THE RELATIONSHIPS BETWEEN OCEANOGRAPHY AND THE DEMOGRAPHY AND FORAGING OF AUKLETS (CHARADRIIFORMES, ALCIDAE: *AETHIA*; MERREM 1788) IN THE ALEUTIAN ISLANDS, ALASKA

By

© Alexander Lyons Bond

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Abstract

I investigated bottom-up climate-mediated control of population of auklets (*Aethia cristatella*, *A. pusilla*, and *A. pygmaea*) in the Bering Sea over two decades of environmental variability. Broadly, this thesis comprises two parts: 1) examining the relationships between chick diet and survival in the context of large-scale climate and oceanographic patterns; and 2) using stable-isotope analysis to infer foraging patterns throughout the annual cycle of different age classes of auklets, using information on chick diet and local oceanography to interpret the results.

I found that large-scale oceanographic patterns during the winter and spring in the North Pacific were related to auklet productivity the following breeding season. I hypothesized bottom-up control of auklet productivity through food limitation, but found that chick meal composition throughout the Aleutian Islands did not differ among years or sites. Auklets' main prey, *Neocalanus* spp. copepods were most prevalent in chick diets when local sea-surface temperature (SST) during the breeding season was around 4.5 ± 1.0°C, and that outside this range, the proportion of biomass represented by *Neocalanus* copepods declined rapidly. There was significant overlap among Least, Crested, and Whiskered Auklets in the composition of chick meals, suggesting little trophic segregation.

Using information on moulting patterns, I found that stable-isotope ratios in the innermost primary feather (grown during incubation) indicated a shift by adult auklets to a more productive foraging location (e.g., oceanic fronts), presumably as a mechanism for reducing their own maintenance costs during chick rearing. I then found that, among three auklet colonies in the Aleutian Islands, there were no differences among sites or years in the foraging patterns of Least Auklets during pre-breeding (breast feathers), incubation (primary 1), or post-breeding (primary 10). There appeared to be some level of segregation among adult Least and Crested Auklets at Gareloi Island.

Together, these results also indicate that local factors, such as introduced Norway rats (*Rattus norvegicus*) at Kiska Island, are important factors in populations' demography, and that demographic responses are not solely driven by bottom-up processes. Future studies should focus on the winter ecology and movements of auklets.

Statement of Coauthorship

Chapters 2-6 were coauthored with Ian L. Jones, my advisor. Ian initiated the work on Kiska Island in 2001, and has been a constant presence in the Aleutian Islands since 1990. Jeffrey C. Williams and G. Vernon Byrd of the Alaska Maritime National Wildlife Refuge contributed diet and reproductive success data from Buldir and Kasatochi, and provided much-appreciated logistical support during my four years in the Aleutians; Jeff and Vernon are coauthors of Chapters 5 and 6. Bill Sydeman (Farallon Institute for Advanced Ecosystem Research) and Shoshiro Minobe (Hokkaido University) contributed greatly to the oceanographic aspects of this research, and are coauthors of Chapter 6 along with former graduate student Heather Major, who did some of the initial demographic work on Kiska. Nikolai Konyukhov of the Russian Academy of Sciences contributed data on Least Auklet moult from Siberia and the Pribilof Islands, and is a coauthor of Chapter 4.

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The desire for knowledge for its own sake is the one which really counts. Exploration is the physical expression of the intellectual passion.

–Apsley Cherry-Garrard (1922)

And Nuh is the letter I use to spell Nutches

Who live in small caves, known as Nitches, for hutches.

These Nutches have troubles, the biggest of which is

The fact there are many more Nutches than Nitches.

Each Nutch in a Nitch knows that some other Nutch

Would like to move into his Nitch very much.

So each Nutch in a Nitch has to watch that small Nitch

Or Nutches who haven't got Nitches will snitch.

"On Beyond Zebra", Dr. Seuss (1955)

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List of Abbreviations and Symbols

$\Delta^{13}C$ – The discrimination factor for $\delta^{13}C$, or the amount of change in $\delta^{13}C$ from a prey mixture to a consumer.

$\delta^{13}C$ – The ratio of the stable carbon isotopes ^{13}C to ^{12}C, compared with the international standard PeeDee Belemnite

$\Delta^{15}N$ – The discrimination factor for $\delta^{15}N$, or the amount of change in $\delta^{13}C$ from a prey mixture to a consumer.

$\delta^{15}N$ – The ratio of stable nitrogen isotopes ^{15}N to ^{14}N, compared with atmospheric nitrogen

ALPI – Aleutian Low Pressure Index

AIC – Akaike's Information Criteria

AIC$_c$ – Akaike's Information Criteria adjusted for small sample size

AMNWR – Alaska Maritime National Wildlife Refuge

$\hat{c}$ – a measure of overdispersion of data given a statistical model

CRAU – Crested Auklet *Aethia cristatella*

DJF – December-January-February

JJA – June-July-August

LEAU – Least Auklet *Aethia pusilla*

MAM – March-April-May

NPI – North Pacific Index

NPGO – North Pacific Gyre Oscillation

P1 – the first, or innermost, primary feather

P10 – the last, or outermost, primary feather

PDO – Pacific Decadal Oscillation

PFMG – Proportion of feather mass grown

$QAIC_c$ – quasi-Akaike's Information Criteria adjusted for small sample size and extra-model variation in error structure

SIA – Stable-isotope analysis

SLP – Sea-level pressure

SST – Sea-surface temperature

U-Z – Underhill-Zucchini moult model

WHAU – Whiskered Auklet *Aethia pygmaea*

w_i – A model's Akaike weight.

‰ – parts per thousand, per-mil notation for stable-isotope ratios

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CHAPTER 1: INTRODUCTION AND OVERVIEW

Seabirds in the marine environment

There is an abundance of literature on the use of seabirds as indicators of various aspects of the marine environment, including the abundance of commercially exploited fish stocks, contaminants, and climate change (Cairns 1987; Bost & Le Maho 1993; Barrett 2002; Frederiksen *et al.* 2007; Piatt *et al.* 2007; Parsons *et al.* 2008; Durant *et al.* 2009). Indeed, seabirds are conspicuous, generally unexploited, secondary and tertiary consumers in marine systems, and can therefore provide a unique opportunity to investigate coupled climate-ecosystem variation (Durant *et al.* 2009).

In order to establish first if seabirds are indeed indicators of ecosystem characteristics (abiotic and biotic), there must be robust, reliable data on the process or state the seabirds may be indicating, as well as the seabirds' response at varying levels of the environment (Cairns 1987). This inverse inference, or using a dependent variable to estimate one or more explanatory variables must be coupled with robust statistical approaches (Durant *et al.* 2009). The use of seabirds as ecological indicators can be strengthened by simultaneous studies of multiple species at multiple sites (Chapters 5, 6).

Climate-mediated bottom-up control

Seabirds' responses to variation in climate and oceanography has been inferred typically to be bottom-up through control of the abundance, distribution, or availability of prey (e.g., Frederiksen *et al.* 2006; Parsons *et al.* 2008). There have, however, been few studies that relate seabird diet to climate or oceanographic conditions (reviewed by Durant *et al.* 2009). Indeed, most studies using seabird diet as an ecological indicator focus on the relationship between seabird diet composition and prey abundance or foraging location (e.g., Montevecchi & Myers 1995; Nel *et al.* 2001). In many studies of seabirds' demographic responses to climate variability, a bottom-up mechanism is often invoked, but seldom tested (e.g., Byrd *et al.* 2008; Hipfner 2008), although several recent studies do present independent data on prey availability in relation to seabirds' demographic responses to climate change (e.g., Durant *et al.* 2003; Watanuki *et al.* 2009).

Approaches to studying bottom-up control

Many ecologists interested in studying diet have adopted advances in analytical chemistry and biochemistry, including analyses of fatty acid profiles (Iverson *et al.* 2004), and ratios of stable isotopes, particularly those of carbon and nitrogen (Peterson & Fry 1987; Kelly 2000). Often, these can be used to compliment traditional diet studies of gut contents or regurgitates (Barrett *et al.* 2007). Recent methodological and statistical advances have made these techniques more accessible and widespread (e.g., Jaeger *et al.* 2010; Parnell *et al.* 2010), but there remain challenges in the interpretation of results (Bond & Jones 2009b), and the development of techniques (Martínez del Rio *et al.* 2009; Wolf *et al.* 2009a). This is not surprising, as all methods for evaluating seabird diet have inherent assumptions and limitations (Duffy & Jackson 1986; Barrett *et* *al.* 2007). I have used two methods for studying the seabird diet – stable-isotope analysis, and prey composition of chick meals delivered by provisioning parents.

Analysis of chick meals

Studies of food delivered or destined for nest-bound chicks (chick meals, food loads, or bill loads) are used frequently to characterize seabirds' foraging behaviour and responses to the environment (e.g., Hall *et al.* 2000; Baillie & Jones 2003). The composition of chick meals can often be measured with minimal disturbance to the parents through direct observation (e.g., Bradstreet & Brown 1985; Bryant *et al.* 1999), or through the simple capture of breeding adults en route to their nest, who regurgitate or drop the chicks' food (e.g., Montevecchi *et al.* 1992; Hunter *et al.* 2002). Chick meals may not, however, be representative of adult diet because adults and chicks have different energetic constraints and demands (Ydenberg 1994; Barrett *et al.* 2007).

As central-place foragers, and long-lived "k-selected" species, adults seabirds should minimize the transit time to food resources (Baird 1991), balancing the trade-off between distance to foraging grounds and the nutritional quality of the resources (Elliott *et al.* 2009), and the evolutionary trade-off of their own survival and future reproduction (Stearns 1992). Adults of some species, mostly Procellariiformes, balance their own energetic requirements with those of their chick by a bimodal foraging strategy whereby adults make frequent, short trips to provide food for chicks, and less-frequent, long trips to restore their own nutrient reserves (Chaurand & Weimerskirch

1994; Weimerskirch *et al.* 1994). This strategy has been described recently in the Dovekie (*Alle alle*), a polar non-Procellariiform (Welcker *et al.* 2009a).

Stable-isotope analysis

There have been several advances in biochemical techniques to studying diet in the last 20 years, including stable-isotope analysis (Hobson 1987; Hobson & Clark 1992a, b) and fatty acid analysis (Iverson *et al.* 2004). These techniques offer several advantages over traditional methods, but have different drawbacks (Bond & Jones 2009b). Stable isotopes of carbon and nitrogen are used frequently in studies of seabird foraging ecology (Barrett *et al.* 2007; Inger & Bearhop 2008). Values are expressed as the parts-per-thousand ratio of the heavier (^{15}N or ^{13}C) to the lighter isotope (^{14}N or ^{12}C) as compared with an international standard (Pee Dee Belemnite for C, atmospheric air for N). $\delta^{15}N$, or the ratio of $^{15}N/^{14}N$, is a continuous measure of trophic position, and it increases between 2-5‰ with each trophic step because ^{14}N is excreted preferentially in nitrogenous waste (Steele & Daniel 1978; Minagawa & Wada 1984; Kelly 2000). There is little trophic enrichment of $\delta^{13}C$ at higher trophic levels (Rau *et al.* 1983; Hobson & Welch 1992), but marine (bicarbonate-based) and terrestrial carbon sources (CO_2-based) differ in their $\delta^{13}C$ values (Peterson & Fry 1987). $\delta^{13}C$ can also provide information on foraging area in the marine environment because of spatial “isoscapes” in the environment (Hobson 1999; Cherel & Hobson 2007; Graham *et al.* 2010; Jaeger *et al.* 2010).

Stable-isotope analysis is also useful for examining foraging behaviour when attaching data loggers is not feasible because of the difficulty in recapturing individuals to retrieve data, or because the species of interest is too small, and gear attachment would affect individuals' behaviour or even survival negatively. Isotope ratios are indicative of the diet at the time of tissue synthesis (Hobson & Clark 1992a). Feathers are sampled frequently because they offer a relatively non-invasive way to sample large numbers of individuals, and if moult patterns are known, different feathers can be sampled to examine foraging throughout the annual cycle (Marra *et al.* 1998; Pyle 2009) because feathers are inert once grown, receiving no additional nutrient input (Hobson & Clark 1992a; Cherel *et al.* 2005a).

Reproductive success

Bottom-up influences on seabird demography will be most evident in annual reproductive success (the number of chicks reared successfully per pair). As long-lived species, seabirds will balance current and future reproduction, as well as reproduction and survival (Dobson & Jouventin 2010a, b). Consequently, reproductive success is more variable than adults' survival (Hamer *et al.* 2002), and in years of poor food availability or increased predation, seabirds will abandon or skip breeding attempts (Schreiber & Schreiber 1984; Whittam & Leonard 1999).

Climate and auklets in the Aleutian Islands

The Aleutian Islands of Alaska span over 2000 km in the Oceanic Domain the North Pacific Ocean. The central and western Aleutians are surrounded by deep oceanic waters with upwelling zones that bring nutrients to the surface, where they are accessible to avian consumers (Kinder *et al.* 1983; Harrison *et al.* 1990; Russell *et al.* 1999).

Climatically, the Aleutians are influenced by basin-wide climatic patterns, including the Pacific Decadal Oscillation, the El Niño-Southern Oscillation, and North Pacific Gyre Oscillation (Mantua *et al.* 1997; Di Lorenzo *et al.* in press). The Aleutian Low Pressure Index (ALPI) measures the strength of the Aleutian Low from December-March over the area 20-70°N, 120°E-120°W (Beamish & Bouillon 1993; Beamish *et al.* 1997), centred roughly over my study area. ALPI is teleconnected to patterns of the El Niño Southern Oscillation (ENSO), as is the North Pacific Gyre Oscillation (NPGO), which measures the sea-surface height and sea-surface temperature anomalies north of 20°N (Di Lorenzo *et al.* in press). Also related is the Pacific Decadal Oscillation (PDO), a measure of sea-surface temperature anomalies over the same area as the NPGO (Mantua *et al.* 1997; Mantua & Hare 2002). Finally, the North Pacific Index (NPI) is the area-weighted sea-level pressure over the region bounded by 30°N-65°N and 160°E-140°W (Trenberth & Hurrell 1994). No single index captures the range of variability of climate in the North Pacific, so using a variety of measures of climate and oceanography is recommended (Bond *et al.* 2003). Previous studies have related auklet demography to these indices (Jones *et al.* 2002; Jones *et al.* 2007).

There has been a long history of ornithological research in the Aleutians, focused primarily on seabirds (Steller 1751; Stejneger 1885; Murie 1959; Gibson & Byrd 2007). Many seabird breeding islands are recovering following the eradiation of introduced Arctic foxes (*Alopex lagopus*), Norway rats (*Rattus norvegicus*), and other alien vertebrate species (Bailey 1993; Ebbert & Byrd 2002). Introduced species have had a negative effect on Aleutian avifauna (Williams *et al.* 2003; Major *et al.* 2006), highlighting the need to understand local effects when interpreting relationships between climate and seabird responses (Chapter 2).

***Aethia* auklets**

Auklets (*Aethia* spp., Merrem, 1788) are the most abundant seabirds in the North Pacific numerically (Sowls *et al.* 1978; Gaston & Jones 1998). Auklets are socially monogamous, lay a single egg per annual breeding attempt, and their chicks have biparental care (Byrd & Williams 1993; Jones 1993a, b). Adults feed chicks by regurgitating food stored in a blind throat pouch (Portenko 1934). Of the four species of *Aethia* auklets, three are considered here.

Least Auklets (*A. pusilla* (Pallas, 1811)) are the smallest auk (85 g). Their chicks are nest-bound for about 26-29 days (Roby & Brink 1986a; Piatt *et al.* 1990b; Renner 2005), during which time they are provisioned with lipid-rich copepods (*Neocalanus* spp.) and smaller amounts of euphausiids (*Thysanoessa* spp.), gastropods, and amphipods (Bédard 1969a; Day & Byrd 1989; Harrison 1990; Gall *et al.* 2006). Parents provision chicks 2-3 times each per day (Roby & Brink 1986a). They are highly sensitive to disturbance at their breeding sites (Piatt *et al.* 1990b), but on average, 50-70% of breeding pairs will rear a chick successfully (Bédard 1969b; Knudtson & Byrd 1982; Sheffield Guy *et al.* 2009). In North America, Least Auklets breed throughout the Bering Sea and Aleutian Islands (Sowls *et al.* 1978; Jones 1993b), and in Russia, they breed on the Chukotka Peninsula, on islands in the Sea of Okhotsk, and on the Kuril Islands (Dement'ev *et al.* 1951; Kozlova 1957; Velizhanin 1977b; Konyukhov *et al.* 1998; Kondratyev *et al.* 2000; Artukhin *et al.* 2001; Zelenskaya 2009). The wintering areas of Least Auklets are poorly known, but are likely in the western North Pacific, off the coast of Japan (Shuntov 1965; Velizhanin 1977a; Vyatkin 1981; Kondratyev *et al.* 2000; Sydeman *et al.* 2010). Previous work has shown that the survival of chicks was related to diet quality (Gall *et al.* 2006; Sheffield Guy *et al.* 2009), and that adult interannual survival was related to large-scale indices of winter climate in the North Pacific (Jones *et al.* 2002).

Crested Auklets (*A. cristatella* (Pallas, 1769)) are similar to Least Auklets ecologically, but are larger (260 g), and their chicks are nest-bound for longer (33 days; Fraser *et al.* 1999). Both parents share the duties of chick rearing, together provisioning the chick 3-5 times per day (Fraser *et al.* 2002). They also tend to provision chicks with larger proportions of euphausiids compared to Least Auklets (Bédard 1969a; Hunt Jr. *et al.* 1981; Day & Byrd 1989). As with Least Auklets, between 50-70% of Crested Auklet breeding pairs raise a chick successfully (Fraser *et al.* 1999; Gall *et al.* 2006; Sheffield Guy *et al.* 2009). Chick survival in Crested Auklets is also related to diet quality (Gall *et al.* 2006). They breed sympatrically with Least Auklets at many sites in the Bering and

Okhotsk seas and on the Kuril Islands (Sowls *et al.* 1978; Jones 1993a; Konyukhov *et al.* 1998; Kondratyev *et al.* 2000; Artukhin *et al.* 2001), and tend to winter in the eastern North Pacific in productive island passes (e.g., Unimak Pass; Renner *et al.* 2008).

Finally, Whiskered Auklets (*A. pygmaea* (Gmelin, 1789)) differ from congeners in that they are active at breeding colonies nocturnally. Because adults feed their chicks only once or twice per night (Konyukhov *et al.* 2000), they tend to provision chicks with larger meals, and for a longer period (Hamer *et al.* 2002; Hunter *et al.* 2002, Chapter 5). Whiskered Auklet chick diet tends to be similar to that of Least Auklets (Day & Byrd 1989; Hunter *et al.* 2002). Unlike Least or Crested Auklets, however, after fledging, young and adult Whiskered Auklets return to the colony at night for several weeks after the breeding season (Konyukhov & Zubakin 1994; Zubakin & Konyukhov 1994), which suggests that they winter in the vicinity of breeding colonies (Stejneger 1885; Byrd & Williams 1993; Gibson & Byrd 2007). Their breeding distribution and population numbers are less known than that of their congeners because of their nocturnal habits, but colonies are found throughout the Aleutian and northern Kuril Islands in areas free of sea ice year round (Yamashina 1931; Sowls *et al.* 1978; Kondratyev *et al.* 2000; Artukhin *et al.* 2001).

Study sites

I studied auklets at four breeding colonies in the central and western Aleutian Islands – Buldir, Kiska, Gareloi, and Kasatochi islands. I also analysed data on auklet moult from St. George and St. Paul islands in the Pribilofs, and from Cape Ulyakhpen on

Russia's Chukotka Peninsula. Buldir Island (52°23'N 175°31'E), the westernmost study site, is approximately 2000 ha, and the most isolated of the Aleutian islands, being the sole landmass in a 200 km pass (Byrd & Day 1986). Approximately 140,000 Least, 280,000 Crested, and 30,000 Whiskered Auklets nest on the island (Byrd *et al.* 2005), although these numbers should be treated with caution as there are currently no reliable methods to census auklets (Sheffield *et al.* 2006; Renner *et al.* 2010). Alien predators such as foxes or rats have never been introduced to Buldir, and so it is one of the most diverse seabird breeding colonies in the world (Byrd & Day 1986). While Buldir is volcanic, both volcanoes on the island have been inactive in the Holocene (Coats 1953; Wood & Kienle 1990), and vegetative succession may be restricting access to breeding sites, causing the auklet populations to decline (IL Jones pers. obs., sensu Roby & Brink 1986b).

Approximately 120 km east of Buldir lays Kiska Island (52°08'N, 177°36'E), the largest island in the Rat Islands group of the Aleutians (28,711 ha). The large auklet colony is situated at Sirius Point at the extreme northern tip of the island and at the base of Kiska Volcano. The colony covers 1.8 km^2 (Jones *et al.* 2001), with 1.16 million Least and 332,000 Crested Auklets breeding, although there is evidence that the Least Auklet population is declining (Byrd *et al.* 2005; Major *et al.* submitted). The colony is situated on the north face of active Kiska Volcano, and on a parasitic lava cone that emerged in 1962 (Coats *et al.* 1961; Miller *et al.* 1998) creating abundant auklet breeding habitat (Jones & Hart 2006). Arctic foxes were introduced to Kiska for fur farming in 1835 (Ashbrook & Walker 1925), and removed in 1986-1987 (Deines &

McClellan 1987a, b). Norway rats were introduced accidentally during military occupation of the island from 1941-1946, and are still present (Murie 1959; Bond *et al.* 2010b).

Gareloi Island (51°46’N, 178°45’W) is the northernmost, and largest (67,200 ha) island in the Delarof Islands group of the Aleutians, and also home to an active volcano. Gareloi Volcano is one of the most active volcanoes in the Aleutians, erupting several times in the last century (Coombs *et al.* 2008). It is home to a large auklet colony, estimated at 186,000 Crested and 402,000 Least Auklets (Byrd *et al.* 2005). Arctic foxes were introduced in 1925, and eradicated in 1996 (Paragi 1996). Gareloi is likely the largest auklet colony in the Aleutian Islands (Jones & Hart 2006).

Kasatochi Island (52°11’N, 175°31’W) in the Andreanof Islands group of the central Aleutians was a 287 ha island home to 20,000 Crested and 15,000 Least Auklets until a catastrophic eruption of Kasatochi Volcano in August 2008 buried the island in pyroclastic lava floes and ash (Williams *et al.* 2010). Although the eruption occurred after most auklets had finished breeding, breeding crevices remained inaccessible. Arctic foxes were present on Kasatochi from 1927-1991 (Scharf *et al.* 1996).

St. George Island (56°35’N, 169°35’W) is a 90-km^2 island in the Pribilof Islands in the Bering Sea with a high diversity of breeding seabirds (Preble & McAtee 1923), and an estimated 250,000 Least Auklets breeding in 1977 (Hickey 1977). At the Ulakaia colony, a photographic count revealed about 88,000 birds (44,000 pairs; Renner & Renner 2010), a decline from the 129,000 birds reported in the 1970’s (Hickey 1977). Vegetative succession, which cuts off access to breeding crevices, and predation by native Arctic foxes have caused the number of auklets to decline in the last century (Roby & Brink 1986b), but because of the challenges of censusing auklets at breeding colonies, it is not possible to compare the two counts directly (Renner & Renner 2010). St. Paul Island (57°11'N, 170°16'W) is a 104-km^2 island also in the Pribilof Islands. The island is home to more than 23,000 Least Auklets (Hickey 1977). The Pribilofs are near the continental shelf break (Hunt Jr. *et al.* 2008), and while sea ice reached the Pribilofs during most winters before 1977, sea ice extent has been considerably variable, and frequently north of the islands since then (Stabeno *et al.* 1999; Overland & Stabeno 2004).

Finally, Cape Ulyakhpen (Russian: Мысе Уляхпэн) on the Chukotka Peninsula (64°23'N, 173°54'W) is on the eastern end of Bezymyannaya Bay, and is one of only four mainland auklet colonies on Chukotka. 1.2 million Least and Crested Auklets nested here in the late 1980s (Konyukhov *et al.* 1998). This area of the northern Bering Sea is covered by sea ice annually (Fetterer *et al.* 2010).

Thesis outline and rationale

In this thesis, I investigate climate-mediated control of reproductive success (Chapter 2) and chick diet (Chapter 3), and attempt to relate foraging patterns of auklets (Chapters 5 & 6), and other life history stages (moult, Chapter 4) to oceanographic conditions in the Bering Sea.

CHAPTER 2: REPRODUCTIVE SUCCESS OF PLANKTIVOROUS SEABIRDS IN THE NORTH PACIFIC IS RELATED TO OCEAN CLIMATE ON DECADAL SCALES

Alexander L. Bond[1], Ian L. Jones[1], William J. Sydeman[2], Heather L. Major[1,3], Shoshiro Minobe[4], Jeffrey C. Williams[5], and G. Vernon Byrd[5]

[1]Department of Biology, Memorial University of Newfoundland, St. John's,
Newfoundland and Labrador, A1B 3X9, Canada

[2]Farallon Institute for Advanced Ecosystem Research, P.O. Box 750756, Petaluma,
California, 94975 USA

[3]Present Address: Centre for Wildlife Ecology, Department of Biological Sciences, Simon
Fraser University, 8888 University Drive, Burnaby, British Columbia, V5N 1S6, Canada

[4]Graduate School of Sciences, Hokkaido University, N10 W8, Sapporo 060-0810, Japan

[5]Alaska Maritime National Wildlife Refuge, United States Fish and Wildlife Service, 95
Sterling Highway, Suite 1, Homer, Alaska, 99603, USA

Abstract

Growing evidence indicates relationships between seabird demography and both large- and small-scale variation in climate and oceanography, yet few studies have examined multiple species and locations simultaneously. As secondary consumers, least, whiskered and crested auklets (*Aethia pusilla*, *A. pygmaea* and *A. cristatella*), congeneric planktivorous seabirds endemic to the Bering and Okhotsk seas, are expected to respond to changes in ocean climate due to their low trophic positioning. From 1990 through 2008, we measured reproductive success (productivity) and breeding phenology (mean hatching date) of auklets at Buldir, Kiska and Kasatochi, three islands spanning 585 km across the Aleutian Islands, Alaska. A model including island, species and the winter Aleutian Low Pressure Index best explained productivity, with reproductive success decreasing among all species with increasing ALPI ($\beta = -0.273 \pm 0.0263$ S.E.), likely through control of water temperature and prey (zooplankton) availability. Auklet productivity also increased with increasing winter sea surface temperature (SST) in the western North Pacific and western Bering Sea (and correspondingly decreased with increasing SST in the Gulf of Alaska) and was correlated negatively with spring sea level air pressure in the North Pacific. These responses are reflective of positive values of the Aleutian Low. Despite the short time span of our data, we found similar correlations between climate and auklet productivity among all species and islands. Together, our results suggested that ocean climatic conditions and reproductive success of planktivorous auklets are related significantly.

Introduction

Climate and oceanographic conditions in the North Pacific Ocean covary on decadal time scales or longer (Overland *et al.* 1999; Biondi *et al.* 2001), often characterized by 'regimes' of 20 - 30 years duration (Hare & Mantua 2000; Biondi *et al.* 2001; d'Orgeville & Peltier 2009). A well known regime shift occurred in 1976-77, with warmer sea surface temperature (SST), lower sea level pressure (SLP), and a more intense Aleutian low pressure system (Hare & Mantua 2000; Rodionov *et al.* 2005). In the North Pacific and Bering Sea, this shift resulted in greater climatic variability (Bond *et al.* 2003; Hunt & Elliott 2004; Rodionov *et al.* 2005), greater stratification of the water column, and increased primary productivity (Trenberth & Hurrell 1994; Iida & Saitoh 2007). Other purported ecosystem shifts have occurred in 1989-1990 and 1998-1999, but these putative shifts in system state have not been well documented (Overland *et al.* 1999; Hare & Mantua 2000; Mueter *et al.* 2007).

Seabirds, as conspicuous, generally unexploited, secondary and tertiary consumers in marine systems, provide a unique opportunity to investigate coupled climate-ecosystem variation (Durant *et al.* 2009). Indeed, the relationship between ocean climate, ranging from direct measures of SST to multivariate climate indices (e.g., Pacific Decadal Oscillation, Mantua & Hare 2002), and seabird breeding performance has been investigated frequently in the North Pacific (e.g., Gjerdrum *et al.* 2003; Abraham & Sydeman 2004; Byrd *et al.* 2008); and elsewhere (e.g., Harris *et al.* 2005; Durant *et al.* 2006; Møller *et al.* 2006; Lavers *et al.* 2008; Jenouvrier *et al.* 2009). Some find significant relationships between large-scale climate indices and seabird demographic rates (Kitaysky & Golubova 2000; Byrd *et al.* 2008; Sandvik *et al.* 2008), whilst others do not (Wanless *et al.* 2009). In the North Pacific, variation in seabird breeding performance is thought to result from “bottom-up” climate forcing of seabird prey abundance (Lehodey 2004).

While linkage between climatic and oceanographic variability has been found in many marine organisms (Beamish *et al.* 1997; Mantua *et al.* 1997; Chavez *et al.* 1999; Hunt Jr. *et al.* 2002; Durant *et al.* 2006; Byrd *et al.* 2008; Hunt Jr. *et al.* 2008), most studies do not address spatial components in climatic and oceanographic variability. Integrating data over large areas can mask smaller-scale variation over space and time. More recently, there has been a focus on examining relationships between seabirds’ demography and oceanographic variables in spatial terms, providing a better understanding of how geographic patterns of climate affect marine animals (Byrd *et al.* 2008; Watanuki *et al.* 2009).

Auklets (Charadriiformes, Alcidae: *Aethia*) are a group of planktivorous seabirds occurring in the Bering and Okhotsk Seas that consume and provision offspring with zooplankton, primarily euphausiid crustaceans and large copepods (Day & Byrd 1989; Flint & Golovkin 2002; Gall *et al.* 2006). Annual reproductive output is reflected by success in the hatching and rearing offspring from a single egg (Byrd & Williams 1993; Jones 1993a, b). Here, we test the hypothesis that the productivity (and timing of breeding) of auklets covaries with ocean climate, and that this covariation is consistent among species and breeding colonies in the western Aleutian Islands. We considered the correlation between productivity, large-scale ocean climate indices (Aleutian Low

Pressure Index, PDO), and direct measures of sea surface temperature and sea level air pressure based on satellite data for three auklet species: least, whiskered and crested auklets (*Aethia pusilla*, *A. pygmaea*, and *A. cristatella*) breeding at Buldir, Kiska, and Kasatochi in the central and western Aleutian Islands, Alaska (Fig. 2-1). Our objectives were to: 1) quantify relationships between auklet reproductive success and indices and direct measures of ocean climate; 2) identify the oceanographic regions where productivity-climate correlations are strongest; 3) examine the covariance in productivity among different island breeding colonies and among different auklet species; and 4) to better understand underlying mechanisms determining demographic variation in planktivorous seabird species in the North Pacific.

Methods

Productivity (the proportion of eggs laid that produced independent young) and phenology (mean date of hatching of eggs) were measured over 18 years (1990-2008) at Main Talus, Buldir (52°22.45'N 175°54.33'E, WGS 84; least, whiskered (1991-2008), and crested auklets), Thundering Talus, Kasatochi (52°10.77'N 175°31.48'W, least and crested auklets, 1996-2008) and at Sirius Point, Kiska (52°08'N 177°36'E, least and crested auklets, 2001-2008), in the Aleutian Islands, Alaska. No data were collected from Buldir in 1999 or from Kiska in 2005 due to logistical constraints.

Auklet productivity

Each year, we checked a sample of auklet breeding nest sites (rock crevices) from late May until early August, encompassing the entire breeding season for all three species using established protocols (for details seeFraser *et al.* 1999; Hunter *et al.* 2002; Major *et al.* 2006). To account for potential variability among islands, years, and observers, one trained observer was stationed on each island in each year to ensure consistency. Within each year, the same individual would check the same nest sites, and all observers used the same methods and criteria (below) for determining nest success (Fraser *et al.* 1999; Major *et al.* 2006). We visited breeding sites every 4-7 days, and determined their status (empty, egg, chick, adult, unknown). New sites were located and included in the sample each year, to account for previously monitored sites that were no longer in use, but the majority of crevice nests in most years were sites that had been monitored in previous years. We assumed that our annual sample of breeding sites monitored at each colony was representative and reflective of productivity at each colony site. We considered sites active when we found an adult on two consecutive visits, or we saw an egg. We scored sites as successful in fledging a chick if the chick disappeared after 25 days (Least Auklets, Roby & Brink 1986a), 26 days (Crested Auklets, Fraser et al. 1999) or 32 days (Whiskered Auklets, Hunter et al. 2002).

Timing of breeding

We estimated date of hatching for a sub-sample of crevice breeding sites monitored. We included only crevices that we scored as an egg on one visit, and as a chick on the very next visit (4-7 days later), and we assumed hatching date to have occurred at the midpoint between the two visits. We then used the mean hatching date for each species-island combination in each year as a measure of timing of breeding.

