NONBREEDING DISTRIBUTIONS AND POTENTIAL CARRYOVER EFFECTS
IN A SENTINEL NORTH PACIFIC SEABIRD, THE CASSIN'S AUKLET

by

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DEDICATION

To Barbara Ryder and Ned Studholme,

for raising me as part of this amazing planet with a desire to respect it, learn from it, give back to it,

and simply revel in it.

To Stephen Glazier,

for being my spark of joy and my even keel, with whom I most enjoy sharing this purpose and revelry.

To Batesville Virginia and Islesboro Maine

for always being my home and the water, wind, and earth behind my inspiration.

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ABSTRACT

Factors influencing animal fitness and population-level processes during nonbreeding are critically important but remain largely unknown in many species due to challenges obtaining individual-level data from this period. Here, I used tracking and physiological sampling techniques to gain insight into nonbreeding distributions, migratory behavior, and potential carryover effects in a North Pacific seabird. From 2014-17, nonbreeding Cassin's auklets from British Columbian colonies routinely occupied nearshore waters from the Gulf of Alaska to Baja California, utilizing regions north of the colony in summer and fall, south of the colony in fall and winter, and returning to the colony region over a month prior to laying in early spring. Within this broad spatial and temporal framework, four general migratory tactics were expressed – North, South, North-South, and Local migration – with individuals exhibiting substantial variability in finer-scale phenology and choice of residency areas. Some variability was explained by sex, year, and colony of origin. These diverse nonbreeding experiences were expected to drive variability in the occurrence and strength of carryover effects on reproduction; however, indicators of pre-breeding physiologic state and diet did not predict reproductive investment (egg size) in an additional year. While significant carryover effects have been shown in similar studies, these differences may be attributable to oceanographic context – with upregulation of corticosterone and high-quality diet being required to achieve larger egg sizes during poor, but not favorable, oceanographic conditions. Overall, this research revealed considerable variability in nonbreeding behavior, experience, and the occurrence of carryover effects in this species. More comprehensive and repeated studies are needed to assess the influence of variation in oceanographic conditions experienced outside the breeding season and to predict population-level responses in the context of climate change.

LIST OF ABBREVIATIONS AND SYMBOLS USED

%	Unit, parts per hundred (percent)
˚C	Unit, degrees Celcius
‰	Unit, parts per thousand
a	Symbol representing statistical confidence level
AIC$_c$	Akaike Information Criterion, corrected for finite sample size
ANOVA	Analysis of Variance
CCS	California Current System
CI	Confidence Interval
cm	Unit, centimeters
Cort	Corticosterone (glucocorticoid homone)
COSEWIC	Committee on the Status of Endangered Species in Canada
CV	Coefficient of Variation
d	Unit, days
EA-IRMS	Elemental Analyzer-Isotope Ratio Mass Spectrometer
EVI	Egg Volume Index (length × breadth^2 × 0.51, units cm^3)
fCort	Feather corticosterone
g	Unit, grams
GLS	Geolocation Sensing logger
HSD	Honest Significant Difference (Tukey)
km	Unit, kilometer
LH	Luteinizing Hormone
LR	Likelihood Ratio
min	Unit, minutes
mL	Unit, milliliters
mm	Unit, millimeters
MODIS	Moderate Resolution Imaging Spectroradiometer
MPA	Marine Protected Area
n	Sample size
NASA	National Aeronautics and Space Administration, USA
NIST	National Institute of Standards and Technology, USA
NOAA	National Oceanic and Atmospheric Administration, USA
NPO	North Pacific Oscillation
NSERC	National Science and Engineering Research Council, Canada
OB.DAAC	Ocean Biology Distributed Active Archive Center (NASA)
PDB	Pee Dee Belemnite, carbon isotope standard
PDO	Pacific Decadal Oscillation
pg	Unit, picograms
PO.DAAC	Physical Oceanography Distributed Active Archive Center (NASA)

RGPIN	Discovery grants program, individual (NSERC)
SD	Standard Deviation
SEM	Standard Error of the Mean
SMI	Standard Mapped Image
SST	Sea Surface Temperature
UD	Utilization Distribution
UV	Ultra-violet light
YOY	Young of the Year
ΔAIC_c	Difference in AIC_c between two models
$\delta^{13}C$	Delta notation, $[(R_{sample}/R_{standard})-1] \times 1000$ (‰) where R is the ratio of ^{13}C to ^{12}C
$\delta^{15}N$	Delta notation, $[(R_{sample}/R_{standard})-1] \times 1000$ (‰) where R is the ratio of ^{15}N to ^{14}N

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CHAPTER 1: INTRODUCTION

1.1 IMPORTANCE OF THE NONBREEDING PERIOD

While factors influencing animal fitness and population-level processes during breeding are more commonly identified and logistically less challenging to study in colonial and aggregate breeders, factors during nonbreeding are also of critical influence. Across taxa, nonbreeding resource availability, broad-scale climatic conditions, short-term events (e.g. storms), physical alterations to habitat, and predation can all be important drivers of vital rates and population dynamics via effects on individual survival and reproduction (Calvert et al., 2009). Many motile species have evolved behavioral strategies to adaptively utilize nonbreeding habitats – including migration, partial migration, year-round residency, and nomadism – with selection due to variation in the predictability, patchiness, and/or seasonality of local resources and environmental conditions (Cresswell et al., 2011; Dingle and Drake, 2007; Jonzén et al., 2011; Shaw and Couzin, 2013). Seasonal differences in survival are typically most pronounced in year-round residents of temperate and polar zones; however, seasonal vital rates and their interactions may also be particularly important to population dynamics in migratory species, due to influences from multiple habitats across broad geographic scales (Calvert et al., 2009).

Effects of nonbreeding experience on future reproduction and survival are an example of carryover effects – features of an organism's current performance that are explained by its past experience (O'Connor et al., 2014). Carryover effects have been identified across a wide range of taxa, including mammals (e.g. Cook et al., 2004), fish (e.g. Midwood et al., 2015), birds (e.g. Legagneux et al., 2012), terrestrial and marine invertebrates (e.g. Dickson et al., 2017; Marshall

and Morgan, 2011), and even plants (e.g. Moreno et al., 2013). Although carryover effects can also act across behavioral states and life history stages, recent ecological studies have focused heavily on effects across seasonal states (Harrison et al., 2011; Norris and Marra, 2007), particularly within the context of avian migration (O'Connor et al., 2014).

