in ocean conditions related to global climate change (Hare and

Mantua 2000, Hunt et al. 2002). While auklet populations currently appear to be thriving on St. Lawrence Island, a population analysis approach can improve the development of a long-term monitoring protocol (Akçakaya et al. 2003). Population models rely on reproductive success, juvenile recruitment, and adult survival to predict trends in population change. Variables such as prey availability, atmospheric indices, and habitat availability can be incorporated into population models to test hypotheses about the causes of population change. For example, if the average temperature in the Arctic region continues to increase and the extent of sea ice and persistence of snow cover are reduced, the onset of egg-laying may gradually advance. I found that early nest initiation was associated with high reproductive success of Least and Crested auklets, but this relationship may not persist if the structure of the zooplankton community in the northern Bering Sea shifts in response to climate change.

The extent and persistence of sea-ice cover has decreased in the northern Bering Sea over the past 3 decades (Hunt et al. 2002), potentially weakening the Anadyr Current and the high productivity associated with it (Roach et al. 1995, Schell 2000). A decrease in currents flowing from the Bering Sea into the Arctic Ocean could reduce the transport of cold, nutrient-rich water, which could have strong effects on the planktivorous auklet colonies of St. Lawrence Island by reducing the availability of large, oceanic copepods. In a year of relatively low reproductive success, I found a high prevalence of neritic copepods in Least Auklet diets and a high prevalence of amphipods in Crested Auklet diets, suggesting that low availability of oceanic copepods over multiple breeding seasons could lead to population declines of Least and Crested auklets. Annual monitoring of reproductive success, adult body mass, colony attendance, and diet composition of plankton-feeding

auklets on St. Lawrence Island will yield empirical data with which to investigate the effects of natural and anthropogenic climate change on the trophic structure and function of the northern Bering Sea.

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APPENDIX

Appendix. Candidate models to evaluate the effects of year and Julian date on adult body mass of Least and Crested auklets on St. Lawrence Island, Alaska during the 2000-2002 breeding seasons.

Species	Model ^a	Parameters	Hypothesis
Least Auklets	Y + D + B + Y*D	6	Patterns of seasonal mass change differed among years, after accounting for differences in body size
	Y + D + B	4	Total body mass differed among years, after accounting for mass change during the season and differences in body size
	Y + B	3	Total body mass differed among years, but was constant within the breeding season
	D + B	2	Total body mass changed within the breeding season, but did not differ among years
	B	1	Total body mass was constant within the breeding season and among years, after accounting for differences in body size
	null	0	
Crested Auklets	Y + D + B + Y*D	6	Patterns of seasonal mass change differed among years, after accounting for differences in body size
	Y + D + B	4	Total body mass differed among years, after accounting for mass change during the season and differences in body size
	Y + B	3	Total body mass differed among years, but was constant within the breeding season
	D + B	2	Total body mass changed within the breeding season, but did not differ among years
	B	1	Total body mass was constant within the breeding season and among years, after accounting for differences in body size
	Y + D + S + Y*D	6	Patterns of seasonal mass change differed among years, after accounting for differences between males and females
	null	0	

^a B = body size, D = Julian date, S = sex, Y = year