Climate and oceanographic data

We used multiple large-scale atmospheric and oceanographic climate indices, and evaluated their relationship to auklet reproductive success. While metrics of climate are interrelated, as might be expected, we chose a variety of indicators since no one index reflects the variability of the North Pacific adequately (Bond *et al.* 2003). The Aleutian Low Pressure Index (ALPI, Beamish & Bouillon 1993; Beamish *et al.* 1997) is the anomaly from the 1950-1997 mean of the area with pressure ≤ 100.5 kPa over the area 20-70°N, 120°E-120°W; positive ALPI values indicate a relatively strong Aleutian low-pressure system. ALPI is centered on our study area (approximately 51-53°N, 175°E-175°W). The related North Pacific Index (NPI) is the area-weighted sea-level pressure over the region bounded by 30°N-65°N and 160°E-140°W (Trenberth & Hurrell 1994). The Pacific Decadal Oscillation (PDO) is a temporally long (20-30 years) ENSO-like oscillation based on the leading principle component of sea surface temperature (SST) north of 20°N (Mantua *et al.* 1997). Finally, the North Pacific Gyre Oscillation (NPGO) is derived output from a model; it represents the second principal component of sea surface height anomalies measured over the same areas as the PDO (Di Lorenzo *et al.* 2008). Several of these indices (PDO, ALPI, NPI) have been related to auklet demography (Jones *et al.* 2002). For sea-surface temperature (SST), we used the 4 km AVHRR Pathfinder Version 5 dataset (available at http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/available.html). We measured SST in a 50km^2 radius around each colony reflecting the likely foraging range of auklets (Obst *et al.* 1995; Thayer *et al.* 2008; Wolf *et al.* 2009b). We assessed SST during June and July when auklets are present at the breeding colonies. For our geospatial approach (see below), large-scale climate data, (SST and SLP) over the North Pacific were taken from the NCEP-NCAR reanalysis (Kalnay et al. 1996).

Statistical procedures

All statistical tests were performed in SPSS 16.0.2 (SPSS Inc., Chicago, USA), and were weighted by the sample size of nest sites studied each year for each species at each island. To investigate whether there were linear trends in productivity or timing of breeding over time, we used a linear regression for each species-island combination. We used nonparametric correlations (Spearman's ρ) to look for covariance among and between species and islands (Byrd *et al.* 2008). To control for multiple comparisons, we used the False Discovery Rate (Benjamini & Hochberg 1995), which is less restrictive and more powerful than a Bonferroni-type family-wise correction (García 2004; Grosbois *et al.* 2008). We use $p < 0.10$ to determine significance. Setting a higher α level is desired when the sample size (in this case, number of years) is low, to increase the power to detect a relationship when one is present (Lebreton *et al.* 1992; Field *et al.* 2004; Grosbois *et al.* 2008). This approach has been used regularly in other studies of seabirds in the North Pacific (e.g., Abraham & Sydeman 2004; Byrd *et al.* 2008).

We used a three-step process to investigate relationships among ocean climate and auklet productivity. First, we used Spearman rank correlations to search for potential relationships to include in a statistical model (see below). Second, as this analysis does not account for spatial variability in variables (e.g., SST and SLP), we examined spatial correlations to provide inference regarding spatial variability (Szép & Møller 2005; Schroeder *et al.* 2009; Watanuki *et al.* 2009); we limited this analysis to the Buldir and Kasatochi time series which were > 10y in duration. Spearman correlation coefficients between reproductive success and SLP or SST were mapped over the North Pacific and Bering Sea and areas of significant correlations ($p < 0.10$) were delineated. We used generalized linear models with a binomial logit-link function (a logistic regression approach), to select the most important climate variables. Variable selection was based upon quasi-Akaike's Information Criteria adjusted for small sample sizes ($QAIC_c$) and extra-binomial variation by including an estimate of model deviance ($\hat{c}$ =model deviance/df for the global model). We chose this information-theoretic approach rather than a null-hypothesis testing because the variation in the dependent variable (productivity) was generally small (9-16% among all species and all islands;

Grosbois *et al.* 2008). We considered the model with the lowest $QAIC_c$ value to be the best fitting model to the data (Burnham & Anderson 2002). We constructed 12 *a prioiri* models composed of biologically plausible combinations of five variables of interest, including a Null Model (intercept only) and a Global Model that included all additive terms and their interactions for species, and islands. Once the best-fitting model was identified, the climate and oceanographic covariates of interest, and biologically important interaction terms were added to subsequent models to examine the effect of climate, a similar procedure to the modelling of recapture rate and then survival rate in mark-recapture studies (Lebreton *et al.* 1992; Grosbois *et al.* 2008). We only included potential climate covariates that were correlated significantly with auklet reproductive performance in our preliminary assessment (see above). This decreases the number of candidate models, and reduces the risk of multi-collinearity in covariates (Grosbois *et al.* 2008). Models with $\Delta QAIC_c > 2$ were considered to have substantially less support, and overall model support was assessed using Akaike weights (wi, Burnham & Anderson 2002). This was done on both the full dataset, and again using data from Buldir and Kasatochi only, as in the geospatial analysis. This is because the dataset from Kiska is shorter (7 years), and because Kiska is anomalous in that is also has introduced predators that affect auklet reproductive performance. Finally, we used the estimated marginal means (EMMs) from the top-ranked generalized linear model to examine differences among species and islands, and differences were considered significant if 95% confidence intervals did not overlap.

Results

We studied between 23-215 breeding pairs of each species on each island in each year (total = 7733 breeding sites over all years and all species, Appendix 1, Fig. 2-2). Auklet productivity ranged from 0.10 to 0.85 chicks/nest for most species for most years, with 2001 and 2002 being unusually low at Kiska and 2003 being an unusually low at Buldir (Appendix 2).

Linear regression identified only one significant trend in reproductive success (or phenology Appendix 2), that being an increase in reproductive success over time for least auklets at Kiska, our shortest dataset ($p = 0.012$, all other $p < 0.11$), we used raw data, not detrended values, for further comparisons.

Reproductive success was correlated more frequently than phenology, and all significant correlations were positive (in phase; Table 2-2). There was a general pattern of correlation among species within islands, and using our shortest time series (Kiska), nine of ten correlations are positive despite the small sample size ($n = 7$ years), providing reasonably strong evidence of covariation (Figure 2-2).

Timing of breeding was rarely correlated among species or islands; crested auklet timing of breeding at Buldir and Kiska was correlated positively (Table 2-1).

Relationships to climate indices

Productivity was related frequently and significantly to ocean climate indices (Table 2-3). Of the climate covariates we considered, the Aleutian Low Pressure Index

(ALPI) and the winter and spring North Pacific Gyre Oscillation (NPGO) were most often related to auklet productivity.

Geospatial mapping of climate and reproductive success correlations

In four cases, geospatial correlation analysis found that reproductive success was correlated with winter (December-January-February) SST (Fig. 2-3), but in different areas of the North Pacific. Productivity of least and crested auklets at Buldir was negatively correlated with SST in the Gulf of Alaska region, while that of whiskered auklets on Buldir was positively related to SST in the western Bering Sea. The spatial correlation pattern for least auklets on Buldir is characterized by a negative correlation along the American west coast and a positive correlation in the central North Pacific, reminiscent of the SST pattern of a negative PDO (Mantua *et al.* 1997), although the PDO pattern does not have another action center with the opposing sign in the western North Pacific. Reproductive success of crested auklets on Kasatochi were positively related to SST in the northwestern Pacific Ocean between 40-50°N (Fig. 2-3). The only relationship between reproductive success and spring (March, April, May) SST was for whiskered auklets breeding at Buldir, and the pattern was identical to that for winter SST. This pattern is similar to the second mode of SST variations (Bond *et al.* 2003), which is closely related to the NPGO (Di Lorenzo *et al.* 2009). This is consistent with the relatively high correlation between productivity and climate indices (Table 2-3). No significant relationships were found between reproductive success and winter SLP, and only two for spring SLP. Whiskered auklet reproductive success on Buldir was negatively related to SLP in the eastern Pacific, while that of least auklets on Kasatochi was negatively related to the spring SLP in the western Pacific (Fig. 2-4).

Factors affecting auklet productivity

Based on the results from our examination of correlation coefficients and spatial correlation analysis, we included only ALPI, NPGO (winter and spring) along with local breeding season SST as covariates in the generalized linear models. The best-fitting model for productivity of all auklets from 1990-2008 included differences among species and islands, ALPI and the island × ALPI interaction term. No other model had $\Delta QAIC_c < 2$, and the top model received 72% support, 3 times more than the second-best model after adjusting for $\hat{c} = 5.62$ (Table 2-4). Parameter estimates are presented in Table 2-5.

Using data from only Buldir and Kasatochi, the top two models included effects of species and ALPI, with one including their interaction. These models were almost equally supported, but were more than 7 times more supported than the third-ranked model after correcting for $\hat{c} = 4.23$ (Table 2-6).

Based on estimated marginal means (EMMs) from the full dataset, Buldir and Kasatochi had similar reproductive success rates during the study and both were higher than Kiska. Among islands, crested and whiskered auklets had higher reproductive success than least auklets (Table 2-7). An increased ALPI was associated with decreased productivity among all species on all islands ($\beta = -0.273 \pm 0.0263$ (S.E.); Fig. 2-5).

Discussion

Our results indicate that auklet reproductive success varied with large-scale climate indices, and that even with a short time series for multi-island comparisons (7 years), the majority (9/10) of correlations were in phase. The combination of only 7 years' data from Kiska, and the potentially confounding effect of introduced Norway rats complicate the interpretation, but performing analysis using data from only Buldir and Kasatochi, combined with independent spatial correlation analysis yielded similar patterns. We note, however, that the oscillation between 'warm' and 'cold' phases of the Pacific Ocean may be masked or accentuated by increasing global temperatures (d'Orgeville & Peltier 2009), and so our correlations should be treated as minimum estimates.

Interestingly, we found no evidence of linear trends in our reproductive success or phenology data, contrary to that found in piscivorous seabirds in the Pribilof Islands (Byrd *et al.* 2008) and North Atlantic (Gaston *et al.* 2005; Moe *et al.* 2009). It is likely that our relatively short time series overall (19 years) was insufficient to document potential climate-linked trends in productivity.

Reproductive success tended to be more correlated among species on the same island than for any single species among islands. Least and crested auklets tend to provision their chicks with diets consisting of euphausiids and calanoid copepods (Bédard 1969a; Day & Byrd 1989; Hunt Jr. & Harrison 1990), so the observed pattern suggests that general prey availability differences among breeding sites was more important that species-specific factors. Several studies have now examined the relationships between climate indices or local oceanographic conditions and timing of breeding in the Alcidae, and found trends for earlier breeding (Gaston *et al.* 2005; Moe *et al.* 2009), later breeding (Byrd *et al.* 2008; Wanless *et al.* 2009), or no trend over time (Abraham & Sydeman 2004; Durant *et al.* 2004, this study). While snow cover, and consequently air temperature, may delay auklet nesting at northern colonies (Sealy 1975; Moe *et al.* 2009), breeding colonies in the Aleutian Islands are snow-free when auklets initiate nesting in late May or early June (authors' pers. obs.).

The influence of climate on reproductive performance

Overall, a higher Aleutian Low Pressure Index (ALPI), which corresponded with a stronger, more intense Aleutian low-pressure system, was associated with decreased productivity in least, whiskered and crested auklets across their range in the Aleutian Islands, Alaska, although the magnitude of this relationship was variable among species and islands. A stronger Aleutian low is supposed to correspond with a larger spring algal bloom in the Bering Sea (Iida & Saitoh 2007), but also possibly with a decrease in zooplankton biomass due to cold temperature limitation (Walsh & McRoy 1986; Huntley & Lopez 1992; Pinchuk *et al.* 2008). In the eastern Bering Sea, warmer SST (and positive values of PDO) were predicted to result in a decrease in zooplankton biomass in surface waters during the auklets' breeding season (Coyle *et al.* 2008; Jin *et al.* 2009), likely caused by the copepods' early descent in the water column to undergo diapause (Miller *et al.* 1984; Miller & Nielson 1988). In the northern Bering Sea, auklets are less selective in the prey species they choose when zooplankton abundance is low (Springer &

Roseneau 1985; Hunt Jr. & Harrison 1990; Russell *et al.* 1999). Under these conditions, prey species that are not typically exploited by auklets because of their lower energy content (e.g., *Calanus marshallae*) are more prevalent in adult and chick diet. The same could be true in the Aleutian Islands during a stronger Aleutian low, leading to a decrease in productivity. Survival of auklet chicks has been shown to be related to the quality of prey items delivered by their parents (Gall *et al.* 2006). In the northern California Current System, Cassin's auklets have low reproductive success in warm years when biomass of their main prey species, *Neocalanus cristatus*, was early, and consequently not abundant in chicks' diet (Sydeman *et al.* 2006). We do not believe that such a mismatch occurred with Aethia auklets in the Aleutian Islands, as chick diet composition has been relatively constant over our study period (authors' unpubl. data).

Aside from indirect effects of ocean climate via effects on productivity, direct effects are also possible and non-mutually exclusive to indirect effects (Jones *et al.* 2007). Heavy rainfall during early chick rearing can flood nesting crevices, resulting in chick death (authors' personal observation). The relative importance of such local, atypical effects as compared with prey availability is unknown.

Another direct affect of stormy weather could operate via increased wave action, that is thought to decrease availability of zooplankton to predators (Wroblewski & Richman 1987). Unfortunately, land-based field observational studies (such as ours) alone do not provide direct information on plankton availability, and are therefore inadequate to confirm the relative roles of direct and indirect effects of ocean climate on auklet breeding success.

ALPI and NPGO

Conveniently, our three study islands lie nearly at the centre of the geographic area used for ALPI calculations. ALPI is also measured over the period December-March, and other studies have found significant relationships between seabird reproductive performance and winter climate (Abraham & Sydeman 2004; Durant *et al.* 2006; Byrd *et al.* 2008; Sandvik *et al.* 2008), presumably through climate-mediated controls on prey development, abundance and distribution (Kitaysky & Golubova 2000; Frederiksen *et al.* 2006; Byrd *et al.* 2008). We previously found that adult survival in whiskered auklets covaried with ALPI as well, through either direct (negative effects of a stormy North Pacific) or indirect effects (i.e., bottom-up control of food supplies, Jones *et al.* 2007). This contrasts partly with recent findings that reproductive success in Cassin's auklet (*Ptychoramphus aleuticus*) is driven by local factors rather than large-scale climatic variables (Wolf *et al.* 2009b). Cassin's auklet chicks are fed only at night by their nocturnally-active parents, grow slower and take much longer to fledge than *Aethia* auklets (Ydenberg 1989), meaning that there is a larger timeframe over which nocturnal species' reproductive success may be affected by climatic variation. Cassin's Auklets breed from southern California to the Aleutian Islands, and so large-scale climate variation is likely to be inherently more variable over their range than that of *Aethia* auklets in our study. Pacific-wide climate patterns affect the coasts of California, British Columbia, and Alaska differently and span several oceanic domains (California Current, North Pacific Current, Alaska Coastal Current). Our study of auklets in the Aleutian

Islands spans one oceanic domain where large-scale climate effects would likely be more consistent than those experienced by Cassin's Auklets in the study by Wolf et al. (2009b).

The NPGO is an index of sea surface height and temperature anomalies over 110-180°W and 25-62°N (Di Lorenzo *et al.* 2008), and tends to explain more of the SST anomaly than the PDO (Bond *et al.* 2003). It is controlled largely by basin-wide variations in upwelling and advection in the ocean, and therefore influences nutrient abundance and salinity directly (Di Lorenzo *et al.* 2009), which in turn affects the abundance of plankton (Di Lorenzo *et al.* 2008). In all cases where the relationship between Aleutian auklet productivity and either winter or spring NPGO was significant, the relationship was negative such that a higher NPGO index corresponded with lower reproductive success. A high NPGO is associated with a stronger Aleutian Gyre in the Gulf of Alaska, and a stronger North Pacific Current, the main warm-water current that runs west-to-east along the south of the Aleutian chain at about 40-50°N. Furthermore, the NPGO mode has been strengthening since about 1993 (Bond *et al.* 2003; Di Lorenzo *et al.* 2008), and may be the result of anthropogenic climate change (Di Lorenzo *et al.* 2008). Furthermore, the NPGO and the Aleutian low-pressure system are linked to El Niño Southern Oscillation (ENSO) dynamics. There is an atmospheric teleconnection between the Aleutian low and ENSO, and the North Pacific Oscillation (which is related to the NPGO) leads ENSO by approximately 8-12 months (Di Lorenzo *et al.* 2010). Biologically, this means that there should be concern about the Aleutian Islands population of auklets, as both increased ALPI and NPGO are related to decreased reproductive success, likely through a bottom-up mechanism of limiting prey availability during either the pre-breeding period (Schroeder *et al.* 2009), or during chick rearing (Gall *et al.* 2006). Combined with vegetative succession (Roby & Brink 1986b), and the detrimental effects of rats at Kiska (Major *et al.* 2006), the effects of oceanography or climate may be masked or dampened by colony effects.

Geospatial mapping of climate and reproductive success

The strongest geospatial correlations provided evidence that reproductive success of least auklets on Buldir might be related to the PDO based on winter SST correlations (Fig. 2-3). Similarly, the correlation map for whiskered auklet reproductive success on Buldir and winter/spring SST (Fig. 2-3) resembled the Victoria mode of SST anomalies (Bond *et al.* 2003). The Victoria mode is the atmospheric expression of the NPGO in the North Pacific Oscillation, an atmospheric SLP pattern, although we again found weak correlations, possibly because of our short time scale.

The negative relationship between auklet productivity and winter SST in the Gulf of Alaska further suggests a bottom-up mechanism. Warmer SST is related to earlier timing of life history events by copepods (Mackas *et al.* 2007), including diapause, which may render the copepods unavailable to auklets (Goldblatt *et al.* 1999; Richardson 2008). Data from continuous plankton recorders in the North Pacific showed a marked decrease in copepod abundance in winter (December-March), although smaller numbers may remain accessible to seabird predators (Fort *et al.* 2010).

Critical to an understanding of geospatial patterns of demography/oceanography relationships in seabirds is an understanding of the birds' spatial distribution during the time of interest, which in our case is winter and spring. Knowledge of the non-breeding distributions of *Aethia* auklets, especially from the ice-free Aleutians, is poor. Whiskered auklets are believed to be non-migratory, spending winters in the vicinity of the breeding colony (Stejneger 1885; Konyukhov & Zubakin 1994; Zubakin & Konyukhov 1994; Gibson & Byrd 2007). Crested auklets winter in the eastern Aleutians, particularly in productive upwelling areas such as Unimak Pass (Renner *et al.* 2008; Sydeman *et al.* 2010), and least auklets are more abundant in the western Pacific during the winter and spring (Vyatkin 1981; Sydeman *et al.* 2010), and some winter in the Sea of Japan off the coast of Primoye, Russia (Shuntov 1965; Velizhanin 1977a; Kondratyev *et al.* 2000), although the extent of mixing between Russian and North American populations is unknown. Nevertheless, large-scale climate patterns would be expected to influence the species differently during the winter, but as the relationships between ALPI and productivity among all species on all islands was similar, the differing effects may manifest in a similar way.

Other factors affecting reproductive success

All species' reproductive success was negatively related to the ALPI across all islands generally, but local factors must also have been important. These factors included variable abundance and predation by avian predation such as Glaucous-winged Gulls (*Larus glaucescens*), Peregrine Falcons (*Falco peregrinus*), and/or Bald Eagles

(*Haliaeetus leucocephalus*), and rainstorms during peak hatching periods when chicks were vulnerable to chilling, and earthquakes collapsing crevices. An extreme example of local effects was the August 7, 2008 eruption at Kasatochi buried the entire auklet colony site under thousands of tons of hot volcanic ash, entombing late auklet chicks and any accompanying adults (Williams *et al.* 2010). Another example is introduced Norway rats that have been present at Kiska since the 1940's (Murie 1959), which were thought to be implicated in severe reproductive failure in least auklets there in 2001 and 2002 (Major *et al.* 2006). Auklets form a considerable portion of the rats' diet, and caches of dead birds were found annually, being especially large in the years of breeding failure (Major *et al.* 2007).

Conclusions

Our results indicated that ocean climate and associated effects on ocean productivity and storminess influences variation in Aleutian *Aethia* auklet reproductive performance. Colony-specific effects, such as variation in the abundance and behaviour of naturally occurring and introduced predators, vegetative succession, and even seismic and volcanic activity must also be considered.

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Figures

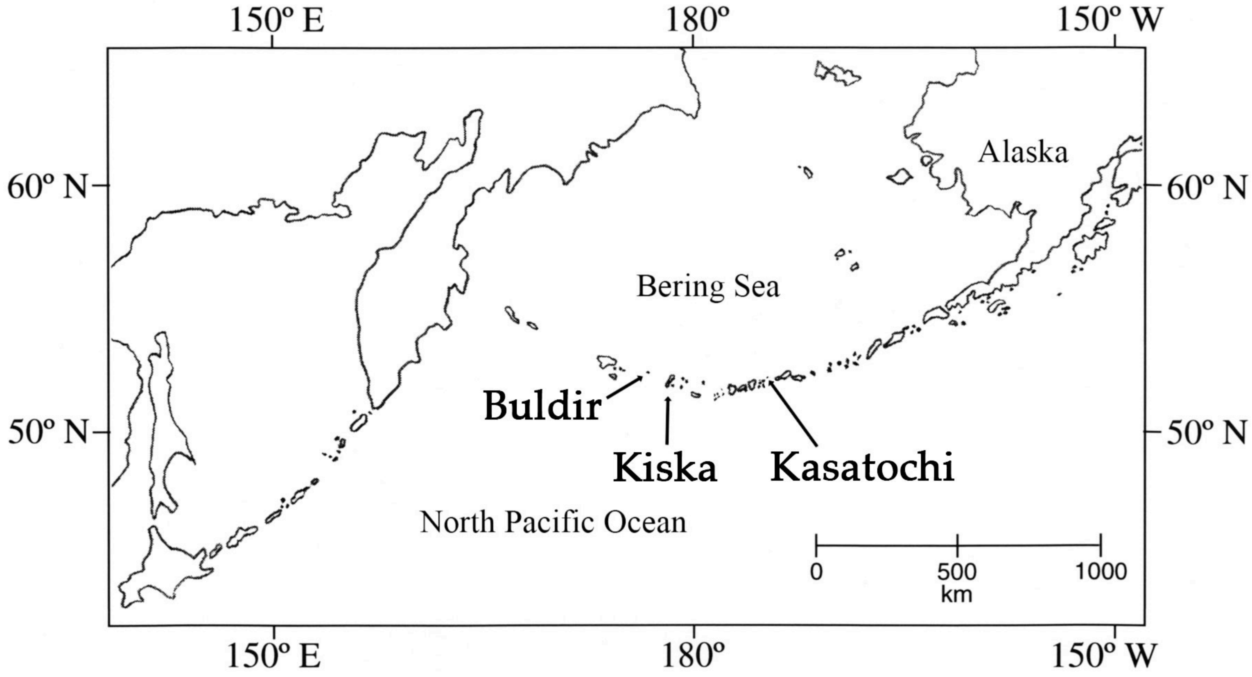

Figure 2-1. Map of the North Pacific Ocean indicating productivity measurement study sites at Buldir, Kiska, and Kasatochi islands, Aleutian Islands, Alaska.

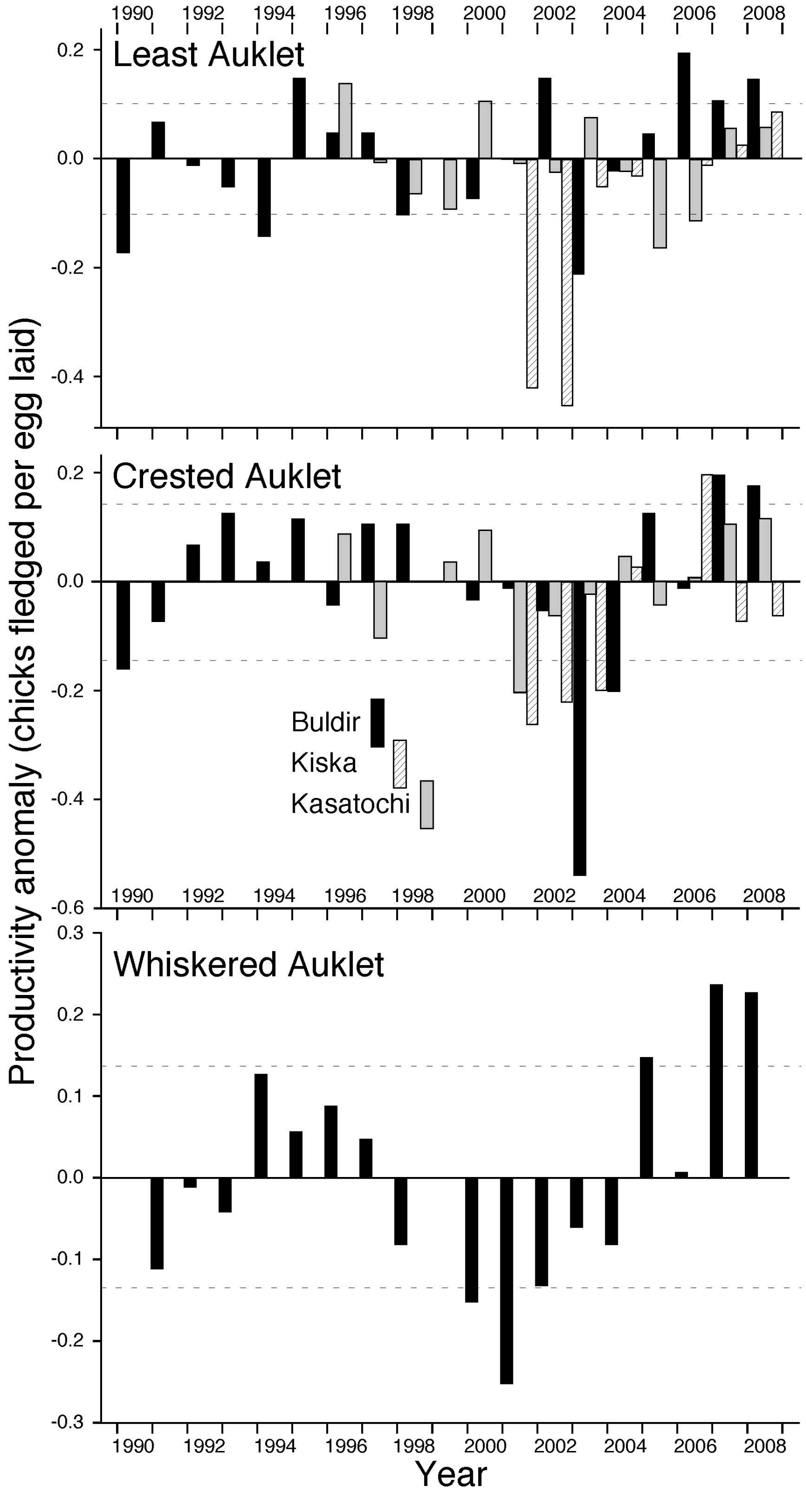

Figure 2-2. Productivity anomalies (differences from the overall mean) of least, crested and whiskered auklets at Buldir, Kiska and Kasatochi, Aleutian Islands, Alaska during 1990-2008.

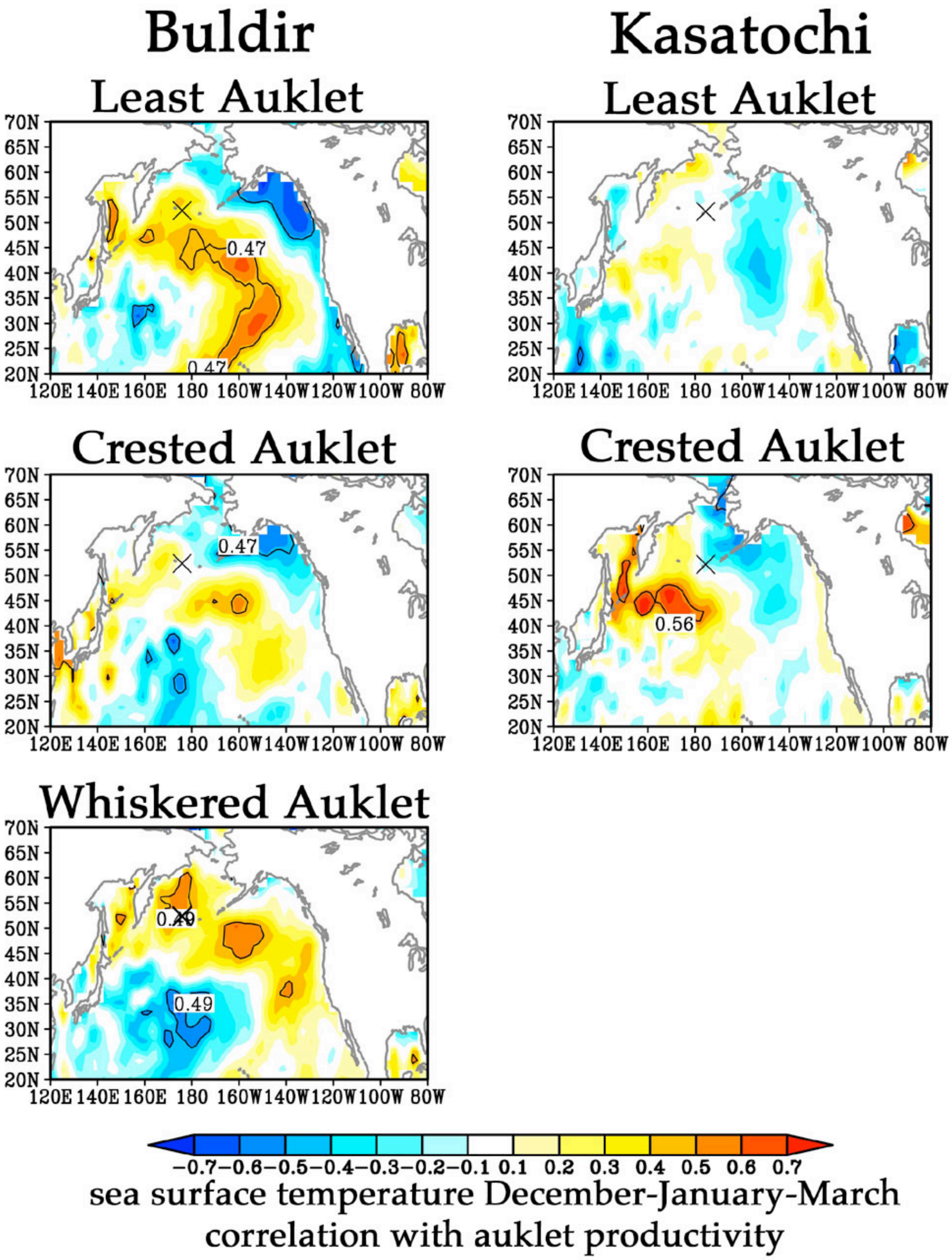

Figure 2-3. Biogeography of Spearman correlation coefficients between least, crested and whiskered auklet productivity at Buldir and Kasatochi and winter sea-surface temperature (SST). Contours indicate significant ($p < 0.10$) Spearman correlations, with the assumption that each year's productivity measure was independent.

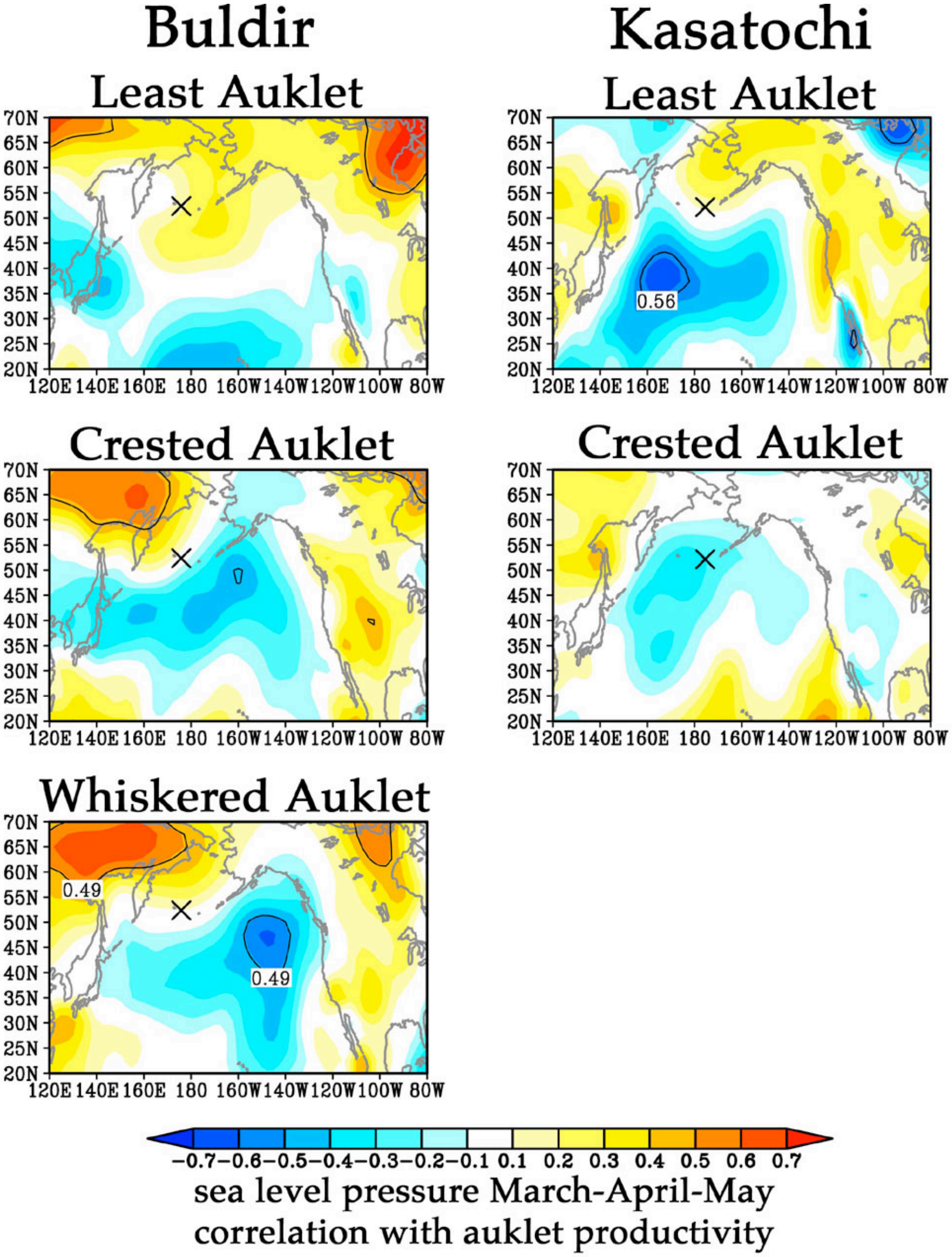

Figure 2-4. Biogeography of Pearson correlation coefficients between least, crested and whiskered auklet reproductive success at Buldir and Kasatochi, and spring sea-level pressure. Contours indicate significant ($p < 0.10$) Spearman correlations, with the assumption that each year's productivity measure was independent.