The physiological mechanisms driving carryover effects remain largely unexplored; however, several have been shown to link nonbreeding season phenomena to reproductive traits. The most commonly reported category of mechanisms is body condition (Cook et al., 2004; Monteith et al., 2014), driven by nonbreeding diet quality (Kennedy et al., 2008), habitat quality (Norris et al., 2004), population density (Betini et al., 2013), or predation stress (Elliott et al., 2016). Physiologic (hormonal) state has been identified as another category of mechanisms, acting via incompatibilities between regulatory systems - such as those for migration and reproduction (Crossin et al., 2012a, 2010). The glucocorticoid hormone corticosterone (Cort) is a candidate mechanism with potential implications for both condition and physiologic state (Goutte et al., 2010). Cort acts as a metabolic regulator and a mediator of physiological response to unpredictable stressors (Landys et al., 2006; Sapolsky et al., 2000; Wingfield et al., 1998) and can be positively, negatively, or neutrally related to fitness (Bonier et al., 2009). Such mechanisms affect reproduction most strongly through maternal tradeoffs and physiological constraints which may drive the decision to breed as well as reproductive timing, investment, and success.

1.2 AN INTRODUCTION TO THE MIGRATORY STRATEGY

Three general movement types have been described in animals: station keeping, ranging, and migration (Dingle, 2014; Kennedy, 1985). In the first two types, movements either within or

beyond an organism's home range cease in response to encountered resources (e.g. in year-round residents and nomads), but this is not the case during migration (Dingle, 2006). While migration has often been defined based on population-level behavioral patterns – such as predictable, coordinated, and/or large-scale movement – individual-based definitions are more inclusive of the extensive, natural variation in this phenomenon (Cresswell et al., 2011). One such definition describes migration as individual movement which 1) is directed or persistent, 2) is deliberately undertaken, and 3) involves temporary suppression of routine station keeping behaviors such as foraging (Kennedy, 1985, 1961). Migratory behavioral phenotypes are expressed due to interactions between individual genetics, physiology, and biomechanics, as well as physical and biological environmental factors (Dingle, 2006; Lennox, 2016). Since migration arose repeatedly across many taxa and mechanisms of expression differ, it is perhaps best to conceptualize migration as a common evolutionary 'syndrome' (Dingle, 2006).

The movements making up migrations are often driven by resource availability ('alimental movement'), abiotic or non-resource biotic conditions (originally 'climatic movement', now includes predation and density-dependent factors), or reproduction ('gametic movement') (Heape, 1931; Shaw, 2016), and are thought to be optimized with respect to energetic costs, time, and predation risk (Alerstam, 2011; Alerstam and Lindström, 1990). These one-way movement types combine to yield the three main categories of round-trip migration: 1) movement away from a primary habitat to avoid temporary unfavorable conditions ('refuge migration' – alimental, 'climatic', and gametic movement), 2) movement between breeding habitat and foraging habitat ('breeding migration' – alimental and gametic movement), and 3) movement in response to spatially shifting resources without a primary habitat ('tracking migration' – alimental movement) (Shaw, 2016). Seasonal refuge and breeding migrations are perhaps the most common across taxa

(Alerstam et al., 2003; Ramenofsky and Wingfield, 2007; Shaw, 2016), particularly among birds, and are of primary interest in this study.

Remarkable individual- and population-level variation exists within the migratory strategy (Cagnacci et al., 2011; Dingle and Drake, 2007; Vardanis et al., 2011). For example, individuals from the same population can migrate to different wintering areas, individuals from different populations can migrate to a shared wintering area, and vice versa. Differences in phenology, routes, stopover habitats, and overwinter location are common both within and among populations and combine to yield many unique migratory patterns or tactics within species. In addition, not all individuals within a population express the same nonbreeding strategy. Many migratory populations are likely 'partially migratory' – where some individuals migrate and others do not (Chapman et al., 2011). While typically defined at the population level, individuals can also exhibit a partially migratory pattern across years since these strategies can be facultative as well as obligate (Terrill and Able, 1988), driven by variable factors such as environmental conditions, population density, individual condition, and/or physiologic state. These same factors may also drive finer-scale variations in migratory tactics within and between populations, along with fixed factors such as genetics, cultural learning, individual quality, sex, size, and age (Alerstam et al., 2003; Cresswell et al., 2011; Dingle, 2006; Shaw, 2016). This variability in strategies and tactics has important implications for energy expenditure and acquisition, breeding habitat occupancy advantages, environmental experience, carryover effects, and mortality (Alerstam et al., 2003; Buehler and Piersma, 2008; Calvert et al., 2009; Cresswell et al., 2011).

1.3 NONBREEDING PERIODS AND MIGRATION IN SEABIRDS

Thanks to advances in tracking technology which enable the determination of individual movement and behavior over extended time scales (Bridge et al., 2011; Burger and Shaffer, 2008), researchers are now addressing significant nonbreeding knowledge gaps for a growing number of species, including seabirds. In particular, the miniaturization of light-based geolocation loggers has increased the number of species which can carry these devices throughout the annual cycle with minimal impact. Prior to these advances, individual nonbreeding distributions for large seabirds could be determined using bulkier, existing tracking technologies (Jouventin and Weimerskirch, 1990; Phillips et al., 2006; Weimerskirch and Wilson, 2000); however, for smaller seabirds, or seabirds with high wing loadings, data on nonbreeding distributions were mostly limited to post-mortality band recoveries and vessel observations. Such datasets can be problematic, the former often hampered by small sample sizes and recovery probability bias (e.g. Mehl et al., 2004; Montevecchi et al., 2012), and the latter often exhibiting incomplete spatiotemporal coverage and providing no information on the provenance of birds. Without sufficient and reliable distributional data, nonbreeding research was largely limited to effects that could be measured at breeding colonies (e.g. reproduction, survival) – inferred at the population level from correlations with broad-scale environmental data (Ainley and Hyrenbach, 2010; Jones et al., 2002; Morrison et al., 2011; Thompson and Ollason, 2001; Zador et al., 2013), or at the individual level using physiological sampling and stable isotope analyses to approximate diet and distribution (Cherel et al., 2006; Inger and Bearhop, 2008; Quillfeldt et al., 2005; Sydeman et al., 1997). Now researchers can move beyond these limitations and are revealing detailed individual

distributions, phenology, and behaviors, as well as their implications for fitness and population-level processes (Crossin et al., 2014).

Seabirds have been found to employ a variety of behavioral strategies to maximize fitness (current and future survival, future reproduction) during the nonbreeding period. While seasonality in breeding habitat is often related to migratory tendency (Cresswell et al., 2011), a great deal of variation in nonbreeding strategy and migratory tactics have been documented independent of breeding latitude. Seabird species can be non-migratory (Ainley, 1995; Crossland, 2012; Croxall and Davis, 1999), migratory (Carey et al., 2014; Egevang et al., 2010; Shaffer et al., 2006), or partially migratory (Croxall et al., 2005; McKnight et al., 2011; Perez et al., 2014; Péron et al., 2013). Among migrants, variation in migratory tactics – combinations of when, where, and how individuals move – exists both among and within populations (Catry et al., 2011; Fifield et al., 2014; Kopp et al., 2011; Weimerskirch et al., 2017) and across years (Dias et al., 2011; Müller et al., 2014; Phillips et al., 2005; Quillfeldt et al., 2010), with consequences for migratory connectivity and variation in nonbreeding experience.

Nonbreeding carryover effects have been documented in many seabirds, including effects on the decision to breed (Crossin et al., 2012a; Goutte et al., 2014), reproductive phenology (Daunt et al., 2014; Salton et al., 2015), egg investment (Crossin et al., 2012b; Sorensen et al., 2009), and fledging success (Harms et al., 2015; Shoji et al., 2015), as well as effects on telomere dynamics, recruitment, and survivorship (Schultner et al., 2014; Szostek and Becker, 2015). As in other taxa, these effects are often correlated with environmental conditions outside the breeding season (Szostek et al., 2015; Zador et al., 2013) and can be mediated by diet (Kouwenberg et al., 2013; Sorensen et al., 2009), body condition (Crossin et al., 2012a; Goutte et al., 2014), and physiologic state (Crossin et al., 2012b, 2010; Pérez et al., 2016). In seabirds, Cort is strongly related to food

availability (Kitaysky et al., 2007; Will et al., 2015) and has been found to mediate nonbreeding carryover effects via physiologic state (Goutte et al., 2011; Kouwenberg et al., 2013). The occurrence, magnitude, and mechanisms of these carryover effects are likely to vary among oceanographic contexts, or even individuals; however, few studies have assessed this potentially variability across years.

Oceanographic change and increasing climatic variability (Cai et al., 2014; IPCC, 2013) are undoubtedly affecting the suitability and predictability of seabird nonbreeding habitat. Seabirds are the most threatened group of avian species (Croxall et al., 2012), and these changes have potentially increasing implications for population-level processes via effects on maternal decisions, carryover effects, and survival. While the main threats to these birds at sea are commercial fisheries and pollution, the potential effects of climate change remain an important knowledge gap (Croxall et al., 2012) – especially given that seabirds are particularly sensitive to rapid changes in their environment (Grémillet and Boulinier, 2009). Since seabirds are also important marine predators, understanding nonbreeding experience and potential carryover effects in the context of a changing ocean is essential to predicting changes in both seabird population dynamics and marine ecosystem health.

1.4   STUDY SPECIES AND APPROACH

With this thesis, I begin to address critical nonbreeding knowledge gaps for a sentinel North Pacific seabird, the Cassin's auklet (*Ptychoramphus aleuticus*), which breeds on offshore islands from Alaska to Mexico. This species is small (~180 g), zooplanktivorous, and lays a single-egg clutch (Ainley et al., 2011), enabling me to assess nonbreeding carryover effects on reproductive

investment at the time of laying. Reproduction and survival in this species also respond strongly to variation in oceanographic conditions (Bertram et al., 2005; Hedd et al., 2002; Morrison et al., 2011). These factors make the Cassin's auklet an ideal study species with which to better understand nonbreeding behavior and carryover effects and how these may vary in different oceanographic contexts.

Prior to this study, as with many small seabirds, nonbreeding distributions of Cassin's auklets were poorly understood with estimates primarily informed by vessel-based surveys and post-mortality band recoveries. The predominant theory was of southern migration for British Columbian and/or Alaskan breeders, due to large numbers observed entering Californian waters from the north in September and October (Briggs et al., 1987), and of sedentary behavior for Californian breeders (Ainley and Boekelheide, 1990), although several radio-tagged birds from southern California moved north following breeding (Adams et al., 2004). Limited band recoveries from British Columbia (Washington [n = 2], Oregon [n = 3], northern Baja [n = 2]; Triangle Island Research Station unpubl. data) and central California (n = 3; Ainley and Boekelheide, 1990) corroborate this theory. While these data are informative, they are limited in space, time, and sample size, and generally lack the individual-level focus required to assess variation in nonbreeding distribution, phenology, environmental experience, and carryover effects within or among colonies and years. Only one study of carryover effects in Cassin's auklets had been published, finding effects of pre-breeding diet on lay date and egg size, but was limited to one year with poor oceanographic conditions. To move beyond these limitations, I employed an individual-level approach across a broad range of oceanographic contexts.

I studied Cassin's auklets from three colonies in British Columbia: Frederick Island (53.93°N, 133.21°W), Rankine Island (52.25°N, 131.05°W), and Triangle Island (50.87°N,