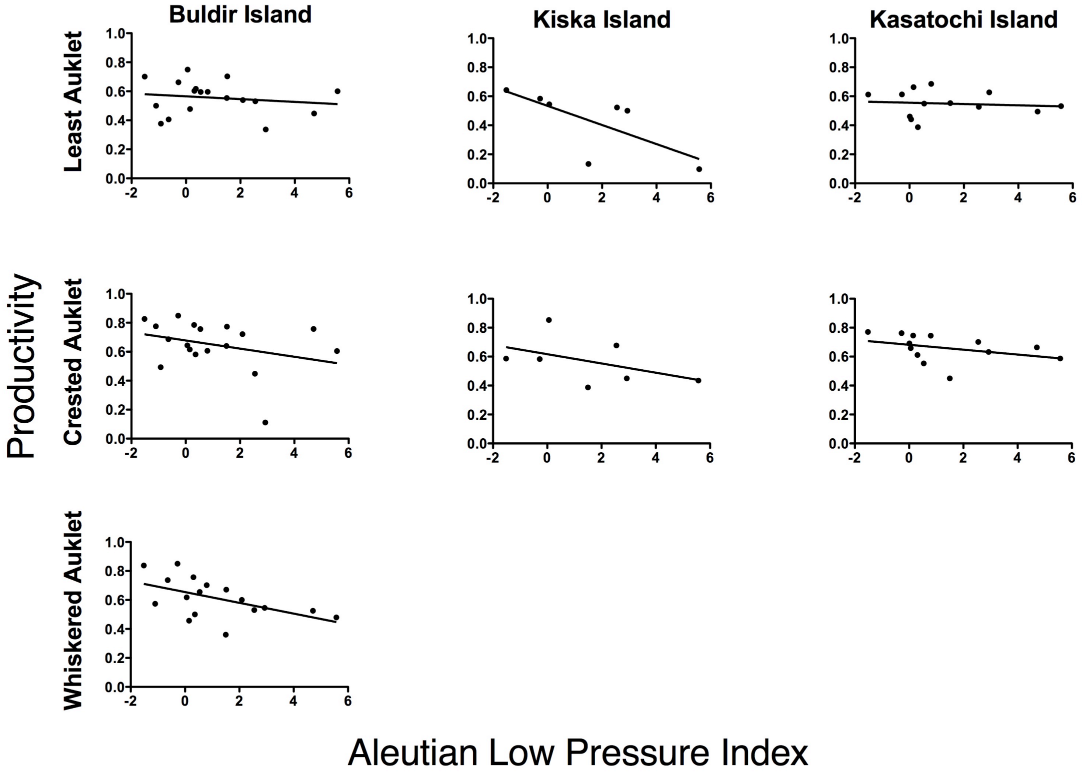

Figure 2-5. Productivity (number of fledglings/number of eggs laid) of least, crested and whiskered auklets at Buldir, Kiska, and Kasatochi during 1990-2008 showing the generally negative relationship with the Aleutian Low Pressure Index (ALPI), least auklets, Buldir (slopes: -0.0096), Kiska (-0.0657), Kasatochi (-0.0045); crested auklets, Buldir (-0.0281), Kiska (-0.0320), Kasatochi (-0.0169); whiskered auklets, Buldir (-0.0372).

Tables

Table 2-1. Spearman's ρ correlation matrix for breeding phenology (mean hatch date) of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) at Buldir, Kiska, and Kasatochi in the Aleutian Islands from 1990-2008. Significant correlations after correcting for false discovery date (see text) are indicated with *.

	Buldir LEAU	**Kiska LEAU**	**Kasatochi LEAU**	**Buldir CRAU**	**Kiska CRAU**	**Kasatochi CRAU**
Kiska LEAU	-0.239					
Kasatochi LEAU	0.458	-0.373				
Buldir CRAU	0.581	-0.108	0.378			
Kiska CRAU	0.667	0.200	0.616	0.900*		
Kasatochi CRAU	0.388	-0.248	0.519	0.208	0.051	
Buldir WHAU	0.452	0.673	-0.196	0.445	0.821	0.092

Table 2-2. Spearman's ρ correlation matrix for productivity of least (LEAU), crested (CRAU), and whiskered auklets (WHAU) at Buldir, Kiska, and Kasatochi in the Aleutian Islands from 1990-2008. Significant correlations after correcting for false discovery date (see text) are indicated with *.

	Buldir LEAU	**Kiska LEAU**	**Kasatochi LEAU**	**Buldir CRAU**	**Kiska CRAU**	**Kasatochi CRAU**
Kiska LEAU	0.206					
Kasatochi LEAU	-0.260	0.216				
Buldir CRAU	0.569	0.090	-0.249			
Kiska CRAU	0.581	0.643	-0.601	0.219		
Kasatochi CRAU	0.162	0.865*	0.373	0.127	0.543	
Buldir WHAU	0.375	0.793	0.018	0.469	0.402	0.565

Table 2-3. Spearman's ρ correlations for productivity and climate indices for least (LEAU), crested (CRAU), and whiskered auklets (WHAU) at Buldir, Kiska, and Kasatochi in the Aleutian Islands from 1990-2008. Significant correlations after correcting for false discovery date (see text) are indicated with *.

	ALPI	**NPGO DEC-FEB**	**NPGO MAR-MAY**	**NPI DEC-MAR**	**NPI AUG-APR**	**PDO DEC-MAR**	**PDO AUG-APR**	**SST**
Buldir								
LEAU	-0.161	-0.127	-0.148	0.258	0.35	-0.532	-0.411	-0.436
Kiska								
LEAU	-0.707	-0.729	-0.528	0.021	0.029	0.281	0.054	0.406
Kasatochi								
LEAU	-0.103	0.283	0.271	-0.133	-0.278	-0.128	-0.142	0.368
Buldir								
CRAU	-0.313	-0.387	-0.297	0.227	0.264	-0.192	-0.295	-0.027
Kiska								
CRAU	-0.469	-0.945*	-0.835*	0.287	0.436	0.029	-0.086	0.091
Kasatochi								
CRAU	-0.373	-0.169	-0.038	0.191	0.128	-0.122	-0.324	0.198
Buldir								
WHAU	-0.529	-0.474	-0.415	0.307	0.231	0.114	0.033	0.053

Table 2-4. Summary of the model set for predicting productivity of least, crested, and whiskered auklets at Buldir, Kiska, and Kasatochi, Aleutian Islands, Alaska from 1990-2008.

Model*	**# Parameters**	**$QAIC_c$**	**$\Delta QAIC_c$**	**w_i**
I+S+ALPI+I*ALPI	8	1818.624	0.000	0.72
I+S+ALPI+I*ALPI+S*ALPI	11	1820.790	2.166	0.24
I+S+ALPI	6	1825.154	6.529	0.03
I+S+ALPI+S*ALPI	8	1826.500	7.876	0.01
I+S+NPGO/DJF	7	1832.111	13.486	0.00
I+S+NPGO/MAM	7	1839.563	20.939	0.00
I+S	5	1844.406	25.782	0.00
I+S+SST	6	1845.380	26.756	0.00
I+S+I*S	8	1847.243	28.619	0.00
S	3	1854.478	35.854	0.00
I	3	1856.643	38.018	0.00
Intercept Only	1	2496.983	678.359	0.00

*Note: Models are sorted by increasing $QAIC_c$ (quasi Akaike's information criteria corrected for small sample size) value with the most parsimonious model at the top. Akaike weight (w_i) is the likelihood that a given model of the model set is the best approximation of the data. Model parameters: I: Island, S: Species, ALPI: Aleutian Low

Pressure Index, NPGO: North Pacific Gyre Oscillation (DJF: December-March; MAM: March-May), SST: Sea Surface Temperature. Model corrected for ĉ = 5.62.

Table 2-5. Parameter estimates from the top-ranked generalized linear model (Table 7) for productivity of least, crested, and whiskered auklets at Buldir, Kiska, and Kasatochi, Aleutian Islands from 1990-2008.

Parameter	**β**	**Std. Error**	**Lower 95% C.I.**	**Upper 95% C.I.**	**Wald χ^2**	**df**	**p-value**
Intercept	0.391	0.1009	0.193	0.588	14.975	1	< 0.001
Crested auklet	0.203	0.0794	0.047	0.358	6.508	1	0.011
Least auklet	-0.274	0.0784	-0.428	-0.121	12.246	1	< 0.001
Whiskered auklet	0[a]	.	.	.	.	.	.
Buldir	0.200	0.0824	0.039	0.362	5.903	1	0.015
Kasatochi	0.148	0.0849	-0.018	0.315	3.049	1	0.081
Kiska	0[a]	.	.	.	.	.	.
ALPI	-0.273	0.0263	-0.325	-0.222	108.252	1	< 0.001
Buldir * ALPI	0.168	0.0317	0.106	0.23	27.926	1	< 0.001
Kasatochi * ALPI	0.220	0.033	0.155	0.285	44.49	1	< 0.001
Kiska * ALPI	0[a]	.	.	.	.	.	.

[a] This parameter is set to 0 because it is redundant.

Table 2-6. Summary of the model set explaining productivity of least, crested, and whiskered auklets in the Aleutian Islands from 1990-2008 using only data from Buldir and Kasatochi.

Model	**# Parameters**	**$QAIC_c$**	**$\Delta QAIC_c$**	**w_i**
S+ALPI+S*ALPI	6	1942.986	0.000	0.49
S+ALPI	4	1943.267	0.281	0.43
S+NPGO/DJF	4	1947.378	4.391	0.05
S+NPGO/MAM	4	1949.853	6.866	0.02
S	3	1951.288	8.302	0.01
S+SST	4	1952.190	9.203	0.00
I+S+I*S	5	1953.267	10.281	0.00
Intercept Only	1	1964.425	21.439	0.00
I	2	1965.426	22.440	0.00

*Note: Models are sorted by increasing $QAIC_c$ (quasi Akaike's information criteria corrected for small sample size) value with the most parsimonious model at the top. Akaike weight (w_i) is the likelihood that a given model of the model set is the best approximation of the data. Model parameters: I: Island, S: Species, ALPI: Aleutian Low Pressure Index, NPGO: North Pacific Gyre Oscillation (DJF: December-March; MAM: March-May), SST: Sea Surface Temperature. Model corrected for $\hat{c}$ = 4.23

Table 2-7. Estimated marginal mean (EMM) productivity for least, crested and whiskered auklets at Buldir, Kiska, and Kasatochi in the Aleutian Islands, 1990-2008 was derived from the top-ranked generalized linear model. Differences were considered significant when confidence intervals do not overlap.

Parameter	**EMM**	**95% Confidence Interval**
Least auklet	0.45	0.43-0.47
Crested auklet	0.60	0.56-0.64
Whiskered auklet	0.62	0.59-0.65
Buldir	0.62	0.60-0.63
Kiska	0.35	0.29-0.41
Kasatochi	0.61	0.59-0.63

CHAPTER 3: DIET OF AUKLET CHICKS IN THE ALEUTIAN ISLANDS, ALASKA: SIMILARITY AMONG ISLANDS, INTER-SPECIES OVERLAP, AND RELATIONSHIPS TO OCEAN CLIMATE

Alexander L. Bond[1], Ian L. Jones[1], Jeffrey C. Williams[2] and G. Vernon Byrd[2]

[1]Department of Biology, Memorial University of Newfoundland, St. John's,
Newfoundland and Labrador, A1B 3X9 Canada

[2]Alaska Maritime National Wildlife Refuge, U.S. Fish and Wildlife Service, 95 Sterling
Highway, Suite 1, Homer, Alaska, 99603 U.S.A.

Abstract

Seabirds are effective samplers of the marine environment, and can be used to measure resource partitioning among species and sites via food loads destined for chicks. We examined the composition, overlap, and relationships to changing climate and oceanography of 3216 food loads from Least, Crested, and Whiskered Auklets (*Aethia pusilla*, *A. cristatella*, *A. pygmaea*) breeding in Alaska, during 1993-2006. Meals comprised calanoid copepods (*Neocalanus* spp.) and euphausiids (*Thysanoessa* spp.) that reflect secondary marine productivity, with no difference among Buldir, Kiska, and Kasatochi islands across 585 km of the Aleutian Islands. Meals were very similar among species (mean Least-Crested Auklet overlap C = 0.68; Least-Whiskered Auklet overlap C = 0.96) and among sites, indicating limited partitioning of prey resources for auklets feeding chicks. The biomass of copepods and euphausiids in Least and Crested Auklet food loads was related negatively to the summer (June-July-August) North Pacific Gyre Oscillation, while in Whiskered Auklets food loads this was negatively related to the winter (December-January-February) Pacific Decadal Oscillation, both of which track basin-wide sea-surface temperature (SST) anomalies. We found a significant quadratic relationship between the biomass of calanoid copepods in Least Auklet food loads at all three study sites and summer (June-July) SST, with maximal copepod biomass between 3-6°C ($r^2 = 0.71$). Outside this temperature range, zooplankton becomes less available to auklets through delayed development. Overall, our results suggest that auklets are able to buffer climate-mediated bottom-up forcing of demographic parameters like

productivity, as the composition of chick meals has remained constant over our study.

Introduction

Seabirds are useful models for investigating dietary resource use and overlap in a community setting. In particular, seabird nestling diets reflect availability, desirability, and perhaps competition for prey in a changing marine environment (Cairns 1987; Piatt *et al.* 2007). During the breeding season, parents are tied to their breeding sites, as chicks cannot feed themselves for several weeks in most species (Hamer *et al.* 2002). Forced into becoming central-place foragers, adults must balance their own energetic investment with the need to obtain and deliver food to the chick (Elliott *et al.* 2009). In environments where food resources are potentially limiting, seabird populations experience bottom-up control (Furness & Birkhead 1984).

Ecologists have long been interested in how multiple similar species coexist in stable communities (Darwin 1859; Wallace 1876), leading to the development of the concepts of “niche” and “niche overlap” (Grinnell 1917; Geisel 1955; Hutchinson 1957; Pianka 1974). The idea that two or more species cannot occupy the same niche in space and time (“competitive exclusion principle”; Gause 1934) has led to innumerable studies of how species accommodate their ecological similarity (Hubbell 2001; Chase & Leibold 2003). This overlap can be reduced by exploiting different resources, or by exploiting the same resources but in different areas or at different times, especially during peak resource demand (Schwemmer *et al.* 2008). Decreasing competition would be expected to benefit individual survival and reproductive success (Hutchinson 1957), and is therefore central to studies of demography. The coexistence of five small planktivorous auklet (Alcidae, genera *Aethia* and *Ptychoramphus*) in the Aleutian Islands (Jones 1999; all five breeding at Buldir Island, Alaska) thus presents a potential test case for evaluating hypotheses about food resource competition.

Seabirds could act as sentinels of climate change over multiple spatial and temporal scales (Parsons *et al.* 2008; Durant *et al.* 2009), a possibility that has led to some studies relating demographic parameters (e.g., breeding success, adult survival) to large-scale multivariate climate indices such as the North Atlantic Oscillation, Pacific Decadal Oscillation, or El Niño Southern Oscillation (e.g., Jones *et al.* 2002; Sandvik *et al.* 2005). Some studies invoked a bottom-up control mechanism whereby oceanographic conditions limit prey availability (e.g., Durant *et al.* 2003; Irons *et al.* 2008; Mills *et al.* 2008) or cause a temporal mismatch between consumer requirements and prey availability (e.g., Hipfner 2008; Gaston *et al.* 2009). Auklet foraging may provide an ideal subject for testing the 'sentinel' hypothesis as foraging by these planktivores would be expected to relate closely to secondary ocean productivity.

In the North Pacific Ocean, changes in climate and oceanography have been well documented (Overland *et al.* 1999; Hare & Mantua 2000; Biondi *et al.* 2001). Following a marked change in climate and oceanography in 1976-77, climatic variability increased (Bond *et al.* 2003), sea surface temperature (SST) increased, and sea-level pressure decreased (Hare & Mantua 2000; Rodionov *et al.* 2005). These changes had demographic consequences for several seabird species (e.g., Gjerdrum *et al.* 2003; Abraham & Sydeman 2004; Jones *et al.* 2007; Byrd *et al.* 2008; Chapter 2).

Least (*Aethia pusilla*, mean adult mass 85 g), Crested (*A. cristatella*, 260 g) and Whiskered (*A. pygmaea*, 108 g) auklets are planktivorous alcids endemic to the Bering and Okhotsk seas of the North Pacific. They breed sympatrically in dense colonies on remote islands, are socially monogamous, and share incubation and chick rearing (Byrd & Williams 1993; Jones 1993a, b). Auklet chick diet consists mainly of calanoid copepods (*Neocalanus* spp.) and euphausiids (*Thysanoessa* spp.), with some amphipods, decapods, and other invertebrates (Day & Byrd 1989; Harrison 1990; Gall *et al.* 2006). The quality of chick diet (e.g., the amount of lipid-rich zooplankton; Roby *et al.* 1986) is related to chick survival in auklets (Gall *et al.* 2006; Sheffield Guy *et al.* 2009), and other seabirds (e.g., Durant *et al.* 2003). Reproductive success of auklets in the Aleutian Islands may be linked to foraging success through climate- and oceanographic-mediated processes (Chapter 2). To explore this possibility further, we quantified auklet chick diet over the same period, and investigated the relationship of auklet chick diet to indices of North Pacific climate and oceanography. Sometimes it is assumed that auklet adult and chick diets are the same, but Crested Auklet adults may feed heavily on cephalopods, which were never fed to chicks (Hunt Jr. *et al.* 1998); our study therefore focuses on food loads captured by adults and destined for their nest-bound chick. Previous work suggested that breeding *Aethia* auklets reduce competition through dietary differences (e.g., Hunt Jr. *et al.* 1998) or spatial separation (Russell *et al.* 1999), ideas that have not been tested at multiple colony sites over time.

Our objectives were to: 1) quantify diet of Least, Crested, and Whiskered Auklet chicks sampled across a 585 km span of the Aleutian Islands from 1993-2006; 2) determine diet variation among species, islands, and stage of the breeding season; 3) examine relationships diet to key indices of annual oceanographic and climatic variability; and 4) investigate correlations between dietary change and climate change.

Methods

Study sites

We collected food brought by parents returning to the colony at three colonies: Main Talus, Buldir Island (52°23'N, 175°55'E; 1993-2006, Crested, Least, and Whiskered Auklets); Sirius Point, Kiska Island (52°08'N, 177°36'E; 2001-2006, Crested and Least Auklets): and Thundering Talus, Kasatochi Island (52°11'N, 175°31'W; 1996-2006, Crested and Least Auklets). These colonies span 585 km of the Aleutian chain (Fig. 3-1), and because auklets forage within 50 km of their breeding colony (Hunt Jr. & Harrison 1990; Obst *et al.* 1995; Flint & Golovkin 2002), we assume that there was little spatial overlap of foraging birds from different sites.

Adults carry food for the chick in a throat pouch (Portenko 1934), and regurgitate this food when captured in a noose carpet or mist net (Jones *et al.* 2002; Jones *et al.* 2004; Jones *et al.* 2007). We sampled food regurgitated by adults throughout the chick-rearing period (late June-early August) in each year. Each year, we collected food samples in the same 24-hour period over 2-calendar days during early, mid, and late chick rearing on each island, weather permitting. *Early* was defined as just after the peak of hatching (late June or early July); *mid* was defined as the period when all chicks had hatched (mid July, about 10 days following the first collection period); and *late* was defined as 10 days after the second collection (just before the start of fledging). We estimated the percentage of food recovered from regurgitated contents to the nearest 5%, and stored samples in 75% ethanol. We identified prey to the lowest taxonomic level possible and counts of individuals were converted into biomass using our own measurements and published data (Appendix 4). The mass of some food loads was estimated based on the proportion (±5%, as noted above) of each food load collected.

To measure pair-wise dietary overlap between species within islands in a given year, we used Horn's (1966) modification of Morisita's Index (1959), as recommended by Diamond (1983). This provides an annual index $0 \le C \le 1$, where identical diets have $C = 1$, and completely dissimilar diets have $C = 0$.

Prey availability

As a measure of prey availability, we used data from a continuous plankton recorder (CPR) during the period of chick rearing (late June to early August) 2000-2006 between 173°W - 173°E and 52-54°N. The Pacific CPR program of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) provided the data. Nets were towed for 18 km at a depth < 15m; further details are in Richardson et al. (2006).

Climatic and oceanographic indices

We used multiple large-scale atmospheric and oceanographic climate indices, as no single index reflects the entire variability of climate or oceanography in the North Pacific Ocean (Bond *et al.* 2003). The Aleutian Low Pressure Index (ALPI, Beamish & Bouillon 1993; Beamish *et al.* 1997) is the anomaly from the 1950-1997 mean of the area with pressure ≤ 100.5 kPa over the area 20-70°N, 120°E-120°W; positive ALPI values indicate a relatively strong Aleutian low-pressure system. ALPI is centred on our study area (approximately 51-53°N, 175°E-175°W). The related North Pacific Index (NPI) is the area-weighted sea-level pressure over the region bounded by 30°N-65°N and 160°E-140°W (Trenberth & Hurrell 1994). The Pacific Decadal Oscillation (PDO) is a long (20-30 years) oscillation based on the leading principal component of sea-surface temperature (SST) north of 20°N (Mantua *et al.* 1997). Finally, the North Pacific Gyre Oscillation (NPGO) is the second principal component of sea surface height anomalies measured over the same areas as the PDO, but also matches the second empirical orthogonal function (EOF; a spatial statistic similar to a principal component score) of SST anomalies closely (Di Lorenzo *et al.* 2008). Several of these indices have been related to auklet demography in previous studies (Jones *et al.* 2002; Jones *et al.* 2007; Chapter 2). These metrics of climate are interrelated, but each is based on slightly different primary components (Trenberth & Hurrell 1994; Bond *et al.* 2003; Di Lorenzo *et al.* 2008). We used seasonal averages of three monthly means (e.g., winter: December-January-February, or DJF) for all indices except ALPI, which is an annual value.

For sea-surface temperature (SST), we used the 4 km AVHRR Pathfinder Version 5 dataset (available at http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/available.html). We extracted SST in a 50 km radius around each colony site, which is the likely foraging range of auklets during June and July (Hunt Jr. & Harrison 1990; Obst *et al.* 1995; Thayer *et al.* 2008; Wolf *et al.* 2009b).

Statistical analyses

All statistical tests were conducted in SPSS 16.0.2 (SPSS Inc., Chicago, IL, USA). For food load size, we fitted a generalized linear mixed model for each species, using island and food-sampling period (early, middle, or late chick rearing) as predictors of load size for each species, and year as a random factor. We used the estimated marginal means and 95% confidence intervals from the parameter estimates to determine significant pairwise differences; pairs with non-overlapping confidence limits were considered to differ statistically.

We used nonparametric correlations (Spearman's ρ) to look for covariance between overlap indices, load composition, and oceanographic or climatic variables. The same approach was used to examine changes in load composition over time. To control for multiple comparisons, we used the False Discovery Rate and $p < 0.10$ (Benjamini & Hochberg 1995; García 2004; Grosbois *et al.* 2008). Setting a higher α level is desired when the sample size (in this case, number of years) is low, as this increases the power for detecting a genuine relationship between climate and ecological variables (Lebreton *et al.* 1992; Field *et al.* 2004; Grosbois *et al.* 2008).

After significant diet-climate relationships were identified, we included those climate variables in a series of generalized linear models with a gamma function error structure and identity link, and used quasi-Akaike's Information Criteria adjusted for small sample sizes and extra-binomial variation ($QAIC_c$) for model selection. Using only a subset of covariates decreases the number of candidate models, and reduces the risk of multicollinearity (Grosbois *et al.* 2008). We considered the model with the lowest $QAIC_c$ value to be the best-fitting model to the data (Burnham & Anderson 2002). We constructed a Null Model (intercept only) and models that included additive terms and their interactions for sampling periods (early, middle, or late chick rearing), and islands (the Global Model). Once the best-fitting model was identified, the climate and oceanographic covariates of interest, and biologically significant interaction terms were added to subsequent models to examine the effect of climate (a procedure similar modelling recapture rate and then survival rate in mark-recapture studies; Lebreton *et al.* 1992; Grosbois *et al.* 2008). Models with $\Delta QAIC_c > 2$ were considered to have substantially less support, and overall model support was assessed using Akaike weights (denoted as wi, Burnham & Anderson 2002). This was done on both the full dataset and on data from Buldir and Kasatochi islands because the dataset from Kiska Island is briefer (5 years), and because Kiska is anomalous because it has introduced predators that might affect provisioning behaviour (Major *et al.* 2006).

Results

We identified 40 prey taxa categories in Least Auklet food loads (*n* = 810), 29 in Crested Auklet food loads (*n* = 1110), and 32 in Whiskered Auklet food loads (*n* = 486; Appendices 5, 6, 7). Food loads were composed mainly of *Neocalanus* copepods and *Thysanoessa* euphausiids (Appendices 5, 6, 7). Fine taxonomic resolution was not possible in all years, so items were grouped for subsequent analysis into higher-level taxa as "*Neocalanus*" or "euphausiids"; other taxa (e.g., amphipods, decapods, *Calanus marshallae*) were not included in analyses because they often comprised < 5% biomass in any given year. Notable exceptions were for Least Auklet on Kasatochi in 1997, 1999, and 2006 (18.9%, 38.5%, and 13.1% decapods, respectively), Crested Auklets on Buldir in 2003 (12.9% *Themisto* amphipods), and on Kasatochi in 2004 (20.5% *Themisto* amphipods; Figures 3-2, 3-3, 3-4).

After correcting for the False Discovery Rate, we found no significant annual trends in the proportion of *Neocalanus* or euphausiids in loads of Least, Crested, or Whiskered auklets (all $P > 0.12$).

Food load size

Food load mass was estimated for 683 Least, 1071 Crested, and 316 Whiskered Auklet food loads (64% of the total). Meal size differed significantly among sampling periods (all $P < 0.01$), but not among islands (all $P > 0.32$). The random effect of year explained less than 5% of the variance in all three species. Based on 95% confidence intervals of marginal means, load sizes increased significantly throughout the chick-rearing period for Crested, and Least Auklets. In Whiskered Auklets, load size was smaller in the early than in the mid period, and load size in the late period did not differ from that in other periods (Table 3-3). As a percentage of adult body mass, Least Auklet loads averaged 3.5-6.1%, Crested Auklets chick meals 3.2-5.7%, and Whiskered Auklet chick meals 7.4-10.1%.

Dietary overlap and similarity among species and islands

Within-island dietary overlap between species was considerable. At Buldir, overlap was highest between Least and Whiskered auklets, followed by Crested and Whiskered auklets, and in many years, overlap between species was > 0.90 (Table 3-1). At Kasatochi, overlap between Least and Crested Auklets was higher than that on Buldir, and was > 0.90 in 5 of 11 years (Table 3-1). At Kiska, overlap between Least and Crested Auklets was low, but based on only three years' data (Table 3-1). Based on 95% confidence intervals given above, we conclude that at Buldir there was more dietary overlap between Least and Whiskered auklets than between other species, and that overlap between Least and Crested Auklets differed among three sites (Kasatochi > Buldir > Kiska). Overlap between Least and Crested auklets on Buldir was positively correlated with overlap between Least and Whiskered Auklets on Buldir after correcting for the False Discovery Rate ($P < 0.001$).

We also used the overlap index C as a measure of dietary similarity within species among islands. Load composition was consistent among islands for all species. Least Auklet diet was identical on all islands. Similarity in Crested Auklet loads was lower than that for Least Auklets, but still high. We conclude that load composition of Least and Crested auklets did not differ among islands (Table 3-2).

Prey availability: CPR data

After correcting for multiple comparisons using the False Discovery Rate, we found no significant relationships between auklet load composition (proportion of *Neocalanus* or euphausiid biomass in chick meals) and total zooplankton biomass, *Neocalanus* (stage V copepodite) biomass, or euphausiid biomass, in plankton tows during chick rearing in 2000-2006.

Relation to climate/oceanographic indices

After correcting for the False Discovery Rate, we identified only two significant correlations between load composition and climate indices. The proportion of euphausiids in Least Auklet loads was positively correlated with winter (December-January-February) NPGO on Buldir ($\rho = 0.72$, $P = 0.006$), and with spring (March-April-May) NPI on Kiska ($\rho = 0.98$, $P = 0.005$). Given the paucity of significant monotonic correlations, and the potential for more complex relationships (e.g., parabolic; Gjerdrum *et al.* 2003), we included all climate and oceanographic variables as covariates in subsequent analyses.

A model that included differences among islands, sampling periods, island x period interaction, and a negative relationship to the summer (June-July-August) NPGO best predicted the biomass of *Neocalanus* in Crested Auklet loads, after correcting for overdispersion by using ĉ = 1.8. This model received 57% of the weight, and 2.6 times more support than the next-ranked model (identical, but with a negative relationship to winter NPGO), which also received considerable support ($\Delta QAIC_c = 1.54$). The same model (covariation with summer NPGO) best predicted euphausiid biomass in Crested Auklet loads (58% weight, 2.2 times more support).

Both *Neocalanus* and euphausiid biomass in Least Auklet loads was best predicted by a model that included differences among islands, periods, period x island interaction, and a negative relationship with summer (June-July-August) PDO (*Neocalanus*: 100% weight, 429 times more support; euphausiids: 100% weight, 427 times more support). Data were not over- or underdispersed, so we did not adjust the model using ĉ.

A model that included only a negative relationship with winter (DJF) PDO best predicted the biomass of *Neocalanus* and euphausiids in Whiskered Auklet loads on Buldir (*Neocalanus* : 98% weight, 96 times more support; euphausiids: 98% weight, 130 times more support). Again, no adjustment using ĉ was required.

Both NPGO and PDO track basin-wide SST anomalies, and as local SST was not among the highly-ranked models, we investigated other possible relationships between food load composition and SST using *Neocalanus* in Least Auklet diet. *Neocalanus* accounted for most biomass in most years, and sample sizes were large on all three islands. We found a parabolic relationship of *Neocalanus* biomass to local summer SST ($r^2 = 0.25$). Major et al. (2006) hypothesized that introduced Norway rats (*Rattus norvegicus*) could affect the provisioning behaviour of auklets at Kiska; when data from Kiska were excluded, the parabolic relationship of *Neocalanus* biomass to SST increased ($r^2 = 0.71$). Maximal *Neocalanus* biomass occurred when summer (June-July) SST was ~4.5°C, was relatively constant between 3-6°C, and declined sharply outside this range (Fig. 3-5).

Correcting for False Discovery Rate, dietary overlap of Least Auklets among all three islands was correlated with winter (DJF) NPGO, and overlap between Kiska and Kasatochi was related to NPGO in spring (March-April-May, MAM) and summer (June-July-August, JJA). Within islands, overlap between Least and Crested Auklets was not related to any climate variable at Kiska or Kasatochi. At Buldir, Least and Whiskered Auklet overlap was related to spring (MAM) NPI.