129.08°W) (Figure 1.1). Research effort was focused at Triangle Island, where ~40% of the world's population breeds (~550,000 pairs; Ainley et al., 2011; Rodway, 1991), located off northwest Vancouver Island at the northern extent of the California Current System. Frederick Island is a large colony (~90,000 pairs; Ainley et al., 2011), located off the northwest coast of Haida Gwaii at the southern extent of the Alaska Current System, and Rankine Island is a mid-size colony (~26,000 pairs; Ainley et al., 2011), located in more protected waters off the southeast coast of Haida Gwaii, in the transition zone between these ecosystems. From 1990 to at least 2009, Cassin's auklets experienced significant population declines, especially on Triangle Island where burrow density declined 2.5% per year, corresponding to an estimated loss of 20% of the global population (Rodway and Lemon, 2011). This decline, along with known sensitivity to large-scale climate effects on their prey, predation at the colony, and vulnerability to oiling, contributed to the Cassin's auklet's designation as a species of 'special concern' in Canada (COSEWIC, 2014). Interestingly, while breeding populations in British Columbia are considered 'vulnerable' to 'imperiled' at the provincial level, they are listed as 'apparently secure' during nonbreeding, despite the paucity of data from that period and the high likelihood that nonbreeding experiences affect reproductive outcomes.
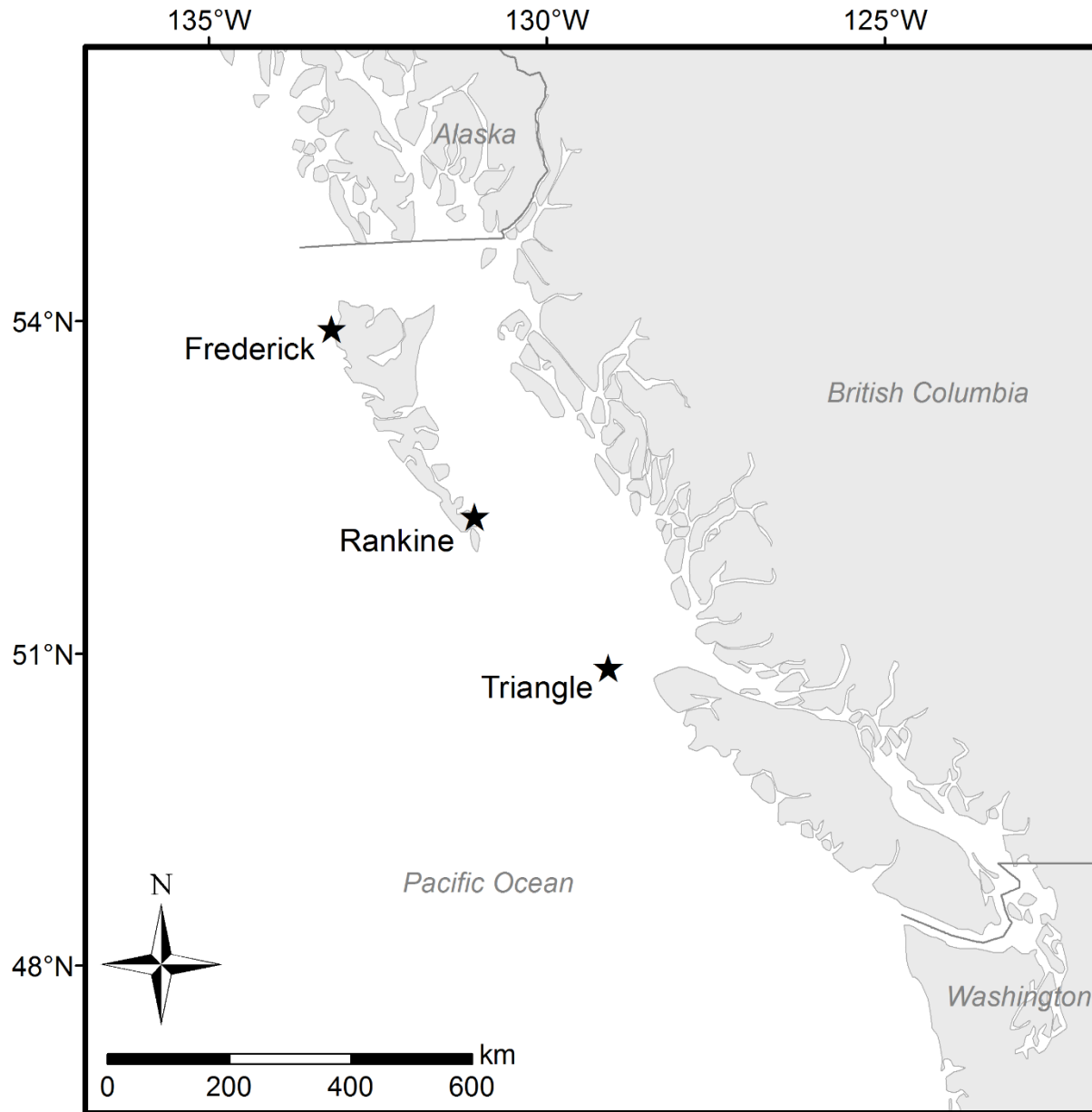
Figure 1.1 Location of study sites (colonies) within British Columbia.

I used three methods to obtain data from the nonbreeding period: 1) light-sensing, archival dataloggers to estimate when and where individual Cassin's auklets moved, 2) satellite imagery to compare these distributions with concurrent sea surface conditions, and 3) breast feather samples to obtain information on physiologic state and diet during the pre-breeding period. Finally, during the breeding season, I measured egg size as a proxy for reproductive investment in order to

investigate potential nonbreeding carryover effects. In the following paragraphs, I briefly introduce these methods.

Due to the small size and high wing-loading of my study species, I used miniature, light-level dataloggers (Intigeo C65, Migrate Technology Ltd., 1.0 g) to determine individual nonbreeding distributions. These loggers have an accurate on-board clock and record ambient light intensity over time. The resulting daily light curves are used to calculate sunrise and sunset event-times based on a standard light intensity threshold (2 lux). These event times are then used to estimate two geographic locations per day, with longitudes calculated from the timing of local noon or midnight and latitudes calculated from day length or night length. These calculations require a user-defined solar elevation angle, an appropriate value of which can be back-calculated using data from a process called 'groundtruthing' where each logger is run at a known location for several days. Following the application of a maximum flight speed filter and two iterations of smoothing (sliding boxcar, 1:2:1 weighted mean), the error in light-level geographic locations is ~169 km (Phillips et al. 2004b), sufficient for observing large-scale migratory movements. Unfortunately, latitude estimates within a few weeks of the equinoxes are unreliable due to the lack of variation in day lengths, leaving these periods poorly resolved. While deployment of similar 2.8 - 5 g devices has caused nest desertion in this species (Elliott et al., 2010), I took precautions to reduce this risk by minimizing logger size (total assembly <2.0 g), selecting chick-rearing birds when possible, and minimizing disturbance during deployment (see section 2.3.2).

Satellite-mounted instruments are continuously recording data from the Earth's surface and atmosphere during their orbits, enabling the comparison of remotely collected distributional data with concurrent environmental characteristics (Robinson, 2004). For example, NASA's Aqua and Terra satellites are equipped with a Moderate Resolution Imaging Spectroradiometer (MODIS)

which records absorption/reflectance, radiation, and backscattering across a broad range of wavelengths, enabling the determination of diverse characteristics such as particulate organic carbon concentrations, sea surface temperature (SST), and atmospheric aerosol optical thickness (haze) (NASA Goddard Space Flight Center, 2018; Robinson, 2004). MODIS-Aqua and -Terra record the entire Earth's surface every two days and the resulting data products are made freely available at daily, 4 km^2 resolution. In this study, I used satellite-derived SST, SST anomaly, and chlorophyll a (chl a) data for the North Pacific to examine potential relationships between these variables and changes in large-scale distributions across both seasons and years – assuming that SST and chl a indicate nonbreeding habitat quality to some extent. SST data are derived from short- (4 µm) or long-wave (11 µm) thermal radiation (NASA Goddard Space Flight Center, 2015), and chl a data, representing near-surface concentrations (mg m^{-3}), are calculated from reflectance in two to four sensor bands within 440 - 670 nm using an algorithm developed from simultaneous in-situ and satellite measurements (NASA Goddard Space Flight Center, 2014).

Information on individual nonbreeding experience and its physiological effects can be obtained via the analysis of feather tissue. As a feather grows, circulating dietary compounds and Cort become fixed within the tissue such that feather isotope ratios and Cort concentrations (fCort) represent integrated measures of diet and physiologic state during the time of growth (Bortolotti et al., 2009, 2008; Fairhurst et al., 2013; Inger and Bearhop, 2008). Cassin's auklets undergo a definitive prebasic molt of both primaries and body feathers which overlaps with breeding and continues through the fall (Ainley et al., 2011; Pyle, 2009, 2008). Prior to breeding, they undergo a definitive prealternate molt with peak body feather replacement during February and March; however, this molt can occur more broadly and has been documented as early as mid-January at lower latitudes (Ainley et al., 2011; Pyle, 2009, 2008). Variation in the timing of molt can also

occur among individuals from similar latitudes and is an important limitation of these methods, requiring assumptions for inter-individual comparisons (Romero and Fairhurst, 2016). Despite this potentially high variability, such feather data have been successfully used identify carryover effects, including links between higher-quality pre-breeding diet, earlier breeding, and larger egg sizes in Cassin's auklets during poor oceanographic conditions (Sorensen et al., 2009).

While very little within-individual variation in avian egg size has been explained by individual or environmental pre-breeding characteristics (Christians, 2002), within-individual variation in Cassin's auklet egg size is unknown and larger eggs may confer a fitness advantage in this species. Larger eggs have higher lipid, protein, and nutrient content (Williams, 1994) and Cassin's auklet mass and size within five days of hatching are positively correlated with egg size (Knechtel, 1998), suggesting it is a good indicator of maternal investment. While an earlier review suggested there was no clear, strong relationship between egg size and fitness across avian species (Williams, 1994), a more recent meta-analysis found that egg size positively affects hatching success, nestling morphological traits, survival, and growth rate, with the strongest relationships occurring in the early post-hatching period when mortality is typically high (Krist, 2011). Early nestling loss in Cassin's auklets is not uncommon, particularly during poor oceanographic conditions (JM Hipfner, unpubl. data), thus greater nutrient stores in nestlings conferred by larger egg size may reduce starvation risk and increase fitness in this species.

1.5   OBJECTIVES AND CHAPTER OUTLINE

The primary objectives of this study were 1) to gain insight into the nonbreeding distributions and migratory behavior of Cassin's auklets breeding in British Columbia and 2) to

begin to assess whether resulting nonbreeding experiences may drive carryover effects onto the breeding season, particularly within the context of oceanographic variability. In Chapter 1, I introduced the key concepts behind this study, highlighted important knowledge gaps for seabirds, and described my study species and methodological approach. In Chapter 2, I characterize individual- and population-level nonbreeding distributions and behavior in three years, evaluate potential drivers of variation in basic migratory characteristics, and assess whether variation in population-level distributions, SST, and chl a suggest fixed or flexible migratory tactics in this species. Nonbreeding experience inevitably affects individual physiology in ways which can result in carryover effects between seasons or life history stages. Therefore, the high variability in migratory behavior and nonbreeding experience I document in Chapter 2 may cause variable occurrence and intensity of carryover effects, both within and among population of this species. In Chapter 3, I characterize nonbreeding physiologic state and diet, specifically during the pre-breeding period, and test whether these parameters carry over to affect individual reproductive performance in the form of egg size during favorable oceanographic conditions. In Chapter 4, I discuss the main findings and implications of this thesis, identify limitations, and provide recommendations for future work. Overall, this research reveals high individual variability in nonbreeding experience and variable effects of oceanographic context, with distributions, phenology, and carryover effects being both affected or unaffected by oceanographic variability.

CHAPTER 2: NONBREEDING BEHAVIOR, DISTRIBUTIONS, AND VARIABILITY AMONG INDIVIDUALS AND YEARS

2.1 ABSTRACT

Nonbreeding distributions and migratory phenology can vary within and among populations of many taxa, including seabirds. Such differences can result in diverse nonbreeding experiences which, in turn, can drive variation in survival and reproduction. Knowledge of where, when, and why individuals move is therefore crucial to understanding and predicting population-level processes, particularly in the context of oceanographic change. Here I present the first year-round tracking data for the Cassin's auklet, a small, zooplanktivorous North Pacific seabird, revealing the nonbreeding behavior of birds from British Columbian colonies across three years of variable oceanographic conditions. These birds moved both north (summer, fall) and south (fall, winter) from their colony of origin, using one of four migratory tactics: North, South, North-South, or Local migration. Within these tactics there was additional variability in the timing of movements and regional habitat use, resulting in highly variable individual nonbreeding experience. Some variability was explained by the sex of individuals, year, and colony of origin. Cassin's auklets appear to target distinct, ecologically differentiated areas within their nonbreeding range which may have, or be expected to have, good quality habitat. Variation in these target regions across years suggests somewhat flexible migratory behavior; however, consistent migration to the Southern California Bight despite very low productivity in one year suggests fixed tactics may exist, at least for some individuals.