Discussion

Overall, our results confirm previous studies of auklet chick diet (using adult food loads as a proxy) in the Aleutian Islands (Day & Byrd 1989) which indicated that Least and Whiskered auklets rely heavily on large-bodied oceanic copepods, whereas Crested Auklet adults also deliver a significant amount of euphausiids to their chicks. Unlike studies from St. Paul Island in the Pribilof Islands, and on the continental shelf and shelf break, we found very few *Calanus marshallae* in chick meals of the three species. The amount of *C. marshallae*, a neritic copepod, in chick meals was negatively related to auklet chick survival at colonies on the continental shelf (St. Lawrence Island, Gall *et al.* 2006). Unlike the larger oceanic copepods *Neocalanus* spp., *C. marshallae* has lower lipid content, and Least Auklets are thought to seek out *Neocalanus* spp. preferentially over less profitable prey resources (Hunt Jr. & Harrison 1990; Hunt Jr. 1997; Russell *et al.* 1999). Oceanic *Neocalanus* spp. copepods (*N. plumchrus*, *N. flemingeri*, and *N. cristatus*) are rich in lipids and wax esters required by auklets (Roby *et al.* 1986). At St. Lawrence Island, oceanic copepods are advected by the Anadyr Current (Springer *et al.* 1989), and contribute to higher chick survival (Gall *et al.* 2006; Sheffield Guy *et al.* 2009). Such oceanographic fronts concentrate zooplankton, including *Neocalanus* spp. (Hunt Jr. & Harrison 1990; Hunt Jr. 1997; Russell *et al.* 1999).

Around St. Lawrence Island, Crested Auklets were often associated with epibenthic advected euphausiid swarms (Russell *et al.* 1999), and their chicks' diet consisted largely of *Thysanoessa* spp. euphausiids (Bédard 1969a; Piatt *et al.* 1990a; Sheffield Guy *et al.* 2009). In addition to euphausiids, Crested Auklets in the Aleutians appear to also rely heavily on calanoid copepods to provision their chicks in most years (Appendix 5, Day & Byrd 1989), unlike their counterparts in the Bering Sea (Bédard 1969a; Hunt Jr. *et al.* 1981; Sheffield Guy *et al.* 2009). Crested Auklets provisioning chicks exploit large bodied oceanic copepods when they are available (Searing 1977), in some years delivering meals consisting wholly of these, consistent with copepods' availability being generally greater in the oceanic domain of the western Aleutian Islands (Hunt Jr. 1997).

Whiskered Auklets have a much smaller breeding range than Least or Crested Auklets, and are restricted to the Aleutian Islands, the Commander Islands, and the northern Kurile Islands (Averin 1957; Byrd & Williams 1993; Kondratyev *et al.* 2000; Artukhin *et al.* 2001). Consequently, much less is known about their diet. Our results agree with previous studies of chick meals on Buldir (Day & Byrd 1989; Hunter *et al.* 2002), but contrast with studies of adult stomach contents in the eastern Aleutians, where euphausiids dominated diet (Troy & Bradstreet 1991), pointing to differences in the provisioning behaviour of adults depending on whether self-feeding or providing meals to chicks, or perhaps geography.

Dietary overlap and similarity among species

In the northern Bering Sea and eastern Aleutians, previous work has suggested that distributional differences among species are related to dietary differences (Hunt Jr. *et al.* 1998; Russell *et al.* 1999). We found considerable dietary overlap between species and among years, could be the result of two non-exclusive hypotheses: adult auklets acquire similar prey from different locations, or, because *Neocalanus* copepods are so abundant (Mackas *et al.* 1998), competition for them is insignificant.

Chick diet of auklets in the Aleutian Islands exhibits high interspecific overlap compared with other seabirds. For example, over 10 years, and nearly 80% of all C-estimates were $\geq$ 0.6, indicating significant overlap (Catry *et al.* 2009). Dietary overlap among Aleutian auklets was similar to that in other subarctic and temperate seabird communities (Pearson 1968; Baltz & Morejohn 1977; Barrett *et al.* 1997; González-Solís *et al.* 1997; Minich 2007), and generally higher than that in tropical communities (Ashmole & Ashmole 1967; Diamond 1983; Catry *et al.* 2009). Overlap among auklets was also higher than among seabirds at the more diverse subantarctic Crozet Island (Ridoux 1994). While this high degree of overlap is noteworthy, it agrees with the prediction that overlap is greater in temperate and sub-polar communities where small numbers of exploited prey taxa are very abundant (Diamond 1983). Dietary overlap was greater in the Aleutians than among auklets breeding at St. Matthew Island in the northern Bering Sea, where overlap between Least and Crested Auklets of $C = 0.52$ was at the lower end of the values we recorded (Harrison 1990).

To our knowledge, ours is the first study of dietary overlap among years, and we have shown that there is considerable variation from year to year and among sites, highlighting the need for long-term investigations to elucidate the ecological relationships among closely-related members of the same foraging guild in the context of coexistence. Dietary overlap at multiple sites has received little attention. We found that Least Auklet chick diet across the Aleutian Islands was nearly identical in all years and exhibited high overlap between islands. These trends, combined with lack of interannual differences in the proportion of *Neocalanus* or euphausiids in chick diet, suggest that auklets were able to locate suitable prey for their chicks in most conditions. Overlap was lower between islands for Crested Auklets but was significant, further supporting the interpretation that chick diet is similar among all three sites. Previous research at Kiska quantified near failure of Least Auklet breeding in 2001 and 2002, with productivity in those years being far lower than recorded at any Least Auklet colony in any year anywhere in Alaska (Major *et al.* 2006; Chapter 2). Most breeding sites failed during the chick rearing stage, with rat activity and nutritional stress being explanatory hypotheses. Our results here are relevant to this issue because we found no difference in Least Auklet chick diet (C = 0.99) between Buldir (where auklets had high productivity; Chapter 2) and Kiska. Food load composition did not correlate with breeding failure at Kiska, nor was it aberrant in any way in the years of failure. This adds to the evidence that introduced Norway rats were responsible for auklet breeding failure in 2001 and 2002 at Kiska.

Food load size

Food load size varied across sampling periods within the breeding season in all three species. In Least and Crested Auklets (and to a certain extent in Whiskered Auklets), food load size increased as the breeding season progressed, paralleling increased energy demands of the chicks. Food load size in the Least Auklet was smaller in our study than load size recorded on the Pribilof Islands, (5.28g, Roby & Brink 1986a). If energy requirements of Least Auklet chicks are the same in the Pribilof and Aleutian islands, then adults in the latter location must deliver food to the chicks more frequently (Roby & Brink 1986a; Roby 1991). To our knowledge, there are no data from Crested of Whiskered auklets to make similar comparisons. The Dovekie (*Alle alle*), similar to auklets ecologically, adapts to changes in zooplankton abundance by increasing the rate of food load deliveries to chicks (Jakubas *et al.* 2007).

Load size was larger relative to adult body mass in the Whiskered Auklet than in Least or Crested auklets. Whiskered Auklet parents provision their chicks only once or twice per night (Konyukhov *et al.* 2000), much less than the other species (Roby & Brink 1986a; Fraser *et al.* 2002). Whiskered Auklets forage in tide rips closer to shore than other auklet species (Byrd & Williams 1993), which may allow them to carry a heavier load over a shorter distance. In addition, because most provisioning of chicks is nocturnal, adults may be under pressure to deliver larger loads to meet their chicks' energy and growth demands, as nocturnal alcids tend to grow slower and fledge at older ages relative to diurnal species (Ydenberg 1989; Hunter *et al.* 2002).

Relationship of food loads to prey availability, and indices of ocean climate

We found no relationship of food load composition to prey availability as assessed by CPR data from near breeding colonies. Auklets generally forage in areas of oceanic fronts and upwelling zones, which have high concentrations of zooplankton (Kinder *et al.* 1983; Hunt Jr. *et al.* 1998; Russell *et al.* 1999); CPR data are averaged over an entire tow, and would not indicate the presence of upwelling areas.

The summer North Pacific Gyre Oscillation (NPGO) predicted food load composition of Crested Auklets, with a higher NPGO value corresponding with a decrease in the biomass of *Neocalanus* copepods and euphausiids. Least Auklet food load composition was related to the summer Pacific Decadal Oscillation (PDO), where a higher PDO value corresponded with a smaller biomass of both *Neocalanus* copepods and euphausiids. The NPGO is an index of sea-surface height and temperature anomalies over 110-180°W and 25-62°N (Di Lorenzo *et al.* 2008), and tends to explain more of the SST anomaly than the PDO (Bond *et al.* 2003). Our examination of the relationship between local summer SST and least Auklet *Neocalanus* biomass showed a parabolic relationship, with copepod biomass peaking between 3-6°C, and declining significantly outside this range. Such a parabolic relationship is found when an optimum exists, such as the relationship between Tufted Puffin (*Fratercula cirrhata*) breeding success and summer SST (Gjerdrum *et al.* 2003). *Neocalanus* copepods require cooler temperatures to develop (ideally less than 10°C; Ikeda *et al.* 1990), but when temperatures are cooler than 3°C, development may be delayed significantly as the copepods take longer to acquire the necessary lipids to grow and moult (Batten *et al.* 2003).

Interestingly, we found a decrease in *Neocalanus* copepods in Least Auklet chick meals at temperatures above 6°C. Such temperatures should be favourable for copepod growth and development (Ikeda *et al.* 1990; Batten *et al.* 2003), meaning that copepod abundance would likely remain high. Warmer temperatures correspond with an earlier start of the peak abundance of *Neocalanus*, and a difference of 4°C in SST between southern and northern sampling stations along the west coast of North American is reflected in a difference of 3-4 weeks in the timing of the *Neocalanus* bloom (Batten *et al.* 2003). Despite this, the variation in local SST measured around auklet breeding islands in June and July each year remained within the thermal limits of *Neocalanus* development (< 10°C; Ikeda *et al.* 1990).

Implications of climate-influenced diet on demography

Many studies of relationships between climate and oceanographic indices and demographic parameters in seabirds suggest bottom-up control mechanisms, although seldom are these tested explicitly (e.g., Durant *et al.* 2004; Votier *et al.* 2005; Chapter 2). In the Aleutian Islands, both adult survival and reproductive success are related to large-scale climate indices (Jones *et al.* submitted; Chapter 2). A more detailed analysis of the relationship between auklet demography and diet is warranted, but the similarity in food load composition from year to year suggests that other factors (e.g., direct predation, density dependence, competition) are regulating auklet populations in the Aleutian Islands.

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We thank the many field workers that collected this abundance of data over the years. Especially noteworthy are the multi-year efforts of several people indicated with a dagger (†). E. Andersen, M. Barrett, D. Barton, G. Beyersdorf†, K. Brenneman, D. Clutter, J. Daniels, E. Drew, B. Drummond†, A. Durand, J. Dussureault†, C. Eggleston†, K. Elkin, J. Fischer†, C. Gray, M. Grinnell, J. M. Hipfner†, S. Hootman, N. Jones, T. Joyce†, P. Kappes, B. Keller, S. Kissler, H. Knechtel†, N. Konyukhov, S. Lantz, K. Lindquist, G. Loh, J. Marais, L. Meehan, J. Mueller, M. Murphy†, R. Orben, M. Ortwerth, A. Palmer, L. Parker, J. Petersen, D. Rehder, H. Renner†, A. Ritchie, N. Rojek†, K. Russell, P. Ryan, S. Sapora, K. Shea, E. Sommer, L. Spitler†, A. Stoertz, A. Stover, S. Syria†, G. Thomson, C. VanStratt, R. Walder and H. Walsh. The M/V *Tiĝlax̂* and her crews provided logistical support. We also thank K. Turco for prey identification. The North Pacific Research Board (Grant No. 638), Natural Sciences and Engineering Research Council of Canada, Alaska Maritime National Wildlife Refuge and Northern Scientific Training Program of Indian and Northern Affairs Canada provided financial support for this research. A consortium managed by the North Pacific Marine Science Organisation supported the North Pacific CPR survey. Consortium members that provided funding for the data used in this study include the North Pacific Research Board and Department of Fisheries and Oceans, Canada. The Institutional Animal Care Committee of Memorial University of Newfoundland (Protocol 09-01-IJ and preceding) approved this project. T.W. Chapman, E.H. Miller, and XX anonymous reviewers provided improvements on previous drafts of this manuscript.

Figures

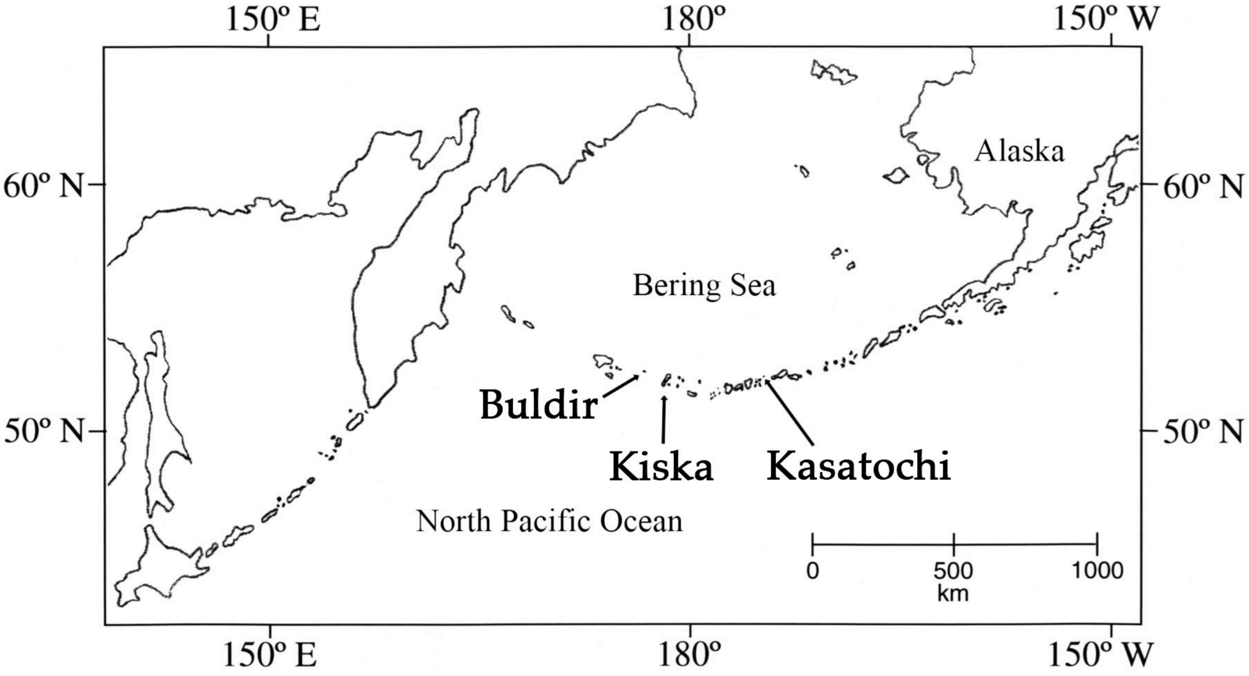

Figure 3-1 – We studied auklet food loads at Buldir, Kiska, and Kasatochi islands, Aleutian Islands, Alaska, from 1994-2006.

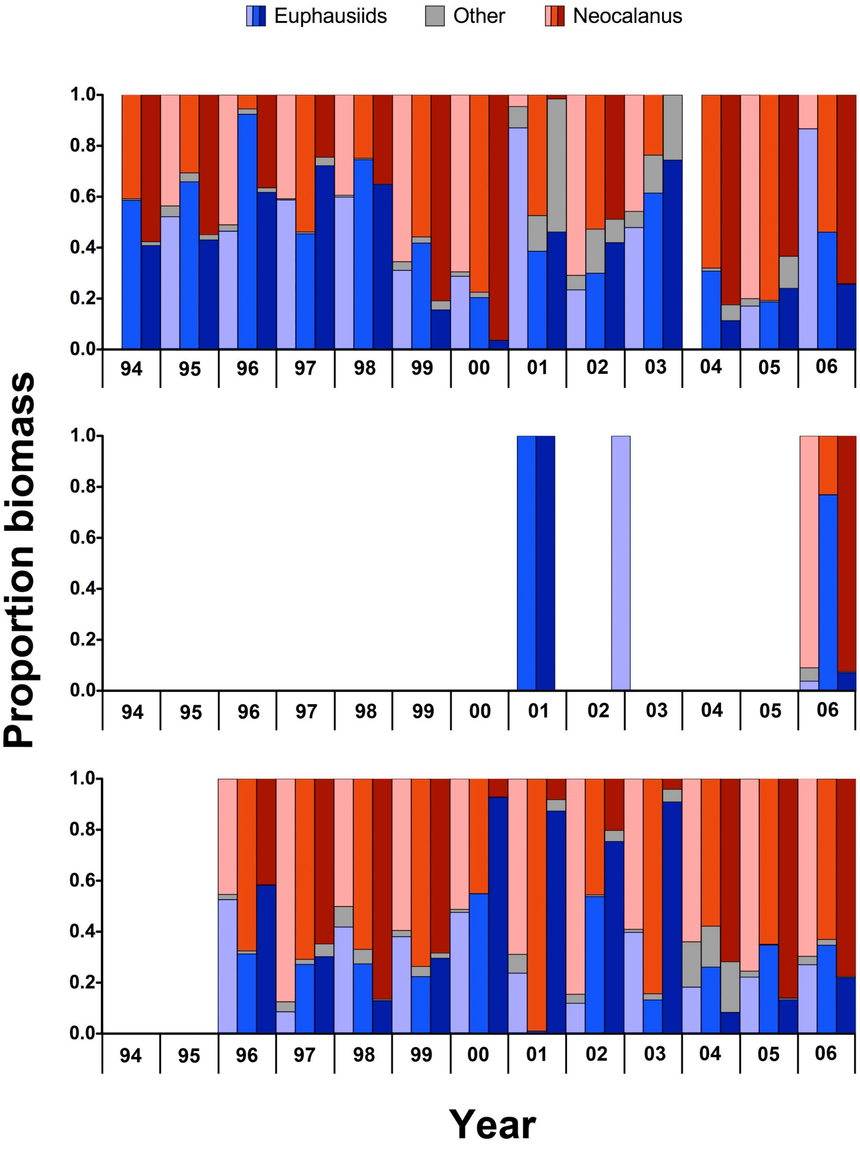

Figure 3-2 – Crested Auklet chick diet (as inferred from adult food loads) had greater proportions of euphausiids than that of Least or Whiskered Auklets. Data are presented as the proportional biomass of *Neocalanus* copepods, euphausiids, and other prey types. Colour shades represent samples from early (light) mid (medium) and late (dark) chick rearing. Data are presented for Buldir (top, 1994-2006), Kiska (middle, 2001-2006), and Kasatochi (bottom, 1996-2006).

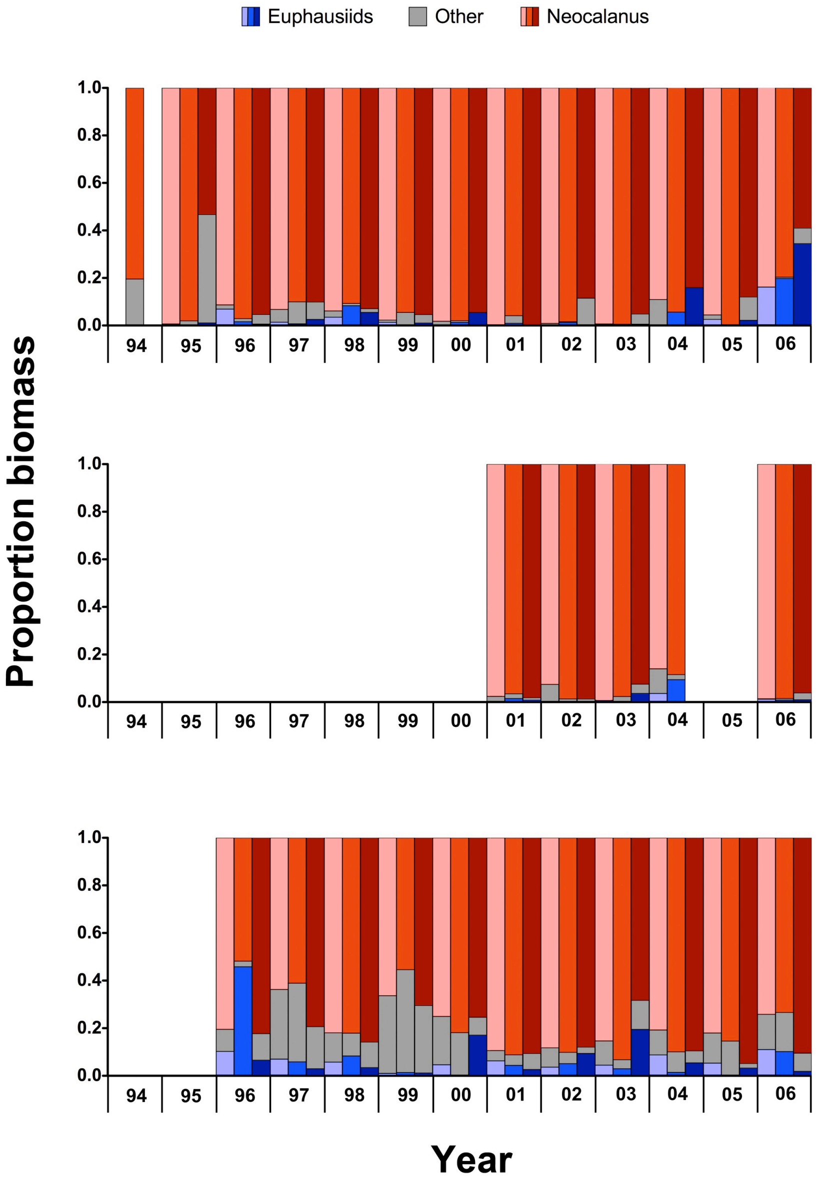

Figure 3-3 – Least Auklet chick diet (as inferred from adult food loads) was almost entirely *Neocalanus* copepods. Data are presented as the proportional biomass of *Neocalanus* copepods, euphausiids, and other prey types. Colour shades represent samples from early (light) mid (medium) and late (dark) chick rearing. Data are presented for Buldir (top, 1994-2006), Kiska (middle, 2001-2006), and Kasatochi (bottom, 1996-2006).

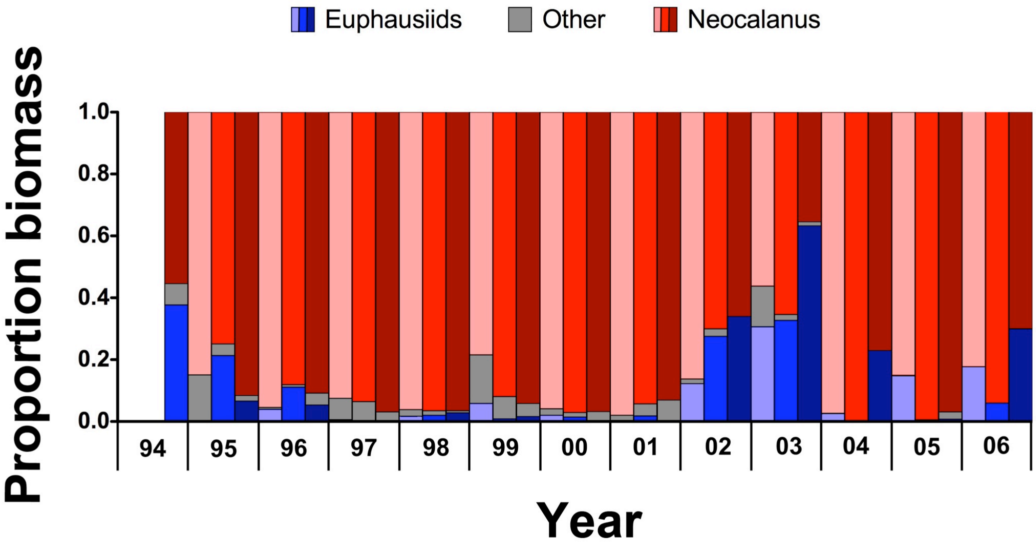

Figure 3-4 Whiskered Auklet chick diet (as inferred from adult food loads) at Buldir (1995-2006) was very similar to that of Least Auklets, with large proportions of copepods. Data are presented as the proportional biomass of *Neocalanus* copepods, euphausiids, and other prey types. Colour shades represent samples from early (light) mid (medium) and late (dark) chick rearing.

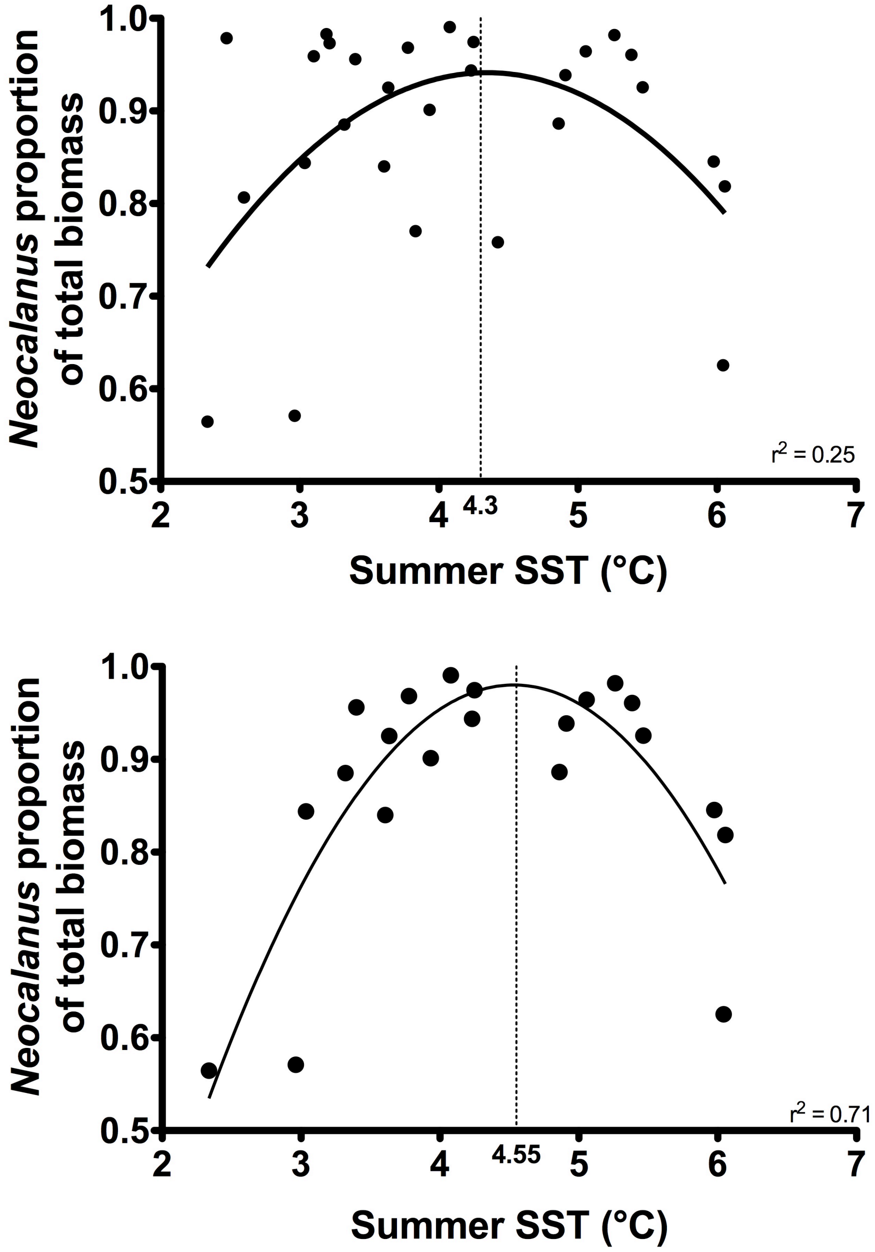

Figure 3-5 – The proportion of *Neocalanus* copepods in Least Auklet food loads was related quadratically to summer SST around all three breeding colonies (a, r^2 = 0.25), and at Buldir and Kasatochi only (b, r^2 = 0.71).

Tables

Table 3-1. The overlap among Least, Crested, and Whiskered auklet food loads at Buldir, Kiska, and Kasatochi islands in 1994-2006 is variable, but consistently high. Values are presented as Horn's (1966) modification of Morisita's (1959) overlap index (C), where C = 0 indicates completely dissimilar diets with no overlap, and C = 1 indicates identical diets (i.e. complete overlap).

	Buldir			**Kasatochi**	**Kiska**
Year	**Crested-Least**	**Crested-Whiskered**	**Least-Whiskered**	**Crested-Least**	**Crested-Least**
1994	0.697	0.981	0.803		
1995	0.634	0.746	0.985		
1996	0.412	0.460	0.998	0.813	
1997	0.513	0.496	0.999	0.949	
1998	0.499	0.469	0.999	0.952	
1999	0.873	0.897	0.995	0.836	
2000	0.977	0.976	1.000	0.553	
2001	0.324	0.328	0.998	0.822	0.010
2002	0.836	0.971	0.932	0.703	
2003	0.170	0.684	0.765	0.740	0.015
2004	0.993	0.990	0.999	0.927	
2005	0.949	0.962	0.999	0.958	

2006	0.915	0.879	0.995	0.953	0.839
Mean	0.676	0.757	0.959	0.837	0.288
95% C.I.	0.149	0.132	0.044	0.077	0.540

Table 3-2. The composition of food loads of Least and Crested auklets at Buldir, Kiska, and Kasatochi islands in 1994-2006 are very similar. Values are presented as Horn's (1966) modification of Morisita's (1959) overlap index (C), where C = 0 indicates completely dissimilar diets with no overlap, and C = 1 indicates identical diets (i.e. complete overlap).

	Crested Auklet			Least Auklet		
Year	Buldir-Kasatochi	Buldir-Kiska	Kasatochi-Kiska	Buldir-Kasatochi	Buldir-Kiska	Kasatochi-Kiska
1996	0.944			0.959		
1997	0.702			0.929		
1998	0.743			0.992		
1999	1.000			0.877		
2000	0.626			0.969		
2001	0.806	0.815	0.527	0.995	1.000	0.996
2002	0.937			0.995	0.999	0.993
2003	0.785	0.897	0.652	0.988	1.000	0.991
2004	0.968			0.995	0.999	0.997
2005	0.998			0.993		
2006	0.945	0.981	0.990	0.973	0.934	0.964
Mean	0.859	0.898	0.723	0.969	0.986	0.988
95% C.I.	0.076	0.094	0.271	0.022	0.026	0.012

Table 3-3. The food load mass for Least, Crested, and Whiskered auklets increases as the breeding season progresses at three breeding sites in the Aleutian Islands, Alaska, in 1994-2006. Samples were pooled among breeding sites and years. Values are estimated marginal means ± S.E. (n) in grams (wet weight). Values sharing the same letter are not significantly different based on overlapping 95% confidence intervals.

Species	**Early**	**Middle**	**Late**
Crested Auklet	8.27 ± 0.83 (282)^{a}	11.77 ± 0.74 (342)^{b}	14.78 ± 0.73 (447)^{b}
Least Auklet	2.94 ± 0.24 (234)^{a}	4.23 ± 0.24 (249)^{b}	5.20 ± 0.24 (200)^{b}
Whiskered Auklet	8.02 ± 0.66 (113)^{a}	10.90 ± 0.67 (108)^{b}	9.29 ± 0.70 (95)^{ab}

CHAPTER 4: INTER-COLONY AND INTER-ANNUAL VARIATION IN TIMING AND RATE OF FLIGHT FEATHER REPLACEMENT BY LEAST AUKLETS (*AETHIA PUSILLA*)

Alexander L. Bond[1], Nikolai B. Konyukhov[2], and Ian L. Jones[1]

[1]Department of Biology, Memorial University of Newfoundland, St. John's,
Newfoundland and Labrador, A1B 3X9, Canada

[2]Bird Ringing Centre of Russia, Institute of Ecology and Evolution, Russian Academy of
Sciences, Vavilova Street, 34, Moscow, 117312, Russia

Abstract

Along with breeding and migration, moult is one of the most energetically expensive components of birds' circannual cycles. Auklets (Alcidae, tribe Aethiini) are apparently unique among the auks in that flight feather moult and breeding overlap. We investigated the degree of overlap of primary moult and breeding in Least Auklets (*Aethia pusilla*) at four colonies – Kiska Island (Aleutian Islands, Alaska, 52°N), St. George Island (Pribilof Islands, Alaska, 56°N), St. Paul Island (Pribilof Islands, 57°N), and Cape Ulyakhpen (Chukotka Peninsula, Russia, 64°N). Flight feather moult commenced during incubation with up to four primaries replaced by the end of chick rearing. We found no difference in moult rate between adult breeders and non-breeders, or between adults and subadults at Kiska. Adult auklets replaced their first four primaries faster and initiated moult later at higher latitudes despite similarities in the length of the breeding season among colonies. The cold-water Anadyr Current, which advects lipid-rich oceanic *Neocalanus* spp. copepods, likely contributes to the increased energetic requirements of Least Auklets breeding and moulting at higher latitudes. In Least Auklets and other members of their tribe Aethiini, sequential primary moult, rather than simultaneous moult typical of other alcids, may be possible because of auklets' lower body mass, wing loading, mass loss at hatching and foraging patterns.