2.2 INTRODUCTION

Fundamentally, animal movement occurs in response to spatial and physical variation in the environment. In the case of migration, animals can respond to semi-predictable, cyclic variation in environmental conditions across the annual cycle (Cresswell et al., 2011). Migration is a widespread phenomenon in terrestrial, aquatic, and aerial taxa, and commonly occurs between breeding and nonbreeding habitats (Alerstam et al., 2003; Ramenofsky and Wingfield, 2007), enabling individuals to optimize their use of variable resources for self-maintenance, growth, development, and reproduction (Dingle and Drake, 2007). Remarkable diversity in migratory tactics has been documented both among and within populations (Cagnacci et al., 2011; Dingle and Drake, 2007; Vardanis et al., 2011). Migratory movements are thought to be optimized with respect to energetic costs, time, and predation risk (Alerstam, 2011; Alerstam and Lindström, 1990); thus, this extensive variability is likely driven by differences in population- or individual-level characteristics with relevance to fitness outcomes.

Like many other migratory taxa, seabirds show considerable diversity in nonbreeding strategy (migratory, nonmigratory) and migratory tactics. Some seabirds appear to be sedentary year-round (Crossland, 2012; Croxall and Davis, 1999), while others make exceptionally long migrations (Egevang et al., 2010; Shaffer et al., 2006), or exhibit a mixed strategy ('partial migration'; Chapman et al., 2011) that includes both migrants and residents (McKnight et al., 2011; Perez et al., 2014). Among migrants of the same species, intra- and inter-population differences can exist in choice of primary overwintering area, stopover locations, and migratory phenology (Catry et al., 2011; Kopp et al., 2011; Weimerskirch et al., 2017), all of which result in varying degrees of spatial segregation and distinct nonbreeding experiences. At both the population- and

individual-level, these migratory tactics can be repeatable year-to-year (fixed) or, in response to environmental variation, they can be flexible (Dias et al., 2011; Phillips et al., 2005; Quillfeldt et al., 2010), often within a relatively consistent large-scale distribution framework (Krietsch et al., 2017; McFarlane Tranquilla et al., 2014). Determining such differences in nonbreeding experience and behavioral flexibility is crucial for understanding the factors driving population-level processes in seabirds and predicting how these processes may be affected by rapid oceanographic change.

Equally important to predicting population-level processes is understanding the fundamental drivers of this behavioral variability. Seabird nonbreeding distributions are affected by intrinsic factors such as sex, age, individual quality, and reproductive status (Fayet et al., 2016; Gutowsky et al., 2014; Phillips et al., 2005), and extrinsic factors such as environmental characteristics, prey distribution, and competition (Fayet et al., 2017; Felicísimo et al., 2008; Phillips et al., 2005). Many additional factors, such as genetics and cultural learning, have been proposed but remain to be tested. The taxonomic coverage of such studies is also far from complete and even in species for which tracking data exist, assessment of these drivers is often hindered by limited spatiotemporal coverage and sample sizes.

The Cassin's auklet (*Ptychoramphus aleuticus*) is a small (~180 g), zooplanktivorous, North Pacific seabird for which reproductive biology has been well studied but basic nonbreeding distributions remain poorly understood (Ainley et al., 2011). Nonbreeding distribution estimates for Cassin's auklets have been based mainly on vessel observations, with high abundances documented over the continental shelf break and slope in the California Current System (Adams et al., 2004; Ainley et al., 2009), as well as in deeper offshore waters (Briggs et al., 1987; Ford et al., 2004). Monthly vessel transect surveys in California from 1975 to 1983 recorded large numbers

entering the region from the north in September and October, roughly doubling the local population and suggesting migration from British Columbia and Alaska (Briggs et al., 1987). In addition, limited radiotelemetry data suggest that birds breeding in southern California may move north toward central California at the beginning of their postbreeding period in June (Adams et al., 2004). Band recoveries appear to corroborate the theory of southward migration from British Columbia (recovered in Washington [n = 2], Oregon [n = 3], and northern Baja [n = 2]; Triangle Island Research Station unpubl. data), and sedentary behavior for central California breeders (n = 3; Ainley and Boekelheide, 1990); however, local currents and differences in shoreline recovery probability make inferences from these recoveries highly speculative.

Individual and colony-specific movement and behavioral data are needed to more directly assess a suite of factors which may affect population-level processes in Cassin's auklets during the nonbreeding period, particularly in the context of increasing oceanographic variability. The purpose of this study was to begin to address these knowledge gaps for colonies in British Columbia, where the majority of this species breeds (~75%; Rodway et al. 1992). This study had two broad aims: 1) to characterize nonbreeding distributions and migratory phenology, including the identification of stopover sites, and 2) to assess whether sex, year, and/or colony can explain variation in basic migratory characteristics (e.g. departure date). I also compared population-level distributions with environmental characteristics within and between three nonbreeding periods to assess whether changes in population-level distributions reflect changes in sea surface temperature (SST) and chlorophyll *a* (chl *a*), particularly in the context of recent, large-scale oceanographic phenomena ('the Blob'; Kintisch 2015).

2.3 METHODS

This research was conducted under permits from Environment Canada (banding permit 10667F; Migratory Birds scientific permits BC-14-0026#1, BC-15-0005, BC-16-0012, BC-17-0028). Wildlife protocols were approved by Simon Fraser University Animal Care Services in 2014 (974B-94), and Environment Canada's Western and Northern Animal Care Committee from 2015-2017 (15MH01, 16MH01, 17MH01).

2.3.1 **Study sites and context**

I tracked 35 breeding Cassin's auklets from two colonies in British Columbia during three nonbreeding periods, spanning 2014 to 2017. These years included unusually positive SST anomalies in the northeast Pacific (up to 4°C), primarily associated with a large, persistent mass of warm ocean water termed 'the Blob' (2013-15; Kintisch 2015, Peterson et al. 2016a) and a very strong El Niño event (2015-16, peak Oceanic Niño Index +2.6; NOAA Climate Prediction Center 2018). The Blob first appeared offshore in fall 2013, shifted alongshore from Alaska to Mexico in spring 2014, and split in two in spring 2015 before temperatures began to moderate (Kintisch, 2015; Peterson et al., 2016a). The Pacific Decadal Oscillation (PDO) was also predominantly positive (warm coastal SST phase) from October 2014 to the end of the study period (NOAA National Centers for Environmental Information, 2018), despite the development of a moderate La Niña in 2016-17 (NOAA Climate Prediction Center, 2018).