Introduction

The regular replacement of feathers through moult is costly both in energy and time (Murphy 1996; Rohwer *et al.* 2009). Despite the importance of moult, studies of inter-annual and inter-colony variation of moult of pelagic seabirds, and possible influencing factors are rare (Emslie *et al.* 1990; Underhill & Crawford 1999). Because of the cost of feather synthesis and the aerodynamic and thermoregulatory costs of missing feathers, understanding patterns of moult can be crucial to investigations of avian physiology, ecology, and behaviour (Hoye & Buttemer 2011). Ecological inference from stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) in animal tissues has increased in recent years (Inger & Bearhop 2008), and feathers are used commonly in such studies because of the ease and minimal invasiveness with which they can be sampled. Essential to understanding and interpreting stable-isotope data from feathers, however, is knowledge of the range of dates over which a feather was grown, as feathers usually incorporate exogenous nutrients from the time of synthesis (Hobson & Clark 1992a) and, in species with moult migrations, endogenously catabolised nutrients that were laid down prior to migration (Fox *et al.* 2009).

Auklets (Aethiini) are unusual alcids because several species moult their primary feathers sequentially beginning during the breeding season (Bédard & Sealy 1984; Emslie *et al.* 1990; Konyukhov 2001, 2009). Most other auks moult all their flight feathers simultaneously after they leave the breeding colony, rendering individuals flightless for several weeks (Stresemann & Stresemann 1966; Harris & Yule 1977; Sealy

1977; Bédard 1985; Ewins 1988; Harris & Wanless 1990b; Bridge 2006; Pyle 2008). Moulting patterns for some species of auk are largely unknown (e.g., Spectacled Guillemot (*Cepphus carbo*), Craveri's Murrelet (*Synthliboramphus craveri*) and Japanese Murrelet (*S. wumizusume*)).

The Least Auklet (*Aethia pusilla*) is endemic to the Bering and Okhotsk seas and adjacent North Pacific Ocean, where they breed at a few dense colonies (Gaston & Jones 1998). In North America, major colonies are in the western Aleutian Islands, on the Pribilof Islands, and in the northern Bering Sea (Jones 1993b). In Russia, Least Auklets breed on Ratmanov (Big Diomede) Island (Bering Strait), on the Chukotka Peninsula, and on islands in the Sea of Okhotsk and Kuril Archipelago (Dement'ev *et al.* 1951; Kozlova 1957; Konyukhov *et al.* 1998; Kondratyev *et al.* 2000; Artukhin *et al.* 2001; Zelenskaya 2009). Northern colonies in the Bering Sea and Sea of Okhotsk are surrounded by sea ice during part of the year, whereas all Aleutian most Kuril Island colony sites are ice-free year round (Fetterer *et al.* 2010).

Moult is often timed with birds' circannual cycles (Dawson 1998; Dawson *et al.* 2001), and in Least Auklets, is probably related to the timing of breeding. Auklet breeding phenology is later at higher latitudes; e.g. Least Auklets nest 3-4 weeks later at St. Lawrence Island (63°24'N) than colonies in the Aleutian Islands (Sealy 1975; Jones 1993b; Gaston & Jones 1998). We therefore predicted that the timing of moult would show a similar gradient in Least Auklets. Such latitudinal variation in timing and rate of moult has been observed in mammals (Todorovič 1955; King & Moody 1982) and land birds (Williamson & Emison 1971; Medwaldt & King 1978; Dawson *et al.* 2000), but ours is the first investigation of this phenomenon in marine birds.

By including data from all major breeding areas (northern Bering Sea, Pribilof Islands, Aleutian Islands, Chukotka Peninsula), our goal was to investigate how the timing of primary replacement varied with breeding phenology, age class, breeding status (breeder vs. non-breeder), and latitude of the colony. Because Least Auklets begin replacing flight feathers during incubation and continue through chick rearing, we predicted that adults from more northerly colonies affected by sea ice and snowmelt would moult later and faster than adults in the south. Based on previous studies we also predicted that subadults would initiate moult later, but replace primaries faster than adults (Bédard & Sealy 1984; Emslie *et al.* 1990). Finally, we evaluated hypotheses to explain why the tribe Aethiini is unique among the Alcidae in overlapping primary replacement and breeding.

Methods

Capture and moult status of wild Least Auklets

We caught Least Auklets at: Sirius Point, Kiska Island, Aleutian Islands, Alaska (52°08’N, 177°37’E) in June-July 2008 and 2009; Ulakaia Ridge, St. George Island, Pribilof Islands, Alaska (56°35’N, 169°35’W) in June-August 2005; Tolstoi Point, East Landing, and Zapadni Point colonies on St. Paul Island, Pribilof Islands, Alaska (57°11’N, 170°16’W) in June-August 2000 and June-July 2004; and Cape Ulyakhpen on the Chukotka Peninsula, Russia (64°23’N, 173°54’W) in June-September 1988-1990 (Fig. 4-1). Summaries of data from St. Paul, St. George, and Cape Ulyakhpen are also presented by Konyukhov (2009). Birds were caught using noose carpets or with a ground net placed over breeding crevices (Konyukhov 2009). We weighed, measured, and banded each bird, and recorded the number of replaced and missing primaries. Adults were identified as having a black forehead with white streaks; subadults (individuals 11-13 months old) have a brown forehead and worn flight feathers (Pyle 2008). On Kiska Island only, we determined the apparent breeding status of each adult by resighting marked birds and recording whether they carried a chick meal, which is evident by the distended throat pouch (Portenko 1934; Bédard 1969a). Individuals were identified as breeders in a given year if they were observed with chick meals at least twice during the chick-rearing period (late June to late July). This underestimates the number of actual breeders, as some captured birds were not seen following release and could have been breeding elsewhere in the colony, and because some breeders whose attempt failed during incubation would not have been seen carrying chick meals (Jones *et al.* 2002).

At St. Paul Island, St. George Island, and Cape Ulyakhpen, newly grown primaries were measured to the nearest 0.1 mm with callipers. At Kiska Island, we recorded the number of newly grown and missing primaries only. We then converted feather lengths to proportion of feather mass grown (PFMG, Underhill & Summers 1993) by assuming that the mass deposition within each new feathers was linear, and using masses of fully grown primaries obtained from auklets encountered dead at Kiska (all feathers) or sampled for stable-isotope analysis (P1 and P10, Table 4-1). PFMG is preferable, as it describes the energetic costs more accurately (Underhill & Zucchini 1988), whereas counting replaced and missing feathers assumes that each feather is energetically identical (Rohwer 2008). Statistical analyses were performed on the PFMG relative to the feather mass of the first four primaries, as only these are replaced during the breeding season (see Results). Data from Kiska were converted to PFMG by assuming that the outermost new primary was half-grown, the next outermost was 75% grown, and all others were fully-grown. This pattern is consistent with our observations based on measured lengths at other colonies (unpubl. data).

Museum specimens

To study Least Auklet moult outside the breeding season, we examined specimens collected between September-January in museum collections in Canada, the United States, and Russia (Appendix 8). As with live auklets, each specimen was aged (adult or subadult), and moult was scored where old feathers received a score of 0, and new feathers 5 (Remisiewicz *et al.* 2010). Because we assumed some mixing of winter populations, and lacked any a priori knowledge about segregation of individual Least Auklets from different breeding areas during the non-breeding season, all specimens from outside the breeding season (mostly autumn) were included in a single analysis.

Statistical methods

Using the mass of each primary (Table 4-1), we converted the measured lengths of feathers to PFMG for analysis in an Underhill-Zucchini type 5 analysis (Underhill & Zucchini 1988; Underhill *et al.* 1990), hereafter "U-Z 5" analysis. U-Z 5 is used when individuals sampled have either not yet started, or are currently moulting primaries, and no individual has finished primary moult at the end of the study (Underhill *et al.* 1990). U-Z models use a maximum likelihood approach to estimate duration (and therefore, rate) or moult and date of moult initiation. Models were constructed using the package 'moult' in R 2.12.1 (R Development Core Team 2010).

Results

Moult of Least Auklets at breeding colonies

The relationship between feather length and mass was not uniform among primaries (Table 4-1); outermost primaries had greater mass per mm than did inner primaries.

On Kiska Island, we examined 214 live birds between 8 June-26 July 2008 and 115 birds between 10 June-19 July 2009. We examined 232 adult birds from St. George Island between 30 June-5 August 2005, and 143 adults between 25 June-31 July 2007. At St. Paul Island, we examined 310 birds between 10 June-9 August 2000, and 182 birds between 29 June-30 July 2004. At Cape Ulyakhpen, we captured 129 adults between 4

June-7 September 1988, 195 adults between 5 June-25 August 1989, and 386 adults between 2 June-31 August 1990. We found that Least Auklets begin growing up to four primary feathers sequentially during late incubation and early chick rearing.

Because of the small number of birds examined on Kiska in 2009 (n = 65), it was not possible to construct a meaningful U-Z model for this group, so it was removed from subsequent analysis. Neither the duration nor start date of primary moult varied among Least Auklet breeders, non-breeders, and subadults, although subadults tended to be more variable in when moult was initiated (Table 4-2). Among colonies, there was much inter-annual variation in both rate and initiation date of moult: rate was faster (i.e. duration was briefer) and moult started later at Cape Ulyakhpen than in the Pribilof or Aleutian Islands (Table 4-3, Fig. 4-2).

Museum specimens

We examined 105 museum specimens. Of these, 35 were collected between September and December. Some birds had completed primary moult by the end of September, and others a month later. No birds were moulting primaries after 27 November (Table 4-4).

Discussion

Least Auklets replace the innermost primary feathers at the breeding colony during chick rearing, and complete primary moult by October or November. Our results contrast with moult patterns of the closely related Cassin's Auklet (*Ptychoramphus aleuticus*) in which subadults tend to moult primary feathers faster, presumably because the costs of breeding reduce the amount of energy and resources available for moulting (Emslie *et al.* 1990). We found no difference: adults (breeders and non-breeders/failed breeders) moulted at the same rate as subadults. Bédard and Sealy (1984) also found no difference in wing moult progress between adult breeders and failed breeders. Bédard and Sealy (1984: 467) defined "subadults" as "birds in their second summer after hatching and in their first Alternate (I) plumage" (i.e. ~23-25 months old), whereas we believe that these birds were in their first summer after hatching, hence only 11-13 months old (Pyle 2008).

The similar moult and duration, but higher variability in primary moult of subadults, likely reflects interaction among several factors. First, young inexperienced birds may be less successful in foraging around breeding colonies, where dense aggregations of experienced adult breeders may outcompete them. Subadults may therefore be unable to sustain their first primary moult at a rate similar to adults, which would be more experienced in acquiring the nutrients required for feather replacement (Barta *et al.* 2008). Body mass is the best indicator of body condition in birds without an established and independently verified body condition index (Schamber *et al.* 2009), and subadult Least Auklets are lighter than adults (Jones 1993b, authors' unpubl. data), which supports the inexperience hypothesis. Second, faster moult is associated with poor feather quality (Dawson *et al.* 2000; Pap *et al.* 2008). Subadults do not expend energy breeding, and may therefore produce feathers of higher quality than breeding adults. We found no difference in moult rate or timing between breeding and non-breeding adults at Kiska (see below), but have observed high inter-annual variability at other colonies. In any case, one of the most distinctive features of subadults is their extremely worn and faded flight feathers (Jones 1993; originally grown a year before as a nestling), which are certainly in need of replacement if this was possible.

We found that breeding status had no relationship to moult progress, as Bédard and Sealy (1984) also noted for wing moult in three *Aethia* auklets. Two points must be considered however: first, our method underestimates the number of actual breeders, as individuals that failed during incubation were not counted, and some breeders may only be seen once with a chick meal. Some birds captured using noose carpets were non-breeders not tied to a specific part of the colony or were breeding birds that bred elsewhere on the colony (Jones *et al.* 2002). Second, timing of primary moult differs among colonies and years. Timing and rate of moult vary considerably across years and in other auklets (Emslie *et al.* 1990).

Birds breeding at high latitudes often experience a briefer summer breeding period (e.g., Summers *et al.* 2004; Coppack 2007), and moult is often faster than at more northerly locations, presumably to minimize overlap of two life-history stages (moult and breeding, Wingfield 2008). Delays in moult can result in an increase in moult rate and decrease in feather quality (Dawson 2004). Interestingly, Least Auklets do not show a compressed breeding season at higher latitudes, where incubation (30 d) and fledging periods (29 d; Piatt *et al.* 1990b) from St. Lawrence Island (63°24’N) are similar in duration to those in the Aleutian Islands (29 d; Renner 2005). There is little information on auklet moult outside the breeding season (e.g. in migration, on wintering grounds) and few museum specimens have been collected between October and May. Auklets from more northerly locations face longer migrations, as colonies in the northern Bering Sea and the Sea of Okhotsk are covered by sea ice, unlike the Aleutian Islands (Fetterer *et al.* 2010), so may have to moult faster (de la Hera *et al.* 2009).

Least Auklets breeding in Chukotka likely exploit the cold-water Anadyr Current, which advects oceanic zooplankton, like *Neocalanus* copepods (Springer *et al.* 1987; Piatt & Springer 2003). Sea-surface temperature of the Anadyr Current is colder than around the Pribilof and Aleutian islands (Piatt & Springer 2003). Combined with the increased rate of moult at Cape Ulyakhpen compared with other colonies in our study, we conclude that northerly-breeding Least Auklets must consume more calories per unit time than their southern conspecifics – a situation made possible by the Anadyr Current's advection of oceanic copepods.

Our estimate of the complete duration of growth of Least Auklets' P1 feather is around 20-30 days (Konyukhov 2009; Rohwer *et al.* 2009). Our modelled values for primary initiation indicated that moult starts during incubation and that the first primary is often replaced by the mean hatch date. The rate of PFMG increase per day is not likely linear among feathers, so estimating a moult completion date in the absence of a large sample of birds is difficult. Based on observations of museum specimens, primary moult concludes before the end of November. This is similar to estimates of moult duration for the congeneric and similar-sized (118 g) Whiskered Auklet (*Aethia pygmaea*) at Buldir Island, Aleutian Islands, where moult was predicted to end around October (Konyukhov 2001). In adult auklets, it is therefore possible to select feathers representing three different times in the annual cycle – the last (outermost) primary grown the previous winter after young have fledged, body feathers grown during the spring (Pyle 2008), and the first primary grown during incubation.

Primary moult in the Alcidae

Least Auklets (subfamily Aethiinae) are the smallest of the auks, and therefore have smaller feathers to replace. Dovekies (*Alle alle*, subfamily Alcinae) are not closely related to the auklets, but are ecologically similar (small planktivorous auks), breed at higher latitudes than auklets and thus experience shorter briefer summers, and have short breeding periods (Stempniewicz 1981). Dovekies are thought to moult their primaries synchronously (Salomonsen 1944; Dement'ev *et al.* 1951; Storer 1960; Stresemann & Stresemann 1966; Bédard 1985), although recent evidence suggests that, like Common Murres (*Uria aalge*), primary moult originates at a single foci between P4 and P7, proceeding in two concurrent waves towards P1 and P10 (Thompson *et al.* 1998); further investigation is required on the precise moulting pattern. Nevertheless, the difference between Dovekies and the Aethiini is clear: Dovekie’s primaries are moulted rapidly and moult is accompanied by a flightless period, whereas auklets have a relatively protracted moult and maintain flying ability. We agree with Thompson et al.

(1998) that this difference is likely because of Dovekie's long-distance post-breeding migration. Unlike auklets, Dovekies travel several thousands of km and must moult before migration. Auklets move on the order of hundreds of km after the breeding season (see below), and are therefore not under as much pressure to complete moult as Dovekies.

The auklets have among the lowest wing loading (body mass per unit wing area) of the alcids (Stempniewicz 1982; Minami *et al.* 1991; Spear & Ainley 1997; Ortega-Jiménez *et al.* 2010) and thus are able to fly with missing primaries. The larger auks (murrelets, puffins, murres, guillemots, and Razorbill) would experience a significant decrease in wing area were they to moult flight feathers sequentially. This would result in greater wing loading (Bridge 2004), likely rendering them flightless for a lengthy period of time (Livezey 1988). In contrast, the flightless Great Auk (*Pinguinus impennis*) likely had a primary moult similar to that of Common Murres (Salomonsen 1945; Thompson *et al.* 1998). Least Auklets experience an abrupt mass loss when chick rearing commences, and may obtain their own food from more inshore areas, which reduces wing loading and flight costs (Jones 1994; Chapter 5). This may be a mechanism to accommodate flight feather replacement while maintaining flying ability. Other auks also decrease in mass during chick rearing, but this is apparently insufficient to allow for a reduction in wing area via moult (Croll *et al.* 1991).

Moult-breeding overlap is also associated with species that have limited post-breeding migration or dispersal (Bridge 2006). Least Auklets' wintering areas are largely unknown, but they are more abundant in the western Pacific during the winter and spring (Vyatkin 1981; Sydeman *et al.* 2010), and some winter in the Sea of Japan off the coast of Primoye, Russia (Shuntov 1965; Velizhanin 1977a; Kondratyev *et al.* 2000). Sea ice cover in the Bering Sea and Sea of Okhotsk, however, requires some auklets to disperse up to 1000 km from their breeding colony (Fetterer *et al.* 2010). Bridge (2006) classified Least Auklets as "dispersive", or "birds that leave the breeding area after fledging chicks but that spend the non-breeding period in the general area or region of the breeding site" (Bridge 2006: 9). It is clear, however, that Least Auklets breeding in the northern Bering Sea (Chukotka Peninsula, Ratmanov, Little Diomede, St. Lawrence, St. Matthew islands) and the Sea of Okhotsk (Yamskiye Islands, and Iona Island, for example) must disperse at least hundreds of km during winter (Fetterer *et al.* 2010).

Our results indicate that primary moult in Least Auklets responds to local oceanographic conditions that differ with latitude, and that, like land birds, auklets' rate of moult is greatest at high latitudes. Physiological and behavioural factors, including mass loss and a change in foraging area, allow Least Auklets to moult during chick rearing, presumably the time of highest food availability.

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Figures

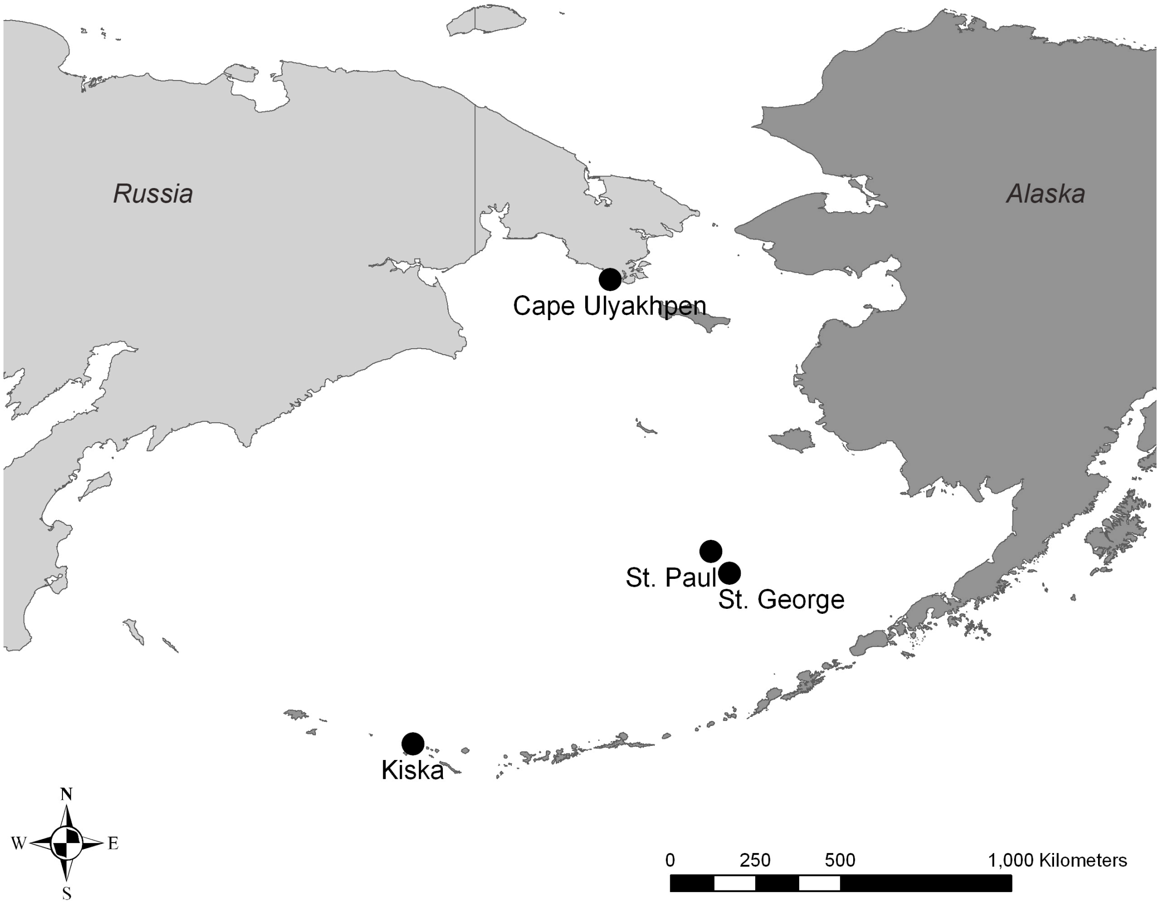

Figure 4-1 – We investigated Least Auklets' primary moult at four colonies throughout their breeding range in the Bering Sea.

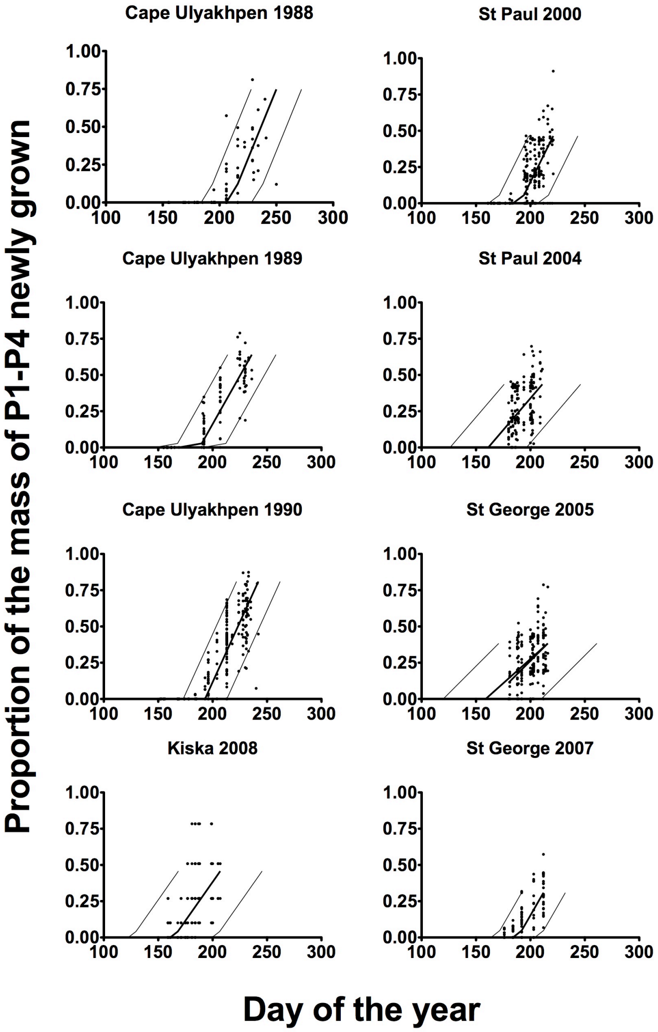

Figure 4-2 – Duration and initiation date of primary moult in Least Auklets varied among years and colonies, with adults from the northern colony (Cape Ulyakhpen) moulting later (higher x-intercept) and faster (shorter duration; greater slope). The solid lines are the mean estimates and 95% confidence intervals, and dots represent individual observations. Researchers arrived after the start of primary moult on St. Paul in 2004, and on St. George in 2005.

Tables

Table 4-1 – The mass and length of Least Auklet primary feathers used to calculate the proportion of feather mass grown for Underhill-Zucchini moult models (n = 5 individuals, except for P1 and P10, where n = 13 individuals). Primary lengths are from Konyukhov (2009). Total feather mass ± S.D. is given for the five individuals for whom all 10 primaries were weighed.

Primary Number	**Mass ± S.D. (mg)**	**Length ± S.D. (mm)**	**Mean mg mm^{-1}**
1	11.1 ± 1.3	43.1 ± 1.7	0.26
2	12.9 ± 2.3	46.0 ± 1.9	0.28
3	14.3 ± 2.7	48.7 ± 1.5	0.29
4	16.5 ± 2.6	51.1 ± 2.0	0.32
5	18.3 ± 2.8	54.5 ± 1.4	0.34
6	19.1 ± 3.2	55.9 ± 1.7	0.34
7	19.8 ± 3.6	57.1 ± 1.6	0.35
8	20.8 ± 3.7	57.8 ± 2.1	0.36
9	22.8 ± 3.4	58.3 ± 1.7	0.39
10	24.5 ± 2.8	56.5 ± 1.8	0.43
Total	176.6 ± 30.0		0.33

Table 4-2 – At Kiska Island in 2008, adult breeding status, and age class had no effect on the duration or initiation date of primary moult in Least Auklets. Subadults' initiation date was significantly more variable than that of adults. Groups sharing the same letter have overlapping 95% confidence intervals and are not considered statistically different.

Group	**n**	**Initiation Date ± S.E. (days)**	**Initiation Date S.D. ± S.E. (days)**	**Duration ± S.E. (days)**
Adult breeders	84	167 ± 5.9^a	18.3 ± 0.2^a	79.5 ± 24.8^a
Adult non-breeders	71	162 ± 3.7^a	18.7 ± 0.2^a	104.5 ± 16.8^a
All adults	155	164 ± 3.0^a	19.5 ± 0.1^a	93.0 ± 12.4^a
Subadults	56	182 ± 7.7^a	24.3 ± 0.5^b	100.7 ± 52.6^a

Table 4-3 – Adult Least Auklets from the most northern colony (Cape Ulyakhpen) tended to moult their primaries faster, and to start their primary moult later than conspecifics in the Pribilofs (St. Paul, St. George), or the Aleutians (Kiska). Groups sharing the same letter have overlapping 95% confidence intervals and are not considered statistically different.

Colony	**Year**	**n**	**Initiation Date ± S.E. (days)**	**Initiation Date S.D. ± S.E. (days)**	**Duration ± S.E. (days)**
Cape Ulyakhpen	1988	129	28 Jul ± 1.8^{c}	11.3 ± 0.1^{b}	54.4 ± 6.6^{a}
Cape Ulyakhpen	1989	195	6 Jul ± 2.5^{b}	11.3 ± 0.1^{b}	75.2 ± 8.3^{ab}
Cape Ulyakhpen	1990	386	12 Jul ± 2.2^{b}	10.2 ± 0.1^{a}	60.5 ± 7.2^{a}
St. Paul	2000	310	9 Jul ± 2.3^{b}	11.5 ± 0.1^{b}	66.1 ± 8.6^{a}
St. Paul	2004	182	10 Jun ± 5.3^{a}	17.9 ± 0.2^{c}	114.0 ± 18.b^{6}
St. George	2005	232	14 Jun ± 6.3^{a}	23.0 ± 0.2^{e}	133.2 ± 23.1^{b}
St. George	2007	143	7 Jul ± 2.2^{b}	10.3 ± 0.1^{a}	76.6 ± 9.1^{ab}
Kiska	2008	214	13 Jun ± 3.5^{a}	19.6 ± 0.1^{d}	93.6 ± 14.3^{ab}

Table 4-4 – The majority of Least Auklets examined from museum collections had completed primary moult by the end of October, and all had completed primary moult by the end of November. Data are pooled among sampling locations, age classes, and years. PFMG = proportion of feather mass grown (P1 through P10).

Month	**n**	**PFMG ± S.D.**	**Range**
Sept	15	0.36 ± 0.22	0.19-1.00
Oct	10	0.96 ± 0.12	0.62-1.00
Nov	4	0.98 ± 0.03	0.93-1.00
Dec	6	1.00 ± 0.00	1.00-1.00

CHAPTER 5: STABLE ISOTOPES REVEAL DAILY VARIATION IN FORAGING ACTIVITY OF INCUBATING LEAST AUKLETS (*AETHIA PUSILLA*)

Alexander L. Bond and Ian L. Jones

Department of Biology, Memorial University of Newfoundland, St. John's,
Newfoundland and Labrador, A1B 3X9 Canada

Abstract

Central-place foraging birds, such as breeding seabirds, face a trade-off between satisfying the energetic demands of growing nestlings and meeting their own nutritional requirements. We investigated the foraging patterns of breeding adult Least Auklets (*Aethia pusilla*) at Kiska Island, Aleutian Islands, Alaska, in 2009. Because of Least Auklets' small size (85 g), suitable attached data recorders were not available at the time of our study, so we used daily within-feather variation in $\delta^{13}C$ and $\delta^{15}N$ stable isotopes of the first primary feather (P1), which is grown during the incubation period. Controlling for individual differences, both $\delta^{13}C$ and $\delta^{15}N$ increased as the breeding season progressed, indicating that Least Auklet adults shifted their foraging patterns significantly. These results could be explained by adults gradually switching to different prey taxa, a seasonal change in isotopic ratios in a constant prey taxon, or a shift to a slightly more productive foraging location, such as an oceanographic front. Other work has shown that no seasonal change in chick diet prey taxa occurs, perhaps pointing to the latter hypothesis, which could involve a mechanism to balance adults' own energetic requirements with the energy required for the successful survival of their single egg and chick. Together, these results indicate that adult Least Auklets may balance their own demands with those of their egg and chick by a shift in foraging activity.

Introduction

Stable-isotope ratios in seabird feathers, which are grown incrementally, provide information about foraging patterns, distribution, and environmental variability experienced by individuals during periods when they are inaccessible outside the breeding season (Cherel & Hobson 2007; Bond *et al.* 2010a). Hidden aspects of breeding birds' foraging activity can be revealed by stable-isotope ratios in feathers that are grown during the breeding season. Apart from advances in laboratory techniques and equipment that have reduced the cost of analyses, many recent advances in the application of stable isotopes to ecological questions have been because tissues such as feathers, blood, or claws can be sampled non-destructively (Hobson & Clark 1992a; Bearhop *et al.* 2004). Because only a small amount of tissue is required for analysis (approximately 0.25 mg), large feathers can be sub-sampled several times to gain insight into species' foraging ecology with greater temporal resolution. Variation in foraging patterns during feather growth will result in within-feather isotopic heterogeneity because exogenous nutrients are incorporated immediately into growing feathers (Murphy 1996).

We examined within-feather variation in δ^{13}C and δ^{15}N in the first primary feather (P1) of Least Auklets (*Aethia pusilla*), a small planktivorous auk endemic to the Bering and Okhotsk seas. Adults eat calanoid copepods, mainly *Neocalanus plumchrus* and *N. flemingeri* (Bédard 1969a; Hunt Jr. *et al.* 1998), which are advected by oceanographic fronts (Hunt Jr. & Harrison 1990; Hunt Jr. 1997; Russell *et al.* 1999).

Nothing is known about differences between adult and chick diet during the nestling stage of the breeding season (Jones 1993b; Chapter 3). Previous studies of adult auklet diet were based on stomach contents (Bédard 1969a; Harrison 1990; Hunt Jr. *et al.* 1998), which often represent the previous meal only, and do not account for temporal variation (Duffy & Jackson 1986). Auklets' foraging distribution has also been studied in relation to oceanographic features (Kinder *et al.* 1983; Harrison *et al.* 1990; Russell *et al.* 1999), but vessel surveys are indicative of population-level patterns, do not address individual differences, and are at too coarse a resolution to infer differences at a fine temporal scale (e.g., within the incubation period). Because of Least Auklets' small size (85 g), and difficulty in recapturing individuals at large colonies (> 1 million individuals; Sowls *et al.* 1978), attached data recorders are not yet practical. The stable-isotope analysis approach therefore offers a unique opportunity to investigate adult foraging activity with a fine temporal resolution, and to examine potential changes in adult self-feeding as chicks' demands increase.

Least Auklets' P1, the innermost primary, is approximately 43 mm long. The old P1 feather is shed near the beginning of incubation, and the new replacement feather takes 20 days to grow at approximately 2.13 mm day^{-1} (Konyukhov 2009; Rohwer *et al.* 2009; Chapter 4). Least Auklets incubate their egg for approximately 30 d (Sealy 1984; Piatt *et al.* 1990b), and at Kiska, peak hatching date is around 30 June ± 3 d (Chapter 2). With a mean moult initiation date at Kiska of 13 June ± 3.5 d (Chapter 4), the majority of the feather is replaced during incubation, when adults must balance their own nutritional requirements with the successful incubation of their egg. Our objectives were to 1) quantify within-feather heterogeneity in δ^{13}C and δ^{15}N in Least Auklet P1 primaries replaced during the incubation period; 2) use these isotopic signatures to elucidate possible changes in adult foraging patterns, and 3) to identify important areas for future investigation of questions related to the trade-off between self-maintenance and parental care in this planktivorous alcid.