Most data in this study were obtained from the world's largest colony of this species, Triangle Island (50.86°N, 129.08°W) in the Scott Islands group, where ~40% of the world's

population breeds (Rodway, 1991). Additionally, I tracked individuals from Frederick Island (53.93°N, 133.21°W), a large colony off the northwest coast of Haida Gwaii during the 2014-15 nonbreeding period (Figure 1.1). In this study I define the nonbreeding period as 1 July - 31 March since most birds left the colony area on or after 1 July, and the earliest estimated lay date for returning tracked birds was 1 April.

2.3.2 Deployment and recovery of loggers

I deployed light-level based Global Location Sensing (GLS) loggers (Intigeo-C65, Migrate Technology Ltd., 1.0 g, range 4, mode 6) on birds at Triangle Island from mid- to late-June during the chick-provisioning period. Deployments of loggers at Frederick Island occurred in late May during incubation. Each logger was pre-attached to a plastic leg band using self-amalgamating tape, epoxy, and a UV resistant zip tie with a stainless-steel barb threaded through two custom holes in the band such that the whole assembly (<2.0 g) could be quickly placed on the tarsus. Loggers were groundtruthed for ≥3 days prior to deployment in 2014 and 2015, and 1 day (n = 7) or 0 days (n = 2) in 2016. At deployment, each bird was removed from its nest chamber, morphometrics were recorded (within 0.05 mm and 0.5 g), a metal band and a logger assembly were applied to the right and left tarsi, respectively, and the bird was returned to its burrow. Sex was assigned based on the bill depth of the loggered bird or its mate (Knechtel, 1998). In April - May of the following breeding season, each burrow was monitored daily for re-occupancy, at which point the logger assembly was retrieved and the bird returned to its incubation chamber. All loggers were groundtruthed again for ≥4 days, except for one logger in 2017 (2 d) and in cases where logger batteries were exhausted (n = 4).

Nest desertion has been documented in Cassin's auklets following the attachment of 2.8 - 5 g leg-mounted devices (Elliott et al., 2010), thus I took precautions to minimize this risk. As recommended by Elliott et al. (2010), I deployed loggers on birds which were rearing chicks whenever possible and which were experienced with human disturbance (from regularly studied areas of the colony), used the smallest available leg-mounted logger assemblies which met my research needs, attached loggers during the day outside the burrow, and minimized disturbance to the bird and its mate (efficient and quiet deployments, no mates tagged). In addition, I elected not to take blood samples at logger deployment to further minimize disturbance and, following deployment, kept burrow entrances covered for ~2 minutes to allow birds to calm down in the dark with their egg, chick, or mate. It was not possible test for logger-induced changes to nonbreeding behavior and, since birds can breed in different burrows among years, failure to recapture a bird during this study does not necessarily indicate mortality.

2.3.3 Logger data processing

All data collected from retrieved loggers were adjusted for logger clock drift except in cases of battery failure (two incomplete datasets and two complete datasets). Daily sunrise and sunset event-times were estimated from light intensity curves in IntiProc 1.03 (Migrate Technology Ltd., Cambridge, UK), using a lux threshold of two. All light curves were visually inspected and clearly erroneous event-times (program-defined sunrises or sunsets occurring within daylight or nighttime periods, or associated with severely truncated light curves) were noted and removed. A standard elevation angle of -6.17° was used when calculating all positional data. I chose this value by estimating the most appropriate angle for each groundtruth period using the

IntiProc calibration tool, calculating the mean of pre- and post-deployment estimates when available, and then calculating the mean for all loggers.

Each dataset was subjected to two quality control filters within the R package GeoLight: 'loessFilter' was used to remove event-time outliers by fitting local polynomial regressions and identifying residuals outside two interquartile ranges, and 'distanceFilter' was used to remove positions requiring unrealistic flight speeds (>1162.8 km d^{-1}). This maximum speed was chosen by multiplying the mean ground speed of small alcids flying offshore with a tailwind (68.4 km h^{-1}; Spear and Ainley, 1997) by the maximum duration of flight per day during the non-breeding period in our study (17 h; Appendix A). All datasets were cropped to the non-breeding period (1 July - 31 March) and equinox periods were removed and saved separately (approx. 5 weeks on the winter side and 2 weeks on the summer side of each equinox; see Appendix B). Positional data were generated from event-times using 'coord' in GeoLight, resulting in two positions per day where complete event-time data were available. As a final quality control step, these periods of positional data for each bird were visualized in ArcMap 10.3 (ESRI, Redlands, CA, USA) to record and remove positions which clearly stood out from the distribution pattern and were greater than 350 km from positions closest in date. Finally, start and end coordinates for the colony of origin were added to the datasets. The mean percent of positions removed per individual across all quality control steps was 7.7% (SD ± 5.6%) during non-equinox periods and 51.9% (SD ± 4.2%) during equinox periods.

Positional data were smoothed twice to improve accuracy (Phillips et al. 2004b), using a sliding boxcar window to calculate a 1:2:1 weighted mean for spherical coordinates. The smoothing function was not applied over periods with gaps in positional data of one day or longer, or over rapid movement periods (changes in latitude or longitude greater than 4° or 6°,

respectively). Smoothing was performed on equinox and non-equinox periods separately so that increased latitudinal error around the equinoxes did not affect position estimates outside those time periods.

2.3.4   Migratory behavior

Migratory tactics (combinations of the direction of migratory movements and the order in which they occurred) were determined by visual inspection of individual movement datasets using the animation tool in Google Earth Pro (Google Inc. 2017, version 7.3.0.3832). Since I was interested in identifying where most birds were distributed during different phases of the nonbreeding period, I used this tool to identify recurrent and distinct nonbreeding residency areas (spatially restricted areas used continuously for ≥20 d by multiple birds in any given year and/or across years). I then divided the coastline into regions bounding each of these residency areas, determined when individual birds first appeared in, and departed from, these regions, and recorded dates of 'regional occupancy' (≥7 days within a region) for each bird. Full datasets were used for this procedure since longitudes during the equinoxes proved informative even when latitudes were erroneous. This was possible because Cassin's auklets predominantly use coastal habitat, thus north-south movement was typically associated with simultaneous east-west movement, driven by the angle of the North American coastline.