Methods

We sampled the right P1 from ten adult Least Auklets at Sirius Point, Kiska Island, Aleutian Islands, Alaska (52°08’N, 177°37’E), in July 2009 (Bond & Jones 2009a). Feathers were 75-100% grown. We cleaned feathers by washing in 0.25M NaOH (Bearhop *et al.* 2000a; Bond & Diamond 2009). Feathers were divided into four regions (A-D), from distal to proximal ends of feathers, each representing approximately 5-8 mm of the feather vane. Approximately 0.25 mg of feather barb was sampled from each region, representing tissue that was grown during days 1-3 (A), 4-8 (B), 9-12 (C), and 13-18 (D) for each feather. Not all vane areas were sampled (e.g., days 19-20), because some feathers were not fully-grown. Each sample was placed in a tin cup, crushed, and combusted at 1800°C in a Carlo Erba NA1500 Series II elemental analyzer for analysis of compounds for isotope ratios. Resultant gases were separated by a packed GC column and analyzed by a Delta V Plus continuous-flow isotope ratio mass spectrometer (CF-IRMS). Isotope values were calibrated using international (mean ± SD of repeated measurements; IAEA-N1 δ^{15}N: 0.52 ± 0.13, IAEA-N2 δ^{15}N: 20.32 ± 0.04, IAEA-CH6 δ^{13}C: -

10.45 ± 0.06, USGS-24 Graphite $\delta^{13}C$: -16.04 ± 0.14, USGS-25 $\delta^{15}N$: -30.25 ± 0.04) and lab standards (MUN Sulphanilamide $\delta^{13}C$: -28.23 ± 0.22, $\delta^{15}N$: -1.51 ± 0.09, MUN-CO-2 $\delta^{13}C$: -40.11 ± 0.09), which cover the range of isotopic values in our samples.

Statistical Analysis

We analysed trends within individuals using a repeated measures ANOVA in SPSS 16.0.2 (SPSS Inc., Chicago, IL, USA), and tested the assumption of sphericity using Maulchy's W (Mauchly 1940) and homogeneity of variance using Levene's test (Levene 1960). We also included a post-hoc analysis to detect any linear or quadratic trends over the feather length of the feather.

Results

Within individuals, the range of values of $\delta^{13}C$ was between 0.70-2.43‰, and differences within feathers in $\delta^{15}N$ were between 0.30-2.42‰. Isotope ratios met the assumptions of the linear model (Levene's test, all $p > 0.10$), but not sphericity for $\delta^{13}C$ (Maulchy's W, $\delta^{13}C$: $p < 0.033$, $\delta^{15}N$: $p = 0.473$). We therefore used the Greenhouse-Geisser (1959) correction for subsequent analyses of $\delta^{13}C$, as $\varepsilon < 0.75$ (Girden 1992). Controlling for individual differences, there were significant within-feather differences in $\delta^{13}C$ ($p < 0.001$) and $\delta^{15}N$ ($p = 0.021$). There were also significant linear trends within individuals, with both $\delta^{13}C$ and $\delta^{15}N$ increasing through the chick-rearing period (mean difference between sections A and D ± SD; δ^{13}C: +1.5 ± 0.7‰, $p < 0.001$, δ^{15}N: + 0.8 ± 0.7‰, $p = 0.022$; Fig. 5-1).

Discussion

Seabirds, as central-place foragers, are expected to minimize transit time between their breeding colony and food resources (Baird 1991), and to balance the trade-off between distance to foraging grounds and the energy and nutrients acquired (Obst *et al.* 1995; Elliott *et al.* 2009). Differences in time allocated to self-maintenance and parental care should balance the life-history trade off between current reproduction and survival in adults (Clark & Ydenberg 1990a; Stearns 1992; Dobson & Jouventin 2010b). In auks that forage by wing-propelled pursuit-diving and have high wing-loadings, such as Least Auklets, the energetic costs of flying between foraging areas and the breeding site are high (Obst *et al.* 1995).

In Least Auklets, we found a consistent shift towards higher δ^{13}C in feather tissue deposited as incubation progressed, with a similar but weaker trend for δ^{15}N. These results could be explained by several processes: 1) adults gradually switched to different prey taxa; 2) a seasonal change in isotopic ratios in prey; 3) a shift in foraging location; or 4) metabolism of endogenous nutrients.

Heterogeneity in feather δ^{13}C and δ^{15}N can reflect changes in the isotopic content of diet (and hence in foraging patterns) at a fine temporal resolution. We did not sample adult stomachs to determine diet, but there were no within-season differences in chick diet during 1993-2006 (Chapter 3), so we have no reason to suspect a diet shift in adults. Least Auklets' primary prey in the Aleutians (*Neocalanus* copepods) are the most abundant zooplankter in the North Pacific Ocean (Mackas *et al.* 1998), and their peak abundance coincides with Least Auklets' nesting period (June and July; Batten & Mackas 2009). We therefore have no a priori reason to suspect that adult diet composition changes throughout the breeding season, although independent verification is required to verify this assertion.

A seasonal change in prey isotopic ratios (hypothesis 2) would explain the change in feather isotope ratios we observed (assuming taxonomic constancy in diet). Such a phenomenon has not been documented in the Bering Sea (but see Rau *et al.* 2003 for discussions on inter-annual variability in plankton stable isotope ratios in the California Current). Because no such data exists for the Bering Sea, we cannot confirm or refute this hypothesis.

Least Auklets lose up to 7% of their body mass around the time the egg hatches, while maintaining a relatively constant mass during incubation. This mass loss is presumably a mechanism to decrease flight costs while adults provision nest-bound chicks (Jones 1994). Mass loss may be related to replacement of up to four flight feathers at the same time (Chapter 4). Metabolising endogenous nutrient reserves (hypothesis 4) could influence the isotopic ratios in feathers during this time (Fox *et al.* 2009), and would be represented in the most proximal feather section (section D) in our study.

A change in foraging behaviour during incubation, such as foraging closer to the colony site, might also explain the results (hypothesis 3). “Isoscapes,” or geographic patterns in stable-isotope ratios, have been described for calanoid copepods in the Bering Sea (Schell *et al.* 1998). These isoscapes show relatively constant δ^{13}C and δ^{15}N values in copepods in the western Aleutian Islands, but at a coarse resolution (areas pooled in 2‰ contours), and there is no information on temporal variability. The consistent shift among individuals along a geographic isotope gradient suggests a geographic shift. Higher δ^{13}C is associated to increase phytoplankton growth as occurs in nutrient-rich waters, such as inshore systems or oceanic fronts (Goericke & Fry 1994; Popp *et al.* 1998; Graham *et al.* 2010). Least Auklets preferred prey, *Neocalanus* copepods, are often concentrated in such fronts in the Bering Sea (Hunt Jr. *et al.* 1998; Russell *et al.* 1999). A shift towards more productive systems at the end of incubation and beginning of chick rearing could be related to adults’ increased energetic demands as chicks hatch, and require their parents to provision them several times per day, with increasing amounts of food (Roby & Brink 1986a; Chapter 3).

During incubation, adults expend energy caring for their egg, and have developed several strategies to accommodate chicks’ demands. Incubation shifts average 23.6 ± 5.6 h (Roby & Brink 1986a), and during this time, off-duty parents can range wider, and exploit more distant resources. Once the chick hatches, it is brooded continuously for the first five days (Jones 1993b), restricting the parents’ ability to travel far. By foraging in highly productive areas, such as oceanic fronts, close to the breeding colony, adults reduce their costs of self-maintenance, and can increase the time allotted to chick provisioning.

There was also a trend in increasing δ^{15}N through the incubation period. This change was small in 7 of 10 cases (range < 1.0‰), but might also reflect a dietary change based on shift in foraging area. Quantitative estimates of adult auklet diet using stable isotope analysis are not possible because discrimination factors, the change in δ^{13}C or δ^{15}N between prey and consumer, are specific to each consumer (Caut *et al.* 2008), and can influence mixing model output greatly (Bond & Diamond 2011); no such discrimination factors are available for auklets.

Continued miniaturization of data loggers will permit telemetric studies in the near future that would provide much more detailed insight into adult auklets' foraging patterns. Isotopic investigations of differences in adult and chick diet are also possible providing that the differences in metabolism between growing chicks and adults can be accounted for (Ponsard & Averbuch 1999; Cherel *et al.* 2008; Sears *et al.* 2009).

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Figures

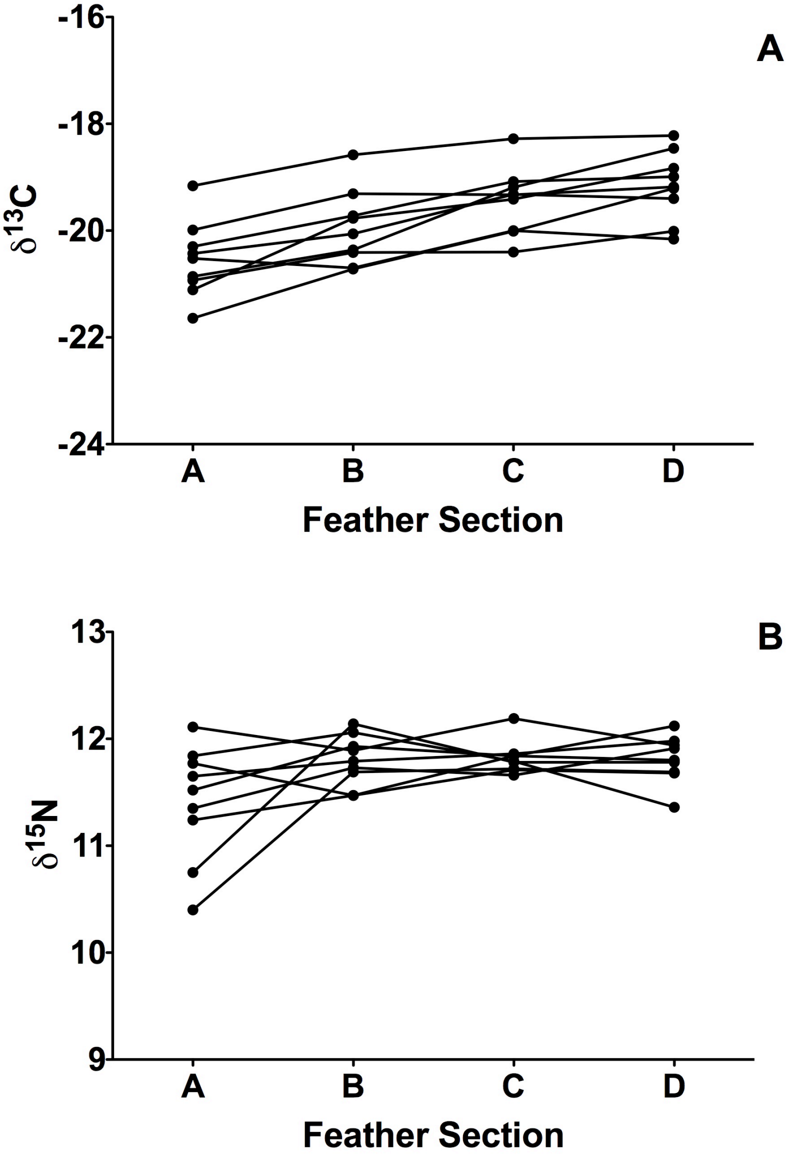

Figure 5-1 – Controlling for individual differences, both $\delta^{13}C$ (A, $p < 0.001$) and $\delta^{15}N$ (B, $p = 0.022$) in individual Least Auklets' first primary feather (P1) increased from incubation (feather section A) to early chick rearing (feather section D). Each line represents isotope values from a single individual.

CHAPTER 6: STABLE ISOTOPES INDICATE SEASONAL AND AGE-RELATED VARIATION IN FORAGING BY LEAST AND CRESTED AUKLETS IN THE ALEUTIAN ISLANDS, ALASKA

Alexander L. Bond and Ian L. Jones

Department of Biology, Memorial University of Newfoundland, St. John's,
Newfoundland and Labrador, A1B 3X9, Canada

Abstract

Least and Crested Auklets (*Aethia pusilla* and *A. cristatella*) replace breast feathers during the pre-breeding period, and primaries form during the incubation and post-breeding periods. Thus, by sampling different feathers from a single individual on one occasion, we can obtain foraging information from the majority of the annual cycle using stable-isotope analysis. (SIA). We sampled adult and subadult Least Auklets and adult Crested Auklets at Buldir, Kiska, and Gareloi Islands, in the western Aleutian Islands, Alaska, from 2007-2010, and Least Auklet chicks at Kiska in 2009. There were no differences in isotope ratios among islands or years, but significant differences between species, among seasons (feather types), and within species between age classes. Adult Least Auklets had higher δ^{15}N than subadults during the pre-breeding period, and chicks during chick rearing. Crested Auklets had higher δ^{15}N than Least Auklets at Gareloi throughout the year. Both species showed a trophic shift during the post-breeding season, characterised by an increase in δ^{15}N, and for Least Auklets, in δ^{13}C as well. Species' isotopic differences were likely caused by differences in diet composition of Crested (euphausiids) and Least Auklets (copepods). Subadults are inherently less experienced than adults, probably still learning to forage during their first winter and thus taking different food items than adults. Least Auklet adults' higher δ^{15}N relative to chicks likely reflects the abundance of zooplankton during the breeding season, and changes in adult physiology and self-feeding patterns during chick rearing. Our results provide hypotheses for testing in future studies using attached data loggers to measure

foraging locations and movement outside of the breeding season.

Introduction

Prey availability and variability in the diet of marine animals have profound influences on demography (Gall *et al.* 2006; Sorensen *et al.* 2009), are influenced by oceanographic and climatic patterns at the landscape level (Durant *et al.* 2003; Hobson *et al.* 2004), and determine individual health and breeding condition (Sorensen *et al.* 2010). During the breeding season, adult seabirds provision nest-bound young, and often face a trade-off between their own energetic demands, and the requirements of their egg or young (Clark & Ydenberg 1990b). This has resulted in a diversification of strategies to balance current reproductive effort with future survival, including alternative strategies when adults self-provision. A frequent assumption of seabird dietary studies is that adult and chick diet are similar, but this is not often the case (Wehle 1982, 1983; Wilson *et al.* 2004). This is best exemplified by the bimodal foraging strategy of some species, where adults make short, frequent trips to provision young, but make longer, less frequent foraging trips to replenish their stores with high energy content prey (e.g., Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994; Welcker *et al.* 2009a). Thus, to gain a full understanding of the foraging behaviour and requirements of adults, quantifying the diet provided to nestlings is insufficient.

In the North Pacific Ocean and Bering Sea, auklets (*Aethia* spp.) are the most numerous seabirds (Gaston & Jones 1998). Auklets breed in dense colonies in the Aleutian Islands, Alaska, and winter in the North Pacific Ocean (Jones 1993a, b). Auklet diet during the breeding season is relatively well studied, although most information concerns nestling diet. In the Aleutian Islands, adults provision chicks with calanoid copepods (*Neocalanus* spp.) and euphausiids (*Thysanoessa* spp.) (Day & Byrd 1989; Chapter 3). Limited information suggests that, in the Aleutians, adults themselves consume copepods, euphausiids, and smaller numbers of amphipods and cephalopods during the breeding season (Day & Byrd 1989; Troy & Bradstreet 1991; Hunt Jr. *et al.* 1998). The winter ecology and behaviour of auklets is largely unknown, and consequently there are few reliable quantitative descriptions of winter diet (Stejneger 1885; Troy & Bradstreet 1991). The diet of subadult Least Auklets, birds in their second year of life is unknown. These individuals attend breeding colonies sporadically as non-breeders and, not burdened with the constraints of raising a chick, their diet may differ from that of breeding adults.

In the past 25 years, biochemical techniques to evaluate avian diet indirectly have been developed (Hobson 1987; Iverson *et al.* 2004). Using these forensic techniques has enabled researchers to study seabird diet during periods when birds are away from breeding colonies, which for many species, covers the majority of the annual cycle. Stable-isotope ratios of carbon and nitrogen are now used frequently to characterize seabird foraging behaviour (Barrett *et al.* 2007). Values are expressed as the parts-per-thousand ratio of the heavier (^{15}N or ^{13}C) to the lighter isotope (^{14}N or ^{12}C) as compared with an international standard (Pee Dee Belemnite for C, atmospheric air for N). $\delta^{15}N$, or the ratio of $^{15}N/^{14}N$, is a continuous measure of trophic position, and it increases between 2-5‰ with each trophic step because ^{14}N is excreted preferentially in nitrogenous waste (Steele & Daniel 1978; Minagawa & Wada 1984; Kelly 2000). There is little trophic enrichment of $\delta^{13}C$ at higher trophic levels (Rau *et al.* 1983; Hobson & Welch 1992), but marine (bicarbonate-based) and terrestrial carbon sources (CO_2-based) differ in their $\delta^{13}C$ values (Peterson & Fry 1987). $\delta^{13}C$ can also provide information on foraging area in the marine environment because of spatial "isoscapes" in the environment (Hobson 1999; Cherel & Hobson 2007; Graham *et al.* 2010). Variation in $\delta^{13}C$ results from varying levels of primary production, with areas of greater phytoplankton growth such as upwellings and inshore areas being enriched in ^{13}C relative to unmixed pelagic systems (Goericke & Fry 1994; Popp *et al.* 1998).

Feathers are very useful for stable-isotope analysis because they can be sampled with minimal invasiveness, stored easily in remote field settings, and because feathers are inert once grown, the isotope ratios will represent the diet at the time of synthesis (Hobson & Clark 1992a; but see Fox *et al.* 2009). Auklets begin moulting primary feathers sequentially, starting near chick hatching, and continuing from P1 to P10 (innermost to outermost primary) until late October or early November (Konyukhov 2009; Chapter 4); the same is likely true for Crested Auklets (Bédard & Sealy 1984; Pyle 2008). Body feathers are replaced during the spring, in March-May (Pyle 2008), thus by sampling three feathers from each individual, we can investigate stable isotopes from late incubation/early chick rearing (P1), autumn post-breeding (P10), and spring pre-breeding (body; Pyle 2009).

Using stable isotope analyses of feathers, our objectives were to 1) compare the spring pre-breeding diet of Least Auklet adults and subadults at Kiska Island between 2007-2010; 2) compare the diet of Least Auklet adults from three breeding colonies throughout the annual cycle; 3) compare the diet of adult Least and Crested Auklets from Gareloi Island throughout the annual cycle; and 4) provide insight into the comparative foraging behaviour and ecology of these closely related planktivores.

Methods

Auklet capture & field sampling

We captured Least Auklets on Main Talus, Buldir Island (52°23'N, 175°33'E; adults in 2008 and 2009), Sirius Point, Kiska Island (52°08'N, 177°35'E; adults and subadults in 2007-2010, chicks in 2008), and Southeast Colony, Gareloi Island (51°46'N, 178°45'W; adults in 2009). Crested Auklets were captured at Gareloi in 2009 only. Birds were captured using noose carpets set in the breeding colony during the auklets' activity period between 0900-1600 Hawaii-Aleutian Daylight Time (Byrd *et al.* 1983; Jones 1992). Adult Least Auklets were those in definitive alternate plumage, indicated by extensive white streaks on the forehead, a redder bill tip, and less-worn primaries. Subadults (birds beginning their second year – 12 months old in July) have a brown forehead with no streaking, worn primaries that appear brown, and a darker bill and often have dark spotted or entirely dark throat feathering (Bédard & Sealy 1984; Jones 1993b). Crested Auklet adults were identified by their large, orange bill rhamphothecae, grey forehead (vs. brown in subadults), and fresher primaries (Jones 1993a). Once aged, birds were measured, banded, and feather samples were taken.

Feathers were then placed in individual paper envelopes, kept cool in the field, and frozen at -20°C upon our return.

Laboratory analysis

Prior to analysis, feathers were washed with 0.25M NaOH and then air dried to remove external contamination (Bearhop *et al.* 2000b; Bond & Diamond 2009). Individual auklet feathers show considerable heterogeneity in stable-isotope ratios (Chapter 5), so we sampled each feather in the same way. Approximately 0.2-0.3 mg from the distal tip of the vane was cut, placed in tin cups, and crushed. Samples were combusted at 1800°C in a Carlo Erba NA1500 Series II elemental analyzer for continuous flow analysis of compounds for isotope ratios. The resultant gases were separated by a packed GC column and analyzed by a Delta V Plus isotope ratio mass spectrometer through a continuous flow interface (CF-IRMS). Isotope values were calibrated using method blanks and standard reference materials IAEA-N2 (mean ± S.D., δ^{15}N: 20.32 ± 0.09‰), IAEA-CH6 (δ^{13}C: -10.45 ± 0.09‰), USGS-24 (graphite, δ^{13}C: -16.11 ± 0.15‰) and USGS-25 (δ^{13}C: -30.25 ± 0.05‰) and internal lab standards MUN-CO-2 (δ^{13}C: -40.11 ± 0.10‰) and MUN Sulfanilamide (δ^{13}C: -28.36 ± 0.81, δ^{15}N: -1.42 ± 0.09). Standards covered the range of isotopic values in our samples. Mean recovery of all standards ranged from 99-101%. Within-run duplicate samples (9% of total samples) yielded mean standard deviations of 0.42‰ for δ^{13}C and 0.45‰ for δ^{15}N.

Statistical methods

Quantitative isotope mixing models are highly sensitive to variation in species-specific discrimination factors, the change in $\delta^{13}C$ or $\delta^{15}N$ between prey and consumer (Bond & Diamond 2011), and because no discrimination factors have been established for auklets, we have restricted our analysis to a comparative description.

All analyses were conducted in SPSS 16.0.2 (SPSS Inc., Chicago, IL, USA). Because $\delta^{13}C$ and $\delta^{15}N$ from the same sample are not independent statistically, we used multivariate analysis of variance (MANOVA) to assess differences among species and age classes in stable-isotope ratios, with univariate analysis of variance (ANOVA) to examine each isotope ratio separately in cases where the MANOVA revealed a significant difference. To test for differences among feather types within individuals, we used repeated measures ANOVA, and tested sphericity using Mauchly's W (Mauchly 1940). When the sphericity assumption was not met, used the Greenhouse-Geisser (1959) correction when $\varepsilon < 0.75$, and the Huynh-Feldt (1976) correction when $\varepsilon > 0.75$ (Girden 1992). We assessed homogeneity of variance using Levene's test (Levene 1960). We used 95% confidence intervals for post hoc comparisons. All tests were considered significant when $p \leq 0.05$. Isotope data are presented as means ± S.D.

Results

Differences among Least Auklet age classes

Variances of δ^{13}C were homogenous, but those of δ^{15}N were not (Levene's test, δ^{13}C: $p = 0.08$, δ^{15}N: $p = 0.03$). MANOVA detected significant differences between age classes in isotope ratios (adults and subadults, Wilks' $\lambda = 0.66$, $F_{2,69} = 17.73$, $p < 0.001$), but not years (Wilks' $\lambda = 0.97$, $F_{6,138} = 0.42$, $p = 0.87$) or the year*species interaction (Wilks' $\lambda = 0.93$, $F_{6,138} = 0.82$ $p = 0.56$). Adults had higher δ^{13}C (-18.81 ± 1.8‰ vs. -19.95 ± 1.88‰, $F_{1,70} = 6.88$, $p = 0.011$) and δ^{15}N (13.21 ± 1.68‰ vs. 11.10 ± 1.44‰, $F_{1,70} = 34.94$, $p < 0.001$) isotope ratios than subadults during the pre-breeding period (Fig. 6-1).

To compare adults and chicks, we used chick breast feathers and adult P1 feathers, which were grown at the same time. Because we found no differences among years in adult P1 feathers (see below), data from Kiska in 2008 and 2009 were pooled. Neither δ^{13}C nor δ^{15}N had homogenous variances (Levene's test, both $p < 0.001$). There were significant differences between age classes in isotope ratios (Wilks' $\lambda = 0.103$, $F_{2,25} = 108.93$, $p < 0.001$). Adults had significantly higher δ^{13}C (-18.98 ± 1.85‰ vs. -20.67 ± 0.35‰, $F_{1,26} = 6.43$, $p = 0.018$) and δ^{15}N (12.30 ± 0.95‰ vs. 8.88 ± 0.23‰, $F_{1,26} = 98.32$, $p < 0.001$) than chicks (Fig. 6-2).

Differences among colonies and seasons

Neither δ^{13}C nor δ^{15}N had homogenous variances (Levene's test, both $p < 0.001$). There were significant differences in Least Auklet isotope ratios among islands, feather types, years, and some of their interactions, so we used repeated measures univariate analyses to examine differences in detail. δ^{13}C did not meet the assumptions of sphericity (Mauchly's W = 0.80, $\chi^2_2 = 9.44$, p = 0.009), and we used the Huynh-Feldt correction ($\varepsilon = 0.94$). There were significant differences among feather types within individuals ($F_{1.89,83.01} = 11.09$, p < 0.001). P10 feathers had a higher $\delta^{13}C$ values than either P1 or breast feathers (Fig. 6-3). Between individuals, there were no differences in $\delta^{13}C$ among the three islands ($F_{2,44} = 1.59$, p = 0.22), or years ($F_{1,44} = 3.48$, p = 0.07), and the island*year interaction was not significant ($F_{1,44} = 0.86$, p = 0.36). $\delta^{15}N$ also did not meet the assumption of sphericity (Mauchly's W = 0.78, $\chi^2_2 = 10.87$, p = 0.004), and we again applied the Huynh-Feldt correction ($\varepsilon = 0.92$). There were significant differences among feather types within individuals ($F_{1.84,81.12} = 13.54$, p < 0.001). P10 were also enriched in ^{15}N compared to P1 and breast feathers (Fig. 6-3). Between individuals, there was no difference in $\delta^{15}N$ among islands ($F_{2,44} = 0.77$, p = 0.47), or years ($F_{1,44} = 1.82$, p = 0.19), and the island*year interaction was not significant ($F_{1,44} = 1.76$, p = 0.19).

Differences among species

Data met the assumptions of our linear models, and variances of both isotopes were equal (Levene's test, both p > 0.20). There were significant differences in isotope ratios among feather types (Wilks' $\lambda = 0.78$, p = 0.01) and species (Wilks' $\lambda = 0.72$, p < 0.001), and the feather type*species interaction was not significant (Wilks' $\lambda = 0.93$, p = 0.42). Both $\delta^{13}C$ and $\delta^{15}N$ met the assumptions of sphericity (Mauchly's W, $\delta^{13}C$: 0.87, $\chi^2_2 = 2.37$, p = 0.31, $\delta^{15}N$: 0.79, $\chi^2_2 = 3.97$, p = 0.14). There were no differences in $\delta^{13}C$ among species at Gareloi ($F_{1,18} = 1.40$, p = 0.25) or feather types ($F_{1,18} = 0.70$, p = 0.41), and the species*feather type interaction was not significant ($F_{1,18} = 0.04$, p = 0.85). Least Auklets had lower $\delta^{15}N$ values than Crested Auklets ($F_{1,18} = 5.15$, p = 0.036, Fig. 6-4), and for both species, P10 was enriched in ^{15}N compared with P1 or breast feathers ($F_{1,18} = 13.06$, p = 0.002. Fig. 6-4). Again, the feather type*species interaction was not significant ($F_{1,18} = 0.62$, p = 0.44).

Discussion

Differences among age classes

Stable isotopes revealed both differences and similarities among groups of auklets that could not have been studied otherwise. We found significant age-related differences in both $\delta^{13}C$ and $\delta^{15}N$ of breast feathers of adult and subadult Least Auklets at Kiska. Breast feathers are replaced during the pre-breeding period in both age classes, around March-May (Pyle 2008). The difference in $\delta^{13}C$ between adults (at least 3 years old) and subadults (approximately 12 months old, Pyle 2008) was about 1‰, a difference within the error estimates of each group of auklets, and that of common prey (Schell *et al.* 1998). There is a known distribution of zooplankton $\delta^{13}C$ in the Bering Sea (Schell *et al.* 1998), with zones defined in 2‰ gradients. Furthermore, very little is known about Least Auklets' pre-breeding distribution, and there is no information on whether there is geographic segregation between ages (Vyatkin 1981; Sydeman *et al.* 2010). Differences in $\delta^{13}C$ are therefore likely the result of variation in the precise time and location of feather replacement among individuals rather than spatial trophic segregation.

The difference between adults and subadults in δ^{15}N, however, was relatively larger (2‰). There are three possible explanations for this difference. First is that adults and subadults forage in separate areas that differ in prey δ^{15}N. Our results showing very small differences among age classes in δ^{13}C make this hypothesis less likely. Second, there may be metabolic differences that cause differences in isotopic discrimination because growing seabirds' discrimination factors differ from adults (Sears *et al.* 2009). While subadult Least Auklets are smaller than adults (Jones 1993b, authors' unpubl. data), Sears et al. (2009) found that once juveniles reached a stable mass, isotopic discrimination was similar to that of fully-grown adults. When Least Auklet chicks depart from Kiska at the end of the breeding season, they are 90% of adult mass (73 g vs. 81 g, Major *et al.* 2006). The mass of subadults we sampled (79 ± 4 g) was similar to that of adults sampled (82 ± 3 g), so differences in isotopic discrimination were not likely the cause of differences in δ^{15}N. The final possibility is that the difference in δ^{15}N between age classes was the result of dietary differences. Quantitative data on the winter diet of Least Auklets is lacking (Stejneger 1885; Troy & Bradstreet 1991), and no data exist on the diet of subadults. In general, diet data for pre-breeding-aged seabirds are sparse because they attend breeding colonies irregularly, and are seldom captured (Hamer *et al.* 2002). Previous studies have found differences in the diets of adult and subadult Tufted Puffins (*Fratercula cirrhata*) in the Aleutian Islands (Wehle 1982) and in the North Pacific (Tanaka 1989). Our results suggest that subadult Least Auklets forage at a lower trophic position than adults during the pre-breeding period. This is most likely the result of subadult birds learning to forage for themselves, as younger birds are often less proficient at finding and capturing high quality prey (Recher & Recher 1969; Cherel *et al.* 2008).

Adult Least Auklets had higher δ^{13}C and δ^{15}N than chicks during the breeding season. As mentioned, growing chicks' metabolism likely contributes to some of these differences, but the magnitude of the differences we found (1.5‰ for δ^{13}C, 3.5‰ for δ^{15}N) are likely larger than growth-related effect (Sears *et al.* 2009). There may also be a small effect of feather type (contour vs. primary), caused by differences in the concentration of the pigment melanin (MIchalik *et al.* 2010; Wiley *et al.* 2010), breast feathers being mostly white, and primaries mostly dark (Jones 1993b). We therefore believe that our qualitative comparisons remain valid (Ponsard & Averbuch 1999; Vanderklift & Ponsard 2003; Cherel 2008) – adults had a different summer diet than the nestlings they were provisioning. Least Auklet chick diet in the Aleutian Islands is well documents, and consists mainly of *Neocalanus* spp. copepods (often > 90% of biomass), and *Thysanoessa* spp. euphausiids (Day & Byrd 1989; Chapter 3). Adult diet during the breeding season is less well known, but the few studies have indicated similar prey in adult stomachs (Bédard 1969a; Harrison 1990; Hunt Jr. & Harrison 1990; Hunt Jr. *et al.* 1998; Russell *et al.* 1999).

Adult Least Auklets experienced a shift in diet through the breeding season, increasing both their δ^{15}N and δ^{13}C values from incubation to early chick rearing (Chapter 5), while the composition of food delivered to chicks remained relatively constant during the same time (Chapter 3). Adults therefore forage for prey from different trophic positions ($\delta^{15}N$) and in different areas ($\delta^{13}C$) depending on whether the prey is meant for self-feeding or delivery to their chick. Increased $\delta^{13}C$ is associated with increased phytoplankton photosynthetic activity and growth (Goericke & Fry 1994; Popp *et al.* 1998), and is characteristic of inshore and upwelling systems (Graham *et al.* 2010; Jaeger *et al.* 2010). Least Auklets forage in upwellings and areas where zooplankton is advected, where *Neocalanus* copepods are concentrated (Springer & Roseneau 1985; Hunt Jr. 1997; Hunt Jr. *et al.* 1998; Russell *et al.* 1999; Piatt & Springer 2003; Springer *et al.* 2007). Nevertheless, the question of why there was a significant difference in stable-isotope ratios between adults in chicks remains puzzling. Least auklet individuals are very difficult to observe at sea, so direct observations are unlikely to provide useful clues, and this species is too small (85 g mean mass) to carry telemetric equipment that would measure foraging behaviour in detail. Further experiments using existing captive populations should quantify Least Auklets' stable-isotope discrimination factors, and use these to construct quantitative isotope mixing models for all age classes.

Our results contrast with bimodal foraging strategies, reported mainly in tropical and subtropical Procellariiformes (Cherel *et al.* 2005b; Congdon *et al.* 2005; Kojadinovic *et al.* 2008; Bond *et al.* 2010a), and recently described for Dovekies (*Alle alle*), a polar non-Procellariiform, and ecological counterpart to Least Auklets in the Atlantic Ocean (Welcker *et al.* 2009b). Bimodal-foraging species alternate between frequent, short trips to provision chicks, and less frequent longer foraging trips to replenish their own nutrient reserves (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994). For several possible reasons, this appears not to be the case in Least Auklets. During the breeding season, auklets forage heavily on *Neocalanus* spp. copepods, the most abundant zooplankter in the North Pacific (Mackas *et al.* 1998), and copepods are advected by oceanic fronts, where auklets are found often in vessel surveys (Kinder *et al.* 1983; Harrison *et al.* 1990; Troy & Bradstreet 1991; Hunt Jr. 1997; Hunt Jr. *et al.* 1998). There is also little annual variation in the proportion of *Neocalanus* spp. copepods in food loads brought by adult Least Auklets to their chick (Chapter 3). Together, this implies that, unlike less productive tropical and subtropical systems, or more variable polar systems, Least Auklets' preferred prey is readily available, and in large supply. Adults' response to increased energetic demand by their chick is likely therefore reflected in a geographic shift and a shortening of their own foraging distance (Chapter 5).

There is no consistent pattern among seabird species in differences in δ^{15}N between adults and chicks. In some studies, chicks' δ^{15}N is higher, presumably because of their increased nutritional demands, and the assumption that higher-δ^{15}N foods are of higher quality (e.g., Bocher *et al.* 2000; Hodum & Hobson 2000; Cherel 2008; Richoux *et al.* 2010). In others, adults' higher δ^{15}N is thought to be because of a bimodal foraging strategy (e.g., Cherel *et al.* 2002; Harding *et al.* 2008; Bond *et al.* 2010a), and in other still, there is no difference (Hedd & Montevecchi 2006; Cherel *et al.* 2008; Davies *et al.* 2009). The difference we found in mean δ^{15}N between adult and chick Least Auklets (3.42‰) is the greatest difference reported where adults have higher δ^{15}N.

Differences among colonies and seasons

We found no differences in $\delta^{13}C$ or $\delta^{15}N$ among Least Auklets from Buldir, Kiska, or Gareloi during any season, represented by different feather types. This suggests that adult Least Auklets feed on similar prey during the breeding season, and likely moult in the same locations during the fall and spring. While attached geolocators were too large for Least Auklets during our study, our results suggest that results from future equipped birds from one colony may be generalized to auklets from other western Aleutian breeding sites. There were also no differences between years in any isotopic comparison, which implies that birds moult in similar areas year to year (Cherel *et al.* 2000).

We documented significant seasonal shifts in $\delta^{13}C$ and $\delta^{15}N$ within individual Least and Crested Auklets. Both species showed a trophic shift following breeding, as P10 feathers (autumn, post-breeding) had higher $\delta^{15}N$ than breast (spring, pre-breeding) or P1 (summer, chick rearing) feathers. The relatively rapid and distinct change in $\delta^{13}C$ in Least Auklets likely resulted from migration to wintering grounds. Unlike the congeneric Whiskered Auklet (*Aethia pygmaea*), which is resident near breeding colonies year-round (Byrd & Williams 1993; Zubakin & Konyukhov 1994), Least Auklets likely disperse to the northwestern Pacific Ocean to areas around Japan (Shuntov 1965; Vyatkin 1981; Kondratyev *et al.* 2000; Sydeman *et al.* 2010). Some Crested Auklets, however, are thought to winter close to the Aleutian Islands (Renner *et al.* 2008), and therefore a less significant change in $\delta^{13}C$ was expected. The similarity between breast and P1 feathers' $\delta^{13}C$ and $\delta^{15}N$ suggests that body contour feathers may be moulted near breeding colonies. When auklets return to Aleutian breeding colonies is not exactly known - adults have been observed at colony sites in April (Jones 1993a, b), and may perhaps arrive earlier. Both species showed a dietary shift during the post-breeding season, and within-individual changes ranged from increases of 0-5.64‰ (mean ± S.D.: 2.05 ± 1.40‰). It is possible that this shift related to adults improving their condition following chick rearing and concurrent primary moult (Chapter 4). A portion of this increase could also be an artefact of protein metabolism resulting in nutritive stress, which can alter $\delta^{15}N$ (Hobson *et al.* 1993; Sears *et al.* 2009). Within species, however, there was a large amount of variation in $\delta^{13}C$ and $\delta^{15}N$ during each season among individuals (Appendix 9). This suggests that there could be considerable individual specialization on certain prey types, or that individuals forage in different areas (Bearhop *et al.* 2006; Cherel *et al.* 2007).

Differences among species

We found significant differences between species sampled at Gareloi. Crested Auklets had higher $\delta^{15}N$ than Least Auklets, and we found no difference in $\delta^{13}C$. In the southern Bering Sea, euphausiids have higher $\delta^{15}N$ than copepods (Schell *et al.* 1998), and remains of higher trophic prey (squid beaks, gadid otoliths) have also been found in adult Crested Auklet stomachs (Bradstreet 1985; Harrison 1990; Hunt Jr. *et al.* 1998), but not at all, or very infrequently in Least Auklets. Together, this suggests some degree of differentiation between Least and Crested Auklets in their foraging patterns, specifically, their food composition, expected between two species that differ by more than a factor of 2 in body size and mass. This contrasts with previous studies near Gareloi that have shown geographic segregation between the two species (Hunt Jr. *et al.* 1998). This segregation is at a much finer spatial resolution, at the level of eddies and upwellings, rather than the more coarse resolution of $\delta^{13}C$ (Schell *et al.* 1998).

Conclusions

Combined with knowledge of moulting patterns, stable isotopes offer unique insight into the foraging patterns of small seabirds, including auklets, for which attached data loggers remain too large. We found significant age differences in foraging of Least Auklets, no variation among breeding colonies spanning over 250 km in the western Aleutian Islands, and a significant trophic shift during the post-breeding season for both Least and Crested Auklets. These differences will serve as testable hypotheses for future studies when data loggers become small enough for reliable use on auklets.

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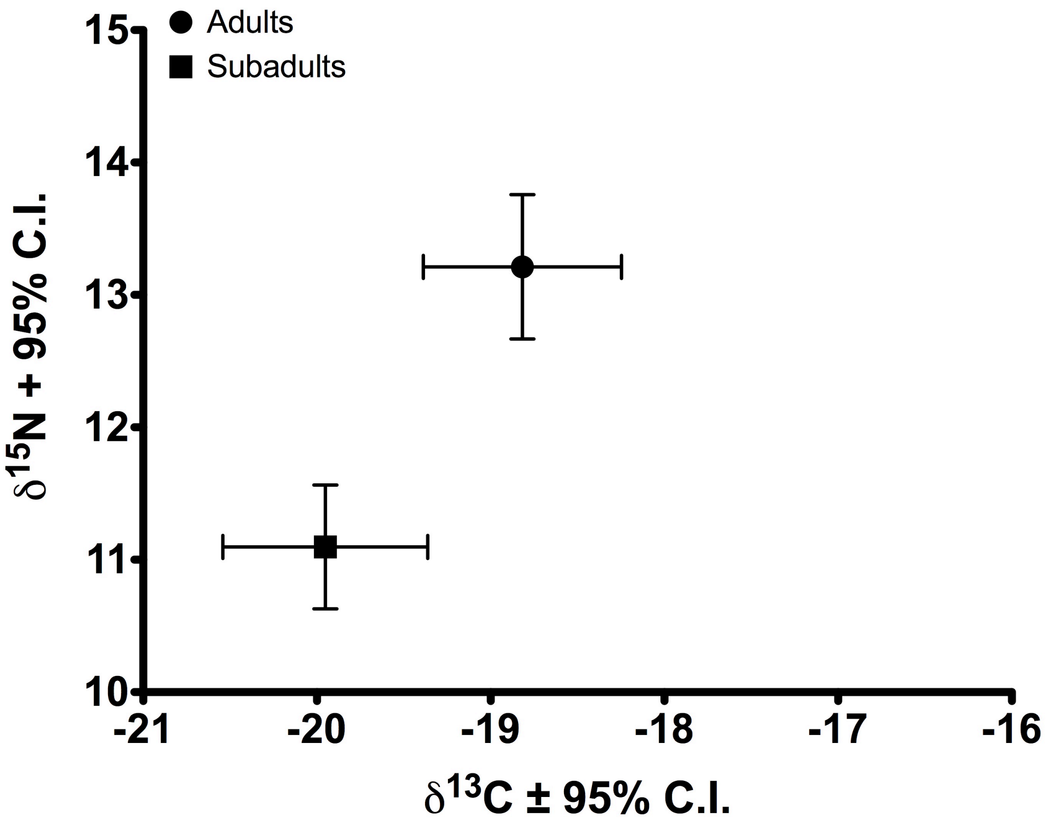

Figure 6-1 – Adult Least Auklets had significantly higher δ^{15}N during the pre-breeding season than subadults sampled in 2007-2010 from Kiska Island, Aleutian Islands, Alaska.

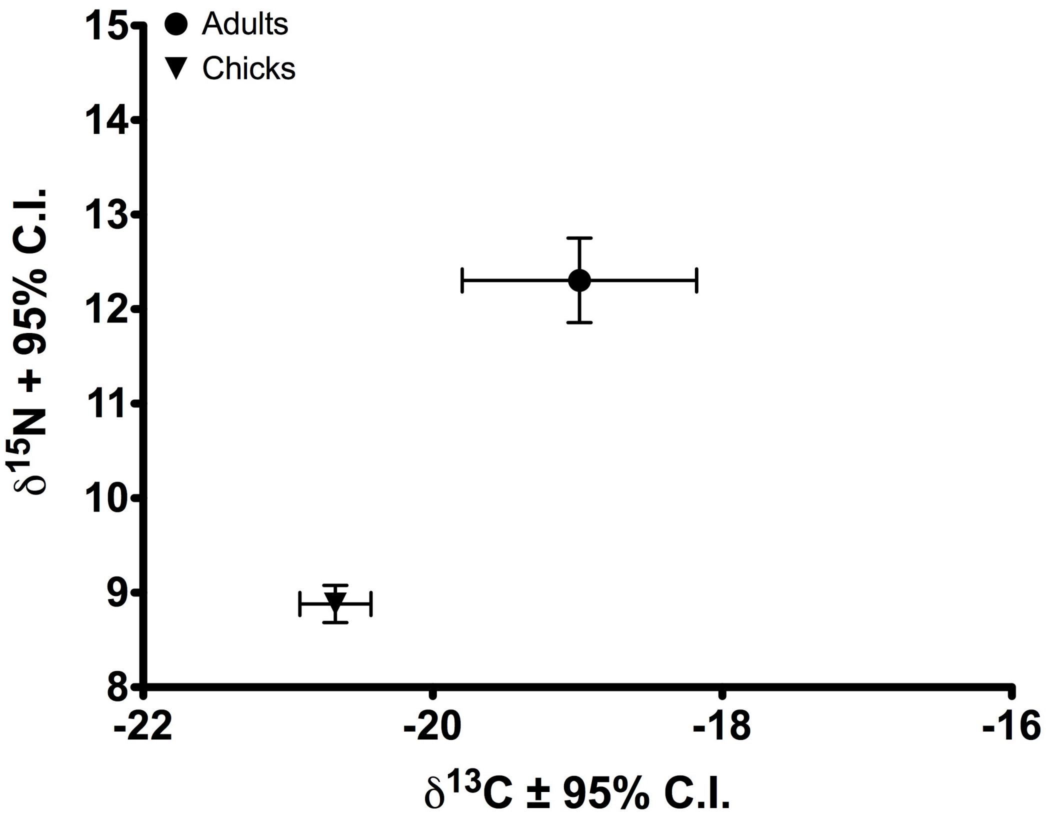

Figure 6-2 – Least Auklet chicks had significantly lower δ^{15}N than adults during the chick-rearing period on Kiska Island, Aleutian Islands, Alaska in 2009.

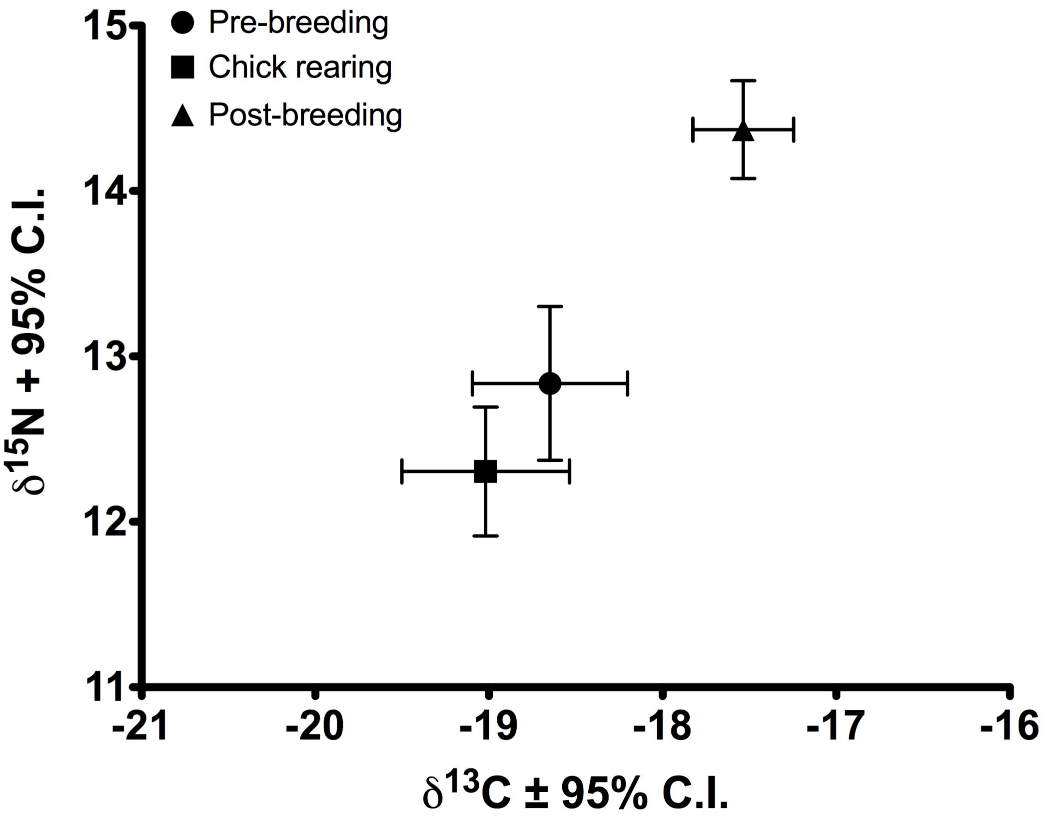

Figure 6-3 – Least Auklets from the Aleutian Islands showed a seasonal dietary shift during the post-breeding season (P10 feather), and no change from pre-breeding (breast feather) to chick rearing (P1 feather).

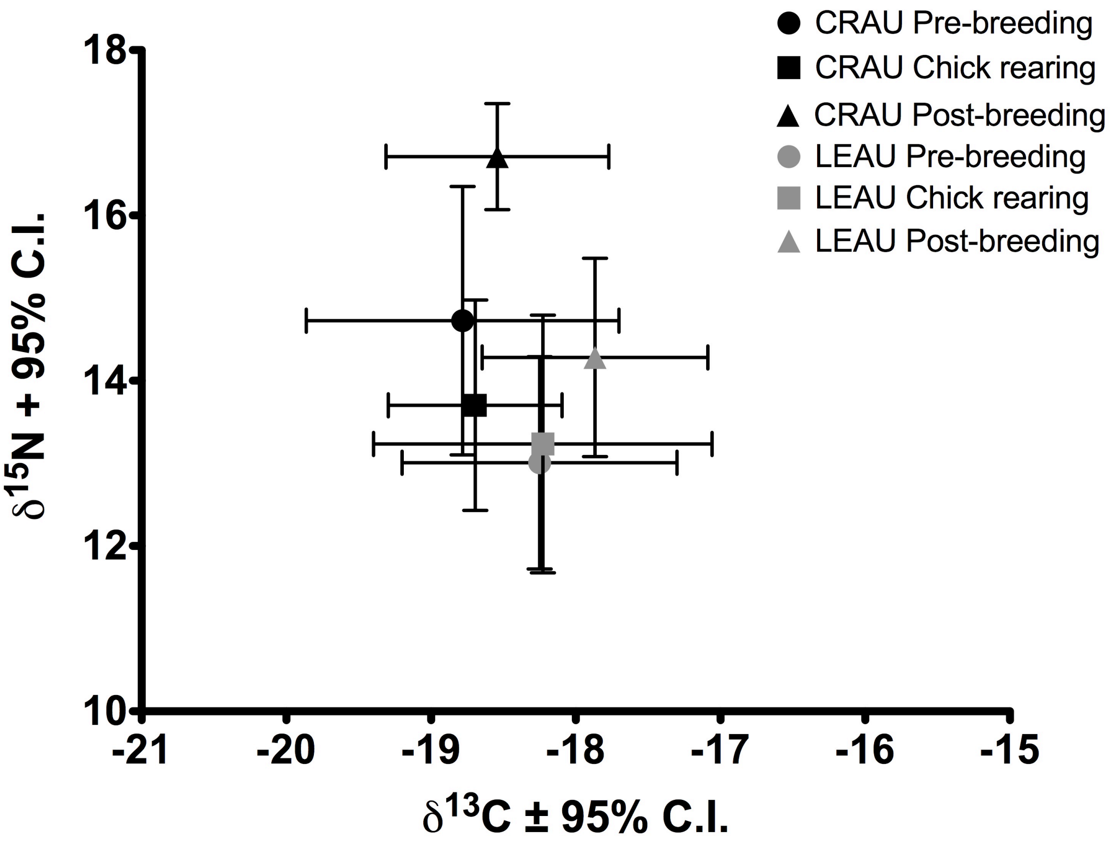

Figure 6-4 – At Gareloi Island, Aleutian Islands, Alaska, there were significant differences in δ^{15}N, but not δ^{13}C between Least and Crested Auklets sampled in 2009.

CHAPTER 7: GENERAL DISCUSSION

Seabirds are useful ecosystem sentinel species for investigating the effects of climate variability on populations over time, and over large spatial extents (Harris & Wanless 1990a; Frederiksen *et al.* 2007). Furthermore, by studying ecological factors and population responses at multiple sites, local effects and population-=specific factors can often be identified (Weise *et al.* 2004; Lavers *et al.* 2009). In this series of studies, I sought to investigate the relationships between large-scale indices of climate in the marine environment, and the responses of planktivorous auklets at multiple sites throughout their breeding range.

An initial hypothesis was that, because auklets are planktivores, changes in oceanographic conditions would affect their primary prey, *Neocalanus* copepods and *Thysanoessa* euphausiids, which could influence reproductive success (Chapter 2). This study was one of the first to investigate the relationships between oceanography and reproductive success in multiple species of seabird at multiple sites over multiple years (Durant *et al.* 2009). We found differences in the number of chicks fledged per nest among species and island, but productivity on all species on all islands was negatively correlated with the Aleutian Low Pressure Index, a measure of the intensity of the Aleutian low pressure system between December and March (Chapter 2). We hypothesized that this relationship was the result of bottom-up control by limiting zooplankton abundance during the following breeding season.

We then addressed this hypothesis by examining the composition of chick meals brought by adults to nest-bound chicks over the same period. We found that breeding-season oceanographic conditions influenced the proportion of main prey taxa in auklets' diet, with the exception of Whiskered Auklets, whose diet composition was related to winter conditions. We noted very little change among years in the proportion of copepods and euphausiids in one of the first studies to relate seabird diet to oceanography (Durant *et al.* 2009). Based on this analysis, we concluded that auklets are able to buffer bottom-up forcing of demographic parameters, like productivity, because the composition of chick meals has remained relatively constant over 14 years of environmental variability in the Bering Sea (Chapter 3).

In addition to breeding, moult is an important, but expensive, life history stage, especially for smaller birds (Holmgren & Hendenström 1995; Schieltz & Murphy 1997; Barta *et al.* 2008; Wingfield 2008; Newton 2009). Unlike many other species, the *Aethia* auklets moult during the breeding season (Bédard & Sealy 1984; Konyukhov 2001; 2009, Chapter 4). We used data collected on the progress of primary feather moult in Least Auklets at four colonies from 52-64°N to test the hypothesis that birds at higher latitudes initiate moult later, and moult faster than southern conspecifics (Medwaldt & King 1978; Hemborg *et al.* 2001; Ryder & Rimmer 2003; Dawson 2004). We found that Least Auklets breeding at higher latitudes did moult later, and faster than those breeding at more southerly latitudes, even though the length of the breeding season is similar among locations (Chapter 4). The cold-water Anadyr Current sweeps south of Cape Ulyakhpen, our most northerly study site, bringing with it oceanic copepods that can fuel auklets' moult-breeding overlap (Pavlov & Pavlov 1996; Stabeno *et al.* 1999; Piatt & Springer 2003; Geinrikh 2005). Detailed descriptions of moulting patterns are required to interpret results of stable isotope analysis from feathers properly (Inger & Bearhop 2008; Bond & Jones 2009b).

We then used our knowledge of moulting patterns in auklets to examine two aspects of their foraging patterns using stable isotope analysis of feathers: seasonal and species differences between Least and Crested Auklets sampled throughout the Aleutian Islands, and within-individual differences during the Least Auklets' incubation period at Kiska Island. Because feathers often represent the foraging activity of birds at the time of tissue synthesis, stable isotope ratios in Least Auklets' innermost primary (P1) will indicate the birds' foraging patterns during incubation (Chapter 4). We found that both δ^{13}C and δ^{15}N increased throughout the 20 days of feather growth, likely indicating a shift in foraging location towards more productive oceanographic fronts that have high concentrations of *Neocalanus* copepods (Harrison *et al.* 1990; Russell *et al.* 1999). This shift, accompanied by the relatively unchanging composition of meals brought to nest bound chicks (Chapter 3), may indicate that adults balance the trade-off between self maintenance and chick provisioning by shifting their own foraging location to more productive oceanographic features in the seascape (Chapter 5).

Feathers moulted at different times of the annual cycle can provide information on birds' foraging away from the breeding colony. Auklets' outermost primary (P10) is moulted in the autumn following breeding (Chapter 3), and breast feathers are replaced during the spring pre-alternate moult (Pyle 2008). We found similar δ^{13}C and δ^{15}N values in each year and at each site within groups. Adult and subadult (one year-old) Least Auklets differed significantly in their foraging patterns during the pre-breeding period, as did adults and chicks during chick rearing. Crested Auklets fed at a consistently higher trophic position than Least Auklets throughout the annual cycle (Chapter 6). These results differ from our observations of chick meal composition (Chapter 3) in that they indicate a lesser degree of overlap among species. Similar to chick meals, however, there were no differences among islands or years. They expand on Chapter 3, however, in elucidating the trophic relationships among species and age classes, showing differences outside the breeding season, and among age classes whose diets are not sampled easily.

Introduced Norway rats at Kiska Island

Since the 1940s, introduced Norway rats have been present at Kiska (Murie 1959). We found significant differences in reproductive success between Kiska and rat-free Buldir and Kasatochi islands, driven primarily by near reproductive failure in 2001 and 2002 (Chapter 2). In an initial assessment (Major *et al.* 2006), two hypotheses were put forward to explain the poor reproductive success: 1) poor food resources around Kiska, and 2) predation and disturbance by rats. We found no significant differences in chick meal composition among years at Kiska, or between Kiska and rat-free islands in the Aleutian Islands (Chapter 3). Furthermore, we found no significant differences in the pre-breeding diet as inferred by stable isotopes between Kiska and rat-free Buldir and Gareloi islands (Chapter 6). These results strongly implicate introduced rats in the breeding failures of 2001 and 2002.

Least Auklet reproductive success was significantly lower on Kiska than on Buldir or Kasatochi, and a paucity of consistent correlations with basin-wide oceanographic or large-scale climatic indices in the North Pacific further suggests that colony-specific factors play an important role in influencing auklet demographics (Chapter 2). The Least Auklet population on Kiska is declining (Major *et al.* submitted), and the Crested Auklet population is also likely declining as well (Bond et al. unbpublished). Long-lived species, such as seabirds, typically have high survival and low fecundity, and survival is often the most influential demographic parameter in determining population growth (Hamer *et al.* 2002). Least and Crested Auklets at Kiska had significantly different survival than those on Buldir or Kasatochi that was often less-related to large-scale indices of climate than their conspecifics on rat-free islands (Jones *et al.* submitted). Together, these results suggest that introduced rats have had a negative effect on the auklet populations at Kiska Island.

Novel techniques and findings

We were the first to incorporate a spatial approach to examining the relationships between oceanographic and climatic variables and the demography of top marine predators. Spatially variable parameters, such as SST or SLP are used often in studies of climate-linked demography (Durant *et al.* 2009), but often over a restricted area. By examining landscape-wide variation in SST and SLP, and its relationship to reproductive success, we moved closer to a mechanistic approach that provided hypotheses for future studies.

In addition, we were also the first to demonstrate a latitudinal gradient in the intensity of primary moult in a marine bird. Such detailed study of moult, and investigation of the moult/breeding overlap in auklets, made detailed study of foraging using stable isotopes available. This included an analysis of auklet foraging during the pre- and post-breeding periods, and of subadults and chicks. Prior to this study, no information on auklet foraging was available for these periods or groups.

Future directions

Future auklet research should focus on three areas: winter ecology, meta-population dynamics, and quantification of isotopic discrimination factors. The first two of these overlap to some degree, since the degree of mixture of breeding populations during the non-breeding period is unknown. The migratory patterns and wintering areas of auklets are known mostly through anecdotal observations and ship-based surveys (Gizenko 1955; Velizhanin 1977a; Vyatkin 1981; Zubakin & Konyukhov 1994; Renner *et al.* 2008). Much of the new information presented here is interpreted in the light of limited data on the winter distribution, behaviour, and ecology of auklets. Least and Whiskered Auklets (85 and 118 g body mass respectively) are, at present, too small for attached telemetry equipment, such as geolocators or satellite transmitters; Crested Auklets (260 g) are more suitable. Such telemetric studies should use a multi-colony approach. There are fundamental differences in the environmental pressures on auklets breeding in the Aleutian Islands, the Pribilof Islands, and the northern Bering Sea, primary among these is the degree of winter sea ice and spring snow cover. Auklets breeding at high latitudes must disperse farther than those breeding in the Aleutians, and may therefore differ in their nutritional requirements, moult characteristics, and demography.

Somewhat related is the degree of inter-colony movement, especially in light of possible population declines throughout the Aleutian Islands. Reliable, repeatable survey methods for *Aethia* auklets are currently lacking, so demographic modelling may provide the only information on population trends. In the Aleutian Islands, Least and Crested Auklets currently breed at six main sites (Buldir, Kiska, Segula, Semisopochnoi, Gareloi, Chagulak), and formerly at Kasatochi, prior to its volcanic eruption in August 2008 (Smith *et al.* 2010; Williams *et al.* 2010). Of these, populations at the two colonies with any monitoring (Buldir, Kiska, Segula) are declining (Renner & Reynolds 2006; Major *et al.* submitted; Bond et al. unpubl. data; IL Jones pers. obs.). Populations in the Bering Sea may also be declining (Roby & Brink 1986b; Renner & Renner 2010), and the status of Russian populations is poorly known (Gaston & Jones 1998; Kondratyev *et al.* 2000). Introduced predators, (Kondratyev *et al.* 2000; Major *et al.* 2006; Major *et al.* 2007), encroaching vegetation (Roby & Brink 1986b; Renner & Reynolds 2006), and volcanism (Williams *et al.* 2010; Bond *et al.* submitted) can threaten auklet populations, and population declines observed at some colonies may also include a certain degree of inter-colony movement. Colonies of millions of auklets and irregular monitoring at most colonies make measuring immigration or emigration challenging. Indeed, as of 2011, there is only one Alaskan auklet colony where demographic information will be collected (Buldir). There is considerably less information on the distribution of nocturnal Whiskered Auklets, despite their listing as a species of Conservation Concern by the U.S. Fish and Wildlife Service (2008).

Second, isotopic studies would be greatly improved by determining stable isotope discrimination factors for auklets. Discrimination factors, the change in δ^{13}C and δ^{15}N between prey and consumer, are tissue- species- and prey-specific (Caut *et al.* 2008, 2009). Captive populations are often required for the accurate determination of discrimination factors, and few exist for *Aethia* auklets. By determining auklet discrimination factors, quantitative isotopic mixing models (e.g., MixSIR, SIAR; Moore & Semmens 2008; Parnell *et al.* 2010) can be used to estimate the proportional contribution of prey types to auklets' diet. By combining isotopic studies with oceanographic sampling during the auklets' pre- and post-breeding season to establish possible prey abundance, and composition, and data from telemetry studies, we can gain further insight into the ecology of these abundant planktivores during the 9 months when they are away from their breeding colonies, and relatively inaccessible to researchers.

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APPENDICES

Appendix 1. The number of breeding pairs of least (LEAU), crested (CRAU) and whiskered auklets (WHAU) studied at Buldir, Kiska, and Kasatochi during 1990-2008.

	Buldir			**Kiska**		**Kasatochi**	
Year	LEAU	CRAU	WHAU	LEAU	CRAU	LEAU	CRAU
1990	61	67	-	-	-	-	-
1991	81	74	46	-	-	-	-
1992	89	79	55	-	-	-	-
1993	44	49	54	-	-	-	-
1994	64	67	57	-	-	-	-
1995	64	66	67	-	-	-	-
1996	57	66	57	-	-	54	43
1997	84	82	90	-	-	91	76
1998	76	70	78	-	-	95	104
1999	-	-	-	-	-	100	110
2000	69	78	70	-	-	89	110
2001	65	75	75	210	31	85	109
2002	50	81	100	205	23	94	109
2003	83	45	44	208	20	110	136
2004	81	67	66	197	31	91	107
2005	73	79	70	-	-	93	103

2006	84	73	68	180	34	77	88
2007	68	66	67	173	36	124	143
2008	67	75	68	157	29	98	109

Appendix 2. Reproductive success (number of chicks fledged/number of eggs laid) of least, crested and whiskered auklets at Buldir, Kiska, and Kasatochi from 1990-2008. Abbreviations and sample sizes are in Appendix 1.

Year	Buldir			Kiska		Kasatochi	
	LEAU	CRAU	WHAU	LEAU	CRAU	LEAU	CRAU
1990	0.38	0.49	-	-	-	-	-
1991	0.62	0.58	0.50	-	-	-	-
1992	0.54	0.72	0.60	-	-	-	-
1993	0.50	0.78	0.57	-	-	-	-
1994	0.41	0.69	0.74	-	-	-	-
1995	0.70	0.77	0.67	-	-	-	-
1996	0.60	0.61	0.70	-	-	0.69	0.74
1997	0.60	0.76	0.66	-	-	0.55	0.55
1998	0.45	0.76	0.53	-	-	0.49	0.66
1999	-	-	-	-	-	0.46	0.69
2000	0.48	0.62	0.46	-	-	0.66	0.75
2001	0.55	0.64	0.36	0.13	0.39	0.55	0.45
2002	0.60	0.60	0.48	0.10	0.43	0.53	0.59
2003	0.34	0.11	0.55	0.50	0.45	0.63	0.63
2004	0.53	0.45	0.53	0.52	0.68	0.53	0.70
2005	0.60	0.78	0.76	-	-	0.39	0.61

2006	0.75	0.64	0.62	0.54	0.85	0.44	0.66
2007	0.66	0.85	0.85	0.58	0.58	0.61	0.76
2008	0.70	0.83	0.84	0.64	0.59	0.61	0.77

Appendix 3. Timing of breeding (mean egg hatch date) of least, crested and whiskered auklets at Buldir, Kiska, and Kasatochi from 1990-2008. Abbreviations are in Appendix 1.

Year	Buldir			Kiska		Kasatochi	
	LEAU	CRAU	WHAU	LEAU	CRAU	LEAU	CRAU
1990	27 June	25 June	24 June	-	-	-	-
1991	30 June	29 June	27 June	-	-	-	-
1992	29 June	26 June	18 June	-	-	-	-
1993	26 June	27 June	22 June	-	-	-	-
1994	24 June	25 June	19 June	-	-	-	-
1995	29 June	29 June	25 June	-	-	-	-
1996	25 June	26 June	22 June	-	-	25 June	30 June
1997	27 June	28 June	24 June	-	-	28 June	01 July
1998	30 June	05 July	23 June	-	-	03 July	03 July
1999	-	-	-	-	-	30 June	29 June
2000	25 June	29 June	17 June	-	-	28 June	29 June
2001	26 June	29 June	22 June	28 June	-	28 June	30 June
2002	25 June	25 June	24 June	5 July	2 July	27 June	27 June
2003	27 June	02 July	25 June	2 July	-	25 June	29 June
2004	28 June	05 July	21 June	27 June	4 July	30 June	28 June
2005	25 June	25 June	18 June	-	-	29 June	29 June
2006	30 June	09 July	27 June	1 July	7 July	03 July	03 July

2007	27 June	23 June	17 June	28 June	28 June	30 June	01 July
2008	24 June	26 June	21 June	28 June	29 June	30 June	02 July

Appendix 4. Taxonomic list of prey taxa, and values used in calculating biomass.

Phylum	**Class**	**Order**	**Suborder**	**Family**	**Genus**	**species**	**Taxa**	**Average estimated mass (g)**
Cnidaria	Scyphozoa						Jellyfish	
Nemata							Nematode	
Arthropoda	Insecta						Insect	0.001
Arthropoda							Unid. crustacean	0.015
Arthropoda	Ostracoda						Ostracoda	0.1
Arthropoda	Maxillopoda	Calanoida		Calanidae			Calanoid spp.	0.002
Arthropoda	Maxillopoda	Calanoida		Calanidae	Neocalanus		*Neocalanus* spp.	0.005
Arthropoda	Maxillopoda	Calanoida		Euchaetidae	Paraeuchaeta	birostrata	*Paraeuchaeta birostrata*	0.002
Arthropoda	Maxillopoda	Calanoida		Euchaetidae	Paraeuchaeta	elongata	*Paraeuchaeta elongata*	0.0044
Arthropoda	Maxillopoda	Calanoida		Augaptilidae	Pseud-haloptilus	pacificus	*Pseudhaloptilus pacificus*	0.002

Phylum	Class	Order	Suborder	Family	Genus	species	Taxa	Average estimated mass (g)
Arthropoda	Maxillopoda						Unid. copepod	0.0075
Arthropoda	Maxillopoda	Calanoida		Calanidae	Calanus	marshallae	*Calanus marshallae*	0.00126
Arthropoda	Maxillopoda	Calanoida		Calanidae	Calanus	pacificus	*Calanus pacificus*	0.0004
Arthropoda	Maxillopoda	Calanoida		Calanidae	Neocalanus	cristatus	*Neocalanus cristatus*	0.0139
Arthropoda	Maxillopoda	Calanoida		Calanidae	Neocalanus	plumchrus/ flemingeri	*Neocalanus plumchrus/ flemingeri*	0.00276
Arthropoda	Malacostraca	Amphipoda					Unid. amphipod	0.0022
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Ischyroceridae	Erichthonius		*Erichthonius* spp.	0.0022
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Eusiridae			Eusiridae	0.05
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Gammaridae			Gammaridae	0.05

Phylum	Class	Order	Suborder	Family	Genus	species	Taxa	Average estimated mass (g)
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Calliopiidae	Halirages	bungei	*Halirages bungei*	0.05
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Hyalidae			Hyalidae	
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Ischyroceridae	Ischyrocerus		*Ischyrocerus* spp.	0.0022
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Lysianassidae			Lysianassidae	0.004
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Eusiridae	Pontogeneia		*Pontogeneia* spp.	0.05
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Stenothoidae			Stenothoidae	0.1
Arthropoda	Malacostraca	Amphipoda	Gammaridea	Talitridae			Talitridae	0.0022
Arthropoda	Malacostraca	Amphipoda	Hyperiidea	Hyperiidae	Hyperia		*Hyperia* spp.	0.002
Arthropoda	Malacostraca	Amphipoda	Hyperiidea	Hyperiidae	Hyperoche	medusarum	*Hyperoche medusarum*	0.00385
Arthropoda	Malacostraca	Amphipoda	Hyperiidea	Phrosinidae	Primno	macropa	*Primno macropa*	0.003

Phylum	Class	Order	Suborder	Family	Genus	species	Taxa	Average estimated mass (g)
Arthropoda	Malacostraca	Amphipoda	Hyperiidea	Hyperiidae	Themisto	pacifica	*Themisto pacifica* (<4mm)	0.00368
Arthropoda	Malacostraca	Amphipoda	Hyperiidea	Hyperiidae	Themisto		*Themisto* spp. (<4mm)	0.00385
Arthropoda	Malacostraca	Tanaidacea					Tanaidacea	0.05
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae	Thysanoessa	inermis	*Thysanoessa inermis* (<7mm)	0.02
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae	Thysanoessa	inermis	*Thysanoessa inermis* (>12mm)	0.075
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae	Thysanoessa	raschii	*Thysanoessa raschii* (<7mm)	0.0305
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae	Thysanoessa	raschii	*Thysanoessa raschii* (>12mm)	0.0978
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae			Euphausiid	0.006

Phylum	Class	Order	Suborder	Family	Genus	species	Taxa	Average estimated mass (g)
							furcilia	
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae			Euphausiid spp. (<7mm)	0.006
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae			Euphausiid spp. (lg, > 7mm)	0.084
Arthropoda	Malacostraca	Euphausiacea		Euphausiidae	Thysanoessa		*Thysanoessa* spp. (>12mm)	0.07895
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Hippolytidae			Hippolytidae juvenile	0.037
Arthropoda	Malacostraca	Decapoda	Pleocyemata				Larval shrimp (<7mm)	0.012
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Pandalidae			Pandalid shrimp (>12mm)	0.04865
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Pandalidae			Pandalid shrimp larvae	0.012

Phylum	Class	Order	Suborder	Family	Genus	species	Taxa	Average estimated mass (g)
Arthropoda	Malacostraca	Decapoda	Pleocyemata				Shrimp zoea	0.01
Arthropoda	Malacostraca	Decapoda	Pleocyemata				Unid. shrimp	0.05
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Paguridae			Paguridae glaucothoe	0.005
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Paguridae			Paguridae megalopa	0.015
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Paguridae			Paguridae zoea	0.00162
Arthropoda	Malacostraca	Decapoda	Pleocyemata	Atelecyclidae			Atelecyclidae megalopa	0.015
Arthropoda	Malacostraca	Decapoda	Pleocyemata				Crab zoea	0.01
Mollusca	Gastropoda	Thecosomata		Limacinidae	Limacina	helicina	*Limacina helicinia*	0.002
Mollusca	Gastropoda	Thecosomata		Limacinidae	Limacina		*Limacina* spp.	0.0035
Mollusca	Gastropoda	Thecosomata					Pterepod spp.	0.001
Mollusca	Gastropoda						Unid. snail	0.005

Phylum	Class	Order	Suborder	Family	Genus	species	Taxa	Average estimated mass (g)
Mollusca	Cephalopoda	Teuthida	Oegopsina	Gonatidae			Gonatidae	0.06
Mollusca	Cephalopoda	Teuthida					Unid. squid	0.06
Chordata	Actinopterygii						Unid. Fish	
Chordata	Actinopterygii						Unid. fish larvae	0.485
Chordata	Actinopterygii	Scorpaeniformes	Hexagrammoidei	Hexagrammidae	Hexagrammos		*Hexagrammos* spp. (1+ yr)	11

Appendix 5. Summary of food load composition of Crested Auklet chick meals.

Table A5-1. Summary of food load composition of Crested Auklets at Buldir, Island 1994-2006. Data are presented as annual values of percent biomass.

Year	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
n	37	46	78	82	103	88	29	45	54	23	33	39	36
Copepoda	**37.13%**	**26.83%**	**75.28%**	**24.75%**	**28.32%**	**83.81%**	**82.74%**	**49.33%**	**71.94%**	**4.37%**	**86.72%**	**81.76%**	**76.92%**
Calanoid spp.	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.53%	0.00%	0.00%	0.00%	0.00%	0.00%
Calanus marshallae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.07%	0.00%
***Neocalanus* Total**	**37.13%**	**26.83%**	**75.28%**	**24.75%**	**28.32%**	**83.81%**	**82.74%**	**48.80%**	**71.94%**	**4.37%**	**86.72%**	**81.69%**	**76.92%**
Neocalanus spp.	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	2.58%	0.00%	0.00%	3.67%	0.00%	0.00%	0.00%
Neocalanus cristatus	37.10%	26.79%	73.45%	21.71%	28.01%	83.13%	79.97%	48.74%	70.21%	0.70%	86.66%	81.13%	74.58%
Neocalanus plumchrus/flemingeri	0.03%	0.04%	1.83%	3.04%	0.31%	0.68%	0.19%	0.06%	1.73%	0.00%	0.05%	0.56%	2.34%
Amphipoda	**0.93%**	**0.80%**	**0.58%**	**0.79%**	**0.14%**	**1.57%**	**0.00%**	**3.03%**	**5.32%**	**12.87%**	**0.17%**	**1.25%**	**0.05%**
Hyperoche medusarum	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%

Year	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Primno macropa	0.04%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Themisto pacifica (<4mm)	0.88%	0.80%	0.57%	0.79%	0.14%	1.56%	0.00%	2.83%	4.89%	0.00%	0.17%	0.01%	0.03%
Themisto spp. (<4mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.20%	0.42%	12.87%	0.00%	1.24%	0.02%
Euphausiacea	**61.79%**	**71.73%**	**23.75%**	**74.38%**	**71.52%**	**13.81%**	**16.56%**	**42.58%**	**20.28%**	**82.43%**	**13.00%**	**16.30%**	**23.03%**
Thysanoessa inermis (<7mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	3.47%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Thysanoessa inermis (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	8.95%	0.00%	0.00%	0.00%	6.64%	0.00%	0.00%
Euphausiid furcilia	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Euphausiid spp. (<7mm)	0.00%	71.73%	23.75%	74.38%	71.52%	13.80%	4.14%	6.13%	8.94%	3.76%	2.41%	3.29%	23.03%
Thysanoessa spp. (>12mm)	61.79%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	36.45%	11.34%	78.67%	3.95%	13.00%	0.00%
Decapoda	**0.16%**	**0.58%**	**0.36%**	**0.06%**	**0.01%**	**0.81%**	**0.69%**	**5.06%**	**2.46%**	**0.33%**	**0.11%**	**0.69%**	**0.00%**

Year	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Hippolytidae juvenile	0.00%	0.00%	0.00%	0.00%	0.00%	0.74%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Pandalid shrimp (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.11%	2.44%	0.00%	0.11%	0.69%	0.00%
Pandalid shrimp larvae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.69%	4.96%	0.00%	0.33%	0.00%	0.00%	0.00%
Shrimp zoea	0.15%	0.52%	0.30%	0.02%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Paguridae megalopa	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Atelecyclidae megalopa	0.00%	0.00%	0.06%	0.04%	0.00%	0.00%	0.00%	0.00%	0.02%	0.00%	0.00%	0.00%	0.00%
Crab zoea	0.00%	0.06%	0.00%	0.00%	0.00%	0.05%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid. squid	0.00%	0.06%	0.03%	0.03%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Table A5-2 - Summary of food load composition of Crested Auklets at Kiska, Island 2001-2006. Data are presented as annual values of percent biomass.

Year	**2001**	**2003**	**2006**
n	7	3	24
Copepoda	**0.00%**	**0.00%**	**87.39%**
***Neocalanus* Total**	**0.00%**	**0.00%**	**87.39%**
Neocalanus cristatus	0.00%	0.00%	87.21%
Neocalanus plumchrus/flemingeri	0.00%	0.00%	0.18%
Amphipoda	**0.00%**	**0.00%**	**0.06%**
Hyperoche medusarum	0.00%	0.00%	0.04%
Themisto pacifica (<4mm)	0.00%	0.00%	0.02%
Euphausiacea	**100.00%**	**100.00%**	**12.10%**
Euphausiid spp. (<7mm)	99.63%	0.00%	0.00%
Euphausiid spp. (lg, > 7mm)	0.37%	100.00%	12.10%

Year	**2001**	**2003**	**2006**
Decapoda	**0.00%**	**0.00%**	**0.38%**
Larval shrimp (<7mm)	0.00%	0.00%	0.38%
Unid. squid	0.00%	0.00%	0.07%

Table A5-3 - Summary of food load composition of Crested Auklets at Kasatochi, Island 1996-2006. Data are presented as annual values of percent biomass.

Year	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
n	36	39	35	36	34	31	39	30	34	35	34
Ostracoda	0.00%	0.19%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Copepoda	**36.58%**	**90.35%**	**73.02%**	**67.04%**	**39.76%**	**90.63%**	**66.07%**	**66.11%**	**74.01%**	**88.48%**	**82.58%**
Unid. copepod	0.04%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Calanus marshallae	0.00%	0.00%	0.00%	0.00%	0.03%	0.00%	0.21%	0.00%	0.00%	0.00%	0.00%
***Neocalanus* Total**	**36.54%**	**90.35%**	**73.02%**	**67.04%**	**39.73%**	**90.63%**	**65.86%**	**66.11%**	**74.01%**	**88.48%**	**82.58%**
Neocalanus cristatus	33.49%	73.14%	67.57%	62.21%	37.72%	90.29%	62.39%	65.81%	74.01%	86.55%	81.65%
Neocalanus plumchrus/flemingeri	3.05%	17.21%	5.44%	4.83%	2.02%	0.34%	3.47%	0.29%	0.00%	1.93%	0.93%
Amphipoda	**0.14%**	**0.33%**	**2.83%**	**1.27%**	**0.09%**	**0.10%**	**1.02%**	**0.03%**	**20.50%**	**0.18%**	**0.13%**
Gammaridae	0.00%	0.05%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Year	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Themisto pacifica (<4mm)	0.14%	0.27%	2.10%	1.27%	0.09%	0.02%	0.19%	0.00%	0.00%	0.00%	0.06%
Pterepod spp.	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.03%
Shrimp zoea	0.00%	0.00%	0.74%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Themisto spp. (<4mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.08%	0.83%	0.03%	20.50%	0.18%	0.05%
Euphausiacea	**63.04%**	**6.75%**	**23.37%**	**30.63%**	**60.07%**	**8.34%**	**32.22%**	**32.03%**	**5.49%**	**10.97%**	**16.46%**
Euphausiid furcilia	0.00%	0.00%	0.00%	0.05%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Euphausiid spp. (<7mm)	0.00%	6.75%	0.00%	0.00%	16.89%	6.98%	27.30%	11.81%	5.49%	8.07%	11.26%
Thysanoessa spp. (>12mm)	63.04%	0.00%	23.37%	30.58%	43.18%	1.36%	4.92%	20.22%	0.00%	2.90%	5.20%
Decapoda	**0.24%**	**2.26%**	**0.18%**	**1.07%**	**0.08%**	**0.92%**	**0.70%**	**1.82%**	**0.00%**	**0.37%**	**0.75%**
Hippolytidae juvenile	0.00%	0.00%	0.00%	0.74%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Larval shrimp (<7mm)	0.17%	1.86%	0.00%	0.00%	0.08%	0.65%	0.14%	0.68%	0.00%	0.30%	0.61%
Pandalid shrimp (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.26%	0.56%	1.07%	0.00%	0.00%	0.00%
Primno macropa	0.00%	0.03%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Paguridae glaucothoe	0.00%	0.00%	0.00%	0.09%	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%

Year	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Paguridae megalopa	0.00%	0.00%	0.05%	0.00%	0.00%	0.00%	0.00%	0.05%	0.00%	0.00%	0.00%
Atelecyclidae megalopa	0.04%	0.29%	0.11%	0.00%	0.00%	0.01%	0.00%	0.03%	0.00%	0.07%	0.14%
Crab zoea	0.03%	0.09%	0.02%	0.24%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid. squid	0.00%	0.11%	0.06%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.07%
Unid. Fish	0.00%	0.00%	0.53%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Appendix 6. Summary of food load composition of Least Auklet chick meals.

Table A6-1 - Summary of food load composition of Least Auklets at Buldir Island, 1994-2006. Data are presented as annual values of percent biomass.

Year	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
n	4	8	15	31	25	32	12	32	31	21	30	24	29
Copepoda	**84.54%**	**94.58%**	**96.06%**	**93.87%**	**94.37%**	**95.59%**	**98.20%**	**96.82%**	**97.45%**	**99.06%**	**92.52%**	**96.43%**	**75.83%**
Paraeuchaeta birostrata	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Calanus marshallae	0.00%	0.00%	0.00%	0.00%	0.04%	0.00%	0.35%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
***Neocalanus* Total**	**84.54%**	**94.58%**	**96.06%**	**93.87%**	**94.33%**	**95.58%**	**97.85%**	**96.82%**	**97.45%**	**99.06%**	**92.52%**	**96.43%**	**75.83%**
Neocalanus spp.	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	3.16%	0.00%	0.00%	84.75%	0.00%	0.00%	0.00%
Neocalanus cristatus	13.95%	1.85%	10.02%	15.56%	25.77%	42.44%	80.95%	20.27%	1.70%	14.31%	3.06%	71.51%	17.87%
Neocalanus plumchrus/flemingeri	70.59%	92.73%	86.04%	78.31%	68.55%	53.15%	13.74%	76.55%	95.75%	0.00%	89.47%	24.91%	57.96%
Amphipoda	**1.48%**	**1.17%**	**0.81%**	**0.88%**	**0.47%**	**0.36%**	**0.02%**	**2.68%**	**1.42%**	**0.42%**	**0.00%**	**0.01%**	**0.06%**

Year	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Erichithonius spp.	0.00%	0.00%	0.00%	0.00%	0.40%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Hyperoche medusarum	0.00%	0.74%	0.07%	0.00%	0.00%	0.00%	0.00%	0.00%	0.02%	0.00%	0.00%	0.00%	0.00%
Primno macropa	0.39%	0.00%	0.00%	0.37%	0.00%	0.14%	0.00%	0.00%	0.02%	0.01%	0.00%	0.00%	0.00%
Themisto pacifica (<4mm)	1.09%	0.43%	0.75%	0.51%	0.07%	0.22%	0.02%	2.68%	1.38%	0.41%	0.00%	0.01%	0.06%
Euphausiacea	**0.00%**	**0.18%**	**2.36%**	**1.46%**	**3.96%**	**0.61%**	**1.66%**	**0.37%**	**0.76%**	**0.47%**	**5.10%**	**1.13%**	**23.00%**
Thysanoessa raschii (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.05%	0.00%
Thysanoessa spp. (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.14%	0.00%	0.00%	0.65%
Euphausiid furcilla	0.00%	0.00%	0.00%	0.00%	2.54%	0.46%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Euphausiid spp. (sm, <7mm)	0.00%	0.18%	2.36%	1.46%	1.42%	0.15%	1.66%	0.37%	0.76%	0.33%	5.10%	0.09%	22.35%
Decapoda	**4.93%**	**2.65%**	**0.62%**	**2.35%**	**0.66%**	**3.16%**	**0.08%**	**0.13%**	**0.38%**	**0.05%**	**0.00%**	**2.31%**	**1.11%**

Year	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Pandalid shrimp (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.35%	0.00%
Pandalid shrimp larvae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.13%	0.38%	0.00%	0.00%	0.00%	0.00%
Larval shrimp (<7mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.91%	0.00%
Hippolytidae juvenile	0.00%	0.00%	0.00%	0.00%	0.00%	2.66%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Shrimp zoea	4.93%	2.65%	0.45%	1.18%	0.56%	0.35%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Paguridae megalopa	0.00%	0.00%	0.00%	0.00%	0.00%	0.10%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Crab zoea	0.00%	0.00%	0.00%	0.20%	0.00%	0.01%	0.00%	0.00%	0.00%	0.02%	0.00%	0.00%	0.00%
Atelecyclidae/crab megalopa	0.00%	0.00%	0.17%	0.96%	0.10%	0.04%	0.08%	0.00%	0.00%	0.03%	0.00%	0.05%	1.11%
Gastropoda	**1.07%**	**1.42%**	**0.15%**	**1.44%**	**0.55%**	**0.10%**	**0.04%**	**0.00%**	**0.00%**	**0.00%**	**0.00%**	**0.13%**	**0.00%**
Limacina spp.	0.00%	0.00%	0.00%	0.00%	0.55%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid. snail	1.07%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Pterepod spp.	0.00%	1.42%	0.15%	1.44%	0.00%	0.10%	0.04%	0.00%	0.00%	0.00%	0.00%	0.13%	0.00%

Year	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Other	**7.98%**	**0.00%**	**0.00%**	**0.00%**	**0.00%**	**0.16%**	**0.00%**	**0.00%**	**0.00%**	**0.00%**	**2.37%**	**0.00%**	**0.00%**
Gonatidae	0.00%	0.00%	0.00%	0.00%	0.00%	0.16%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid. fish larvae	7.98%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	2.37%	0.00%	0.00%

Table A6-2 - Summary of food load composition of Least Auklets at Kiska Island, 2001-2006. Data are presented as annual values of percent biomass.

Year	**2001**	**2002**	**2003**	**2004**	**2006**
n	59	17	31	23	30
Insect	0.00%	0.01%	0.00%	0.00%	0.00%
Copepoda	**97.30%**	**97.86%**	**95.91%**	**80.65%**	**98.29%**
Calanus marshallae	0.03%	0.00%	0.00%	0.00%	0.00%
***Neocalanus* Total**	**97.27%**	**97.86%**	**95.91%**	**80.65%**	**98.29%**
Neocalanus spp.	0.00%	95.98%	0.00%	0.00%	0.00%
Neocalanus cristatus	8.09%	1.88%	0.00%	3.47%	3.19%
Neocalanus plumchrus/flemingeri	89.18%	0.00%	95.91%	77.18%	95.10%
Amphipoda	**0.26%**	**0.05%**	**0.15%**	**0.32%**	**0.02%**
Hyperoche medusarum	0.00%	0.00%	0.00%	0.13%	0.01%

Year	**2001**	**2002**	**2003**	**2004**	**2006**
Primno macropa	0.01%	0.01%	0.00%	0.00%	0.01%
Themisto pacifica (<4mm)	0.59%	0.00%	0.09%	1.03%	0.02%
Themisto spp. (<4mm)	0.45%	0.21%	0.51%	0.10%	0.05%
Euphausiacea	**1.06%**	**0.05%**	**2.02%**	**9.06%**	**0.67%**
Euphausiid spp. (lg, > 7mm)	0.87%	0.00%	1.80%	0.00%	0.00%
Euphausiid spp. (sm, <7mm)	0.19%	0.05%	0.21%	9.06%	0.67%
Decapoda	**0.14%**	**1.67%**	**1.36%**	**0.07%**	**0.92%**
Larval shrimp (<7mm)	0.12%	0.00%	0.00%	0.07%	0.85%
Pandalid shrimp (>12mm)	0.00%	1.65%	0.00%	0.00%	0.00%
Paguridae zoea	0.01%	0.00%	0.00%	0.00%	0.00%
Atelecyclidae/crab megalopa	0.00%	0.00%	0.00%	0.00%	0.04%
Crab zoea	0.00%	0.03%	1.36%	0.00%	0.03%

Gastropoda	**0.45%**	**0.19%**	**0.11%**	**0.51%**	**0.03%**

Year	**2001**	**2002**	**2003**	**2004**	**2006**
Limacina helicinia	0.00%	0.19%	0.00%	0.00%	0.00%
Pterepod spp.	0.45%	0.00%	0.11%	0.51%	0.03%
Unid. fish larvae	0.00%	0.00%	0.00%	8.45%	0.00%

Table A6-1 - Summary of food load composition of Least Auklets at Kasatochi Island, 1996-2006. Data are presented as annual values of percent biomass.

Year	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
n	19	51	36	33	33	33	37	24	33	29	28
Unid. crustacean	0.10%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Copepoda	**62.53%**	**57.09%**	**84.00%**	**56.46%**	**81.85%**	**90.12%**	**92.55%**	**84.39%**	**88.53%**	**88.63%**	**77.02%**
Calanus marshallae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.34%	0.09%	0.00%	0.00%	0.00%
***Neocalanus* Total**	**62.53%**	**57.09%**	**84.00%**	**56.46%**	**81.85%**	**90.12%**	**92.21%**	**84.30%**	**88.53%**	**88.63%**	**77.02%**
Neocalanus cristatus	4.23%	5.42%	11.96%	18.92%	9.33%	0.27%	2.58%	1.86%	1.55%	42.96%	22.88%
Neocalanus plumchrus/flemingeri	58.31%	51.67%	72.04%	37.54%	72.52%	89.84%	89.63%	82.44%	86.97%	45.67%	54.14%
Amphipoda	**0.51%**	**10.91%**	**1.22%**	**1.74%**	**4.74%**	**0.00%**	**1.13%**	**0.85%**	**0.23%**	**0.48%**	**0.00%**
Erichithonius spp.	0.00%	0.00%	0.48%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Eusiridae	0.00%	0.00%	0.00%	0.00%	2.92%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Year	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Gammaridae	0.00%	10.11%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Halirages bungei	0.00%	0.00%	0.00%	1.42%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Ischyrocerus spp.	0.00%	0.00%	0.00%	0.00%	0.26%	0.00%	0.44%	0.19%	0.16%	0.06%	0.00%
Pontogeneia spp.	0.00%	0.00%	0.00%	0.07%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Stenothoidae	0.00%	0.36%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Talitridae	0.02%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Hyperoche medusarum	0.46%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Primno macropa	0.00%	0.30%	0.00%	0.03%	0.00%	0.00%	0.00%	0.01%	0.01%	0.00%	0.00%
Themisto pacifica (<4mm)	0.04%	0.13%	0.75%	0.20%	1.56%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Themisto spp. (<4mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.70%	0.65%	0.06%	0.42%	0.00%
Tanaidacea	0.00%	0.00%	0.00%	0.00%	0.71%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Euphausiacea	**31.30%**	**11.07%**	**5.53%**	**1.70%**	**4.09%**	**4.73%**	**3.12%**	**10.36%**	**3.84%**	**1.26%**	**8.82%**
Euphausiid furcilla	0.00%	0.00%	5.10%	0.64%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Euphausiid spp. (sm, <7mm)	0.00%	0.00%	0.00%	0.00%	3.95%	4.73%	2.43%	10.36%	3.84%	1.26%	8.82%

Year	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Thysanoessa spp. (>12mm)	31.30%	11.07%	0.43%	1.06%	0.14%	0.00%	0.68%	0.00%	0.00%	0.00%	0.00%
Decapoda	**3.68%**	**18.89%**	**5.56%**	**38.51%**	**5.10%**	**4.49%**	**2.86%**	**4.41%**	**5.10%**	**8.74%**	**13.09%**
Hippolytidae juvenile	0.00%	0.00%	0.00%	38.22%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Larval shrimp (<7mm)	2.38%	17.03%	0.00%	0.00%	4.76%	2.44%	2.31%	2.02%	4.60%	8.70%	12.95%
Pandalid shrimp (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	1.92%	0.42%	1.93%	0.00%	0.00%	0.00%
Shrimp zoea	0.00%	0.00%	5.10%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Paguridae glaucothoe	0.00%	0.00%	0.15%	0.16%	0.02%	0.00%	0.00%	0.30%	0.00%	0.00%	0.00%
Paguridae zoea	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.02%	0.00%	0.00%	0.01%
Atelecyclidae/crab megalopa	1.13%	1.42%	0.16%	0.09%	0.32%	0.12%	0.13%	0.15%	0.50%	0.03%	0.14%
Crab zoea	0.17%	0.44%	0.15%	0.04%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Gastropoda	**1.88%**	**2.04%**	**3.68%**	**1.59%**	**3.51%**	**0.67%**	**0.33%**	**0.00%**	**2.30%**	**0.89%**	**1.07%**
Limacina spp.	0.00%	0.00%	3.68%	1.59%	3.51%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Pterepod spp.	1.88%	2.04%	0.00%	0.00%	0.00%	0.67%	0.33%	0.00%	2.30%	0.89%	1.07%

Appendix 7. Summary of food load composition of Whiskered Auklet chick meals.

Table A7-1 - Summary of food load composition of Whiskered Auklets at Buldir Island, 1993-2006. Data are presented as annual values of percent biomass.

Year	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
n	23	16	48	71	36	26	38	33	28	32	31	37	31	36
Unid. crustacean	7.40%	0.00%	0.26%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Copepoda	**19.14%**	**43.88%**	**76.67%**	**93.29%**	**93.39%**	**96.95%**	**93.54%**	**96.70%**	**99.68%**	**85.39%**	**39.55%**	**98.32%**	**96.19%**	**91.42%**
Calanoid spp.	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	2.82%	0.00%	0.00%	0.00%	0.00%	0.00%
Paraeuchaeta birostrata	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.18%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Paraeuchaeta elongata	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.13%	0.12%	0.00%	0.00%	0.00%	0.00%
Pseudhaloptilus pacificus	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.25%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Calanus marshallae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.46%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Calanus pacificus	0.00%	0.00%	0.06%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
***Neocalanus* Total**	**19.14%**	**43.88%**	**76.61%**	**93.29%**	**93.39%**	**96.95%**	**93.11%**	**96.24%**	**96.73%**	**85.27%**	**39.55%**	**98.32%**	**96.19%**	**91.42%**
Neocalanus spp.	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	5.08%	49.31%	0.00%	0.00%	0.00%	0.00%	0.00%
Neocalanus cristatus	11.48%	36.80%	36.09%	36.19%	15.50%	75.57%	92.49%	70.04%	47.42%	71.96%	8.36%	19.01%	17.71%	58.35%
Neocalanus plumchrus/flemingeri	7.66%	7.08%	40.53%	57.10%	77.88%	21.38%	0.61%	21.12%	0.00%	13.32%	31.19%	79.32%	78.49%	33.07%
Amphipoda	**0.09%**	**4.37%**	**1.28%**	**0.26%**	**0.25%**	**0.09%**	**0.33%**	**0.00%**	**0.00%**	**0.00%**	**0.91%**	**0.00%**	**0.01%**	**0.00%**
Hyalidae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.90%	0.00%	0.00%	0.00%
Lysianassidae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%
Hyperoche medusarum	0.00%	0.00%	1.11%	0.26%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Primno macropa	0.01%	3.82%	0.00%	0.00%	0.24%	0.09%	0.33%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Themisto pacifica (<4mm)	0.00%	0.55%	0.17%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Themisto spp. (<4mm)	0.08%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.01%	0.00%
Euphausiacea	**60.22%**	**48.80%**	**20.07%**	**5.99%**	**0.23%**	**1.81%**	**1.37%**	**1.57%**	**0.30%**	**13.52%**	**52.03%**	**1.61%**	**3.14%**	**8.45%**

Year	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Euphausiid furcilia	0.00%	0.00%	0.00%	0.00%	0.00%	0.35%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Euphausiid spp. (lg, > 7mm)	0.00%	0.00%	20.07%	5.99%	0.23%	1.46%	1.37%	1.57%	0.30%	11.73%	4.23%	0.51%	3.03%	8.45%
Thysanoessa spp. (>12mm)	60.22%	48.80%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.79%	47.80%	1.09%	0.11%	0.00%
Decapoda	**0.00%**	**2.79%**	**1.50%**	**0.34%**	**5.53%**	**0.59%**	**2.89%**	**1.70%**	**0.02%**	**0.69%**	**7.52%**	**0.07%**	**0.66%**	**0.12%**
Hippolytidae juvenile	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.98%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Larval shrimp (<7mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.59%	0.12%
Pandalid shrimp (>12mm)	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.58%	7.49%	0.00%	0.00%	0.00%
Pandalid shrimp larvae	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.02%	0.10%	0.03%	0.00%	0.00%	0.00%
Shrimp zoea	0.00%	2.79%	1.50%	0.14%	4.43%	0.59%	1.92%	1.70%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Atelecyclidae megalopa	0.00%	0.00%	0.00%	0.16%	0.71%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.04%	0.04%	0.00%
Crab zoea	0.00%	0.00%	0.00%	0.04%	0.39%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.03%	0.03%	0.00%

Year	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Gastropoda	**0.02%**	**0.00%**	**0.21%**	**0.11%**	**0.61%**	**0.55%**	**1.87%**	**0.03%**	**0.00%**	**0.40%**	**0.00%**	**0.00%**	**0.00%**	**0.00%**
Limacina helicinia	0.02%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Limacina spp.	0.00%	0.00%	0.00%	0.00%	0.00%	0.55%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Pterepod spp.	0.00%	0.00%	0.21%	0.11%	0.61%	0.00%	1.87%	0.03%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Unid. snail	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.40%	0.00%	0.00%	0.00%	0.00%
Unid. squid	0.00%	0.16%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Hexagrammos spp. (1+ yr)	13.13%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Appendix 8. Catalogue numbers of Least Auklet specimens examined at the American Museum of Natural History (AMNH), Academy of Natural Sciences, Philadelphia (ANSP), Cowan Vertebrate Museum (CVM), Delaware Museum of Natural History (DMNH), Denver Museum of Nature and Science (DMNS), Moscow State University Zoological Museum (MSUZM), and University of Michigan Museum of Zoology (UMMZ).

AMNH: 30040, 30043, 653500, 748234, 748235, 748241, 749236, 749240, 753496, 753497, 753498, 753499, 753501, 753503, 753504; ANSP-55379, 148119, 148121; CVM-13290; DMNH-55060; DMNS-11636; MSUZM-42421, 42724, 64650, 70035, 70777, 79193, 81118, 85668, 98295, 98296, 98297, 119171; UMMZ-150027.

Appendix 9. Means, standard deviations, and sample sizes from stable-isotope analysis of Least and Crested Auklets at Buldir, Kiska, and Gareloi Islands, Aleutian Islands, Alaska, from 2007-2010. There were no significant differences within species among islands, or among years, so data were pooled. Data are from breast (pre-breeding), P1 (chick rearing), and P10 (post-breeding) feathers.

Species	**Age class**	**Season**	**n**	**δ^{13}C ± S.D.**	**δ^{15}N ± S.D.**
Crested Auklet	Adult	Pre-breeding	10	-18.78 ± 1.74	14.73 ± 2.27
		Chick rearing	10	-18.70 ± 0.97	13.70 ± 1.78
		Post-breeding	10	-18.54 ± 1.24	16.71 ± 0.90
Least Auklet	Adult	Pre-breeding	50	-18.65 ± 1.63	12.84 ± 1.63
		Chick rearing	50	-19.02 ± 1.71	12.30 ± 1.37
		Post-breeding	50	-17.54 ± 1.03	14.37 ± 1.04
Least Auklet	Subadult	Pre-breeding	39	-19.95 ± 1.88	11.10 ± 1.44
Least Auklet	Chick	Chick rearing	8	-20.67 ± 0.35	8.88 ± 0.23