To visualize regional occupancy over time, violin plots were generated for each region in each year by combining the sequences of dates for which each bird was resident in each region. Estimated dates for colony region departure and return, as well as lay dates, were plotted in the same manner but using a single date record for each bird. Since Cassin's auklets typically alternate

incubation duties daily and only depart and arrive from the colony between dusk and dawn (Ainley et al., 2011), I was able to identify incubation in the light data as regularly occurring 'dark' daytime periods and estimated lay dates as the first 'dark day' in these series.

All statistical analyses were run in R version 3.4.1 (R Core Team, 2017). Sex, year, and colony were assessed as potential drivers of migratory tactics using multinomial logistic regressions ('multinom', package 'nnet'). Each migratory tactic was used in turn as the reference level against which the relative likelihood of each additional tactic was determined for different levels of predictor variables (e.g. how much more likely a bird is to use the South tactic rather than the North tactic given that it is male rather than female). Overall significance of terms was determined using ANOVA using type III sum of squares (wherein the effect of each parameter is evaluated after accounting for the variance explained by all others; 'Anova', package 'car'), and post-hoc analyses were conducted using two-tailed Z-tests. The effects of sex, year, colony, and tactic on basic migratory phenology were also assessed, including (1) departure date from the colony region, (2) return date to the colony region, and (3) duration of residence in the colony region prior to lay date ('pre-lay duration'). The distributions of these three dependent variables most closely resembled Gamma distributions following inversion of the return dates, therefore I used Gamma family generalized linear models with inverse link functions ('glm', package 'stats'). Significance of terms was determined using ANOVA (type III sum of squares) and post-hoc analyses were performed using pairwise comparisons of estimated marginal means and the Tukey method for p-value adjustment ('emmeans', package 'emmeans').

2.3.5   Nonbreeding distributions

Utilization distribution (UD) kernels were generated for each bird using Geospatial Modelling Environment 0.7.4 (Beyer 2014, Spatial Ecology LLC), with a search radius of 170 km (based on the approximate error of twice-smoothed GLS logger positions; Phillips et al. 2004a) and a cell size of 50 km. These individual UDs were then summed using Cell Statistics in ArcMap to generate best-estimate population UDs while preventing bias due to variation in the number of positions per bird. This method was used to create UDs for all years combined and for each year separately (excluding equinox periods), and for five 'periods of interest': the post-breeding summer period (1 July - 7 Sept), two winter periods (26 Oct - 20 Dec, 21 Dec - 13 Feb), and each equinox period (8 Sept - 25 Oct, 14 Feb - 31 March). The winter period was split so changes in distribution and environmental conditions could be assessed across roughly equal intervals (non-equinox periods ~2 months, equinox periods ~1.5 months). For each UD probability surface, isopleths were generated at 5% intervals from 25-90% using Geospatial Modelling Environment.

All maps were produced using ArcMap 10.3 (projection WGS1984). Isopleths were plotted as UD contours in our yearly composite plots and represent the boundaries of the core (50% isopleth) and general use (90% isopleth) areas in each 'period of interest' plot. Core and general use isopleths are shown in dashed lines during equinox periods to signify that only longitudinal data are reliable.

2.3.6   Oceanographic context

Regional SST and chl *a* data were obtained using Marine Geospatial Ecology Tools 0.8a68 (Roberts et al., 2010) in ArcMap, which retrieves raster formatted data from the NASA Goddard Space Flight Center OceanColor Group (Greenbelt, MD, oceancolor.gsfc.nasa.gov) via the Physical Oceanography and Ocean Biology Processing Group Distributed Active Archive Centers (NASA: PO.DAAC, OB.DAAC). Global Level 3 SMI SST (°C) and chl *a* (mg m^{-3}) products, derived from Aqua MODIS satellite data, were downloaded at daily, 4 km resolution for the Northeast Pacific for each year. These data were then used to create custom composites for each period of interest by averaging cell data with the Cell Statistics tool in ArcGIS Spatial Analyst. I downloaded SST anomaly data (°C) as composite datasets for each period of interest from the NOAA Earth System Research Laboratory, Physical Sciences Division (Boulder, CO, esrl.noaa.gov/psd) at 0.25° global grid resolution, calculated against 1971-2000 mean SST (dataset: NOAA OI.v2 high-resolution blended analysis of daily SST). I then overlaid the corresponding 50% and 90% UD contours on each composite dataset to enable initial insight into habitat use and the environmental conditions experienced by these birds during the different phases of each nonbreeding period and among years.

Although satellite-derived SST and chl *a* data represent only sea surface conditions and are limited in their suitability as indicators of higher trophic-level productivity (e.g. Grémillet et al., 2008), Cassin's auklets are relatively shallow divers (commonly <15 m, >30 m rare) and feed close to primary productivity (Ainley et al., 2011) – thus these data are likely to be useful when assessing broad variations in Cassin's auklet nonbreeding distributions. Bathymetry, fronts, eddies, and terrestrial nutrient inputs (estuaries) are also likely to influence and indicate the distribution of

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phytoplankton and, by extension, the availability of zooplanktonic prey. However, fine-scale, individual-level assessments of these features as potential drivers of habitat selection were precluded by relatively low-resolution positional data which required a conservative, population-level approach to assessing potential patterns in habitat use.

2.4   RESULTS

I obtained 33 complete and two partial nonbreeding spatial datasets from individual Cassin's auklets with a mean colony-year recovery rate of 33%. Recovery rates following the 2014-15 nonbreeding season were notably lower than in subsequent years (Table 2.1), most likely due to winter mortality or skipped breeding associated with particularly unfavorable nonbreeding conditions in that year ('the Blob'). Although I cannot confirm whether logger deployment induced any nest desertion (burrows were not monitored after deployment to minimize disturbance), no birds left the colony region immediately after logger deployment or before a feasible fledging date. The total numbers of birds informing this study in each non-breeding period were 10 (2014-15), 16 (2015-16), and 9 (2016-17), 25 of which were female, 9 male, and 1 unknown (Table 2.1).

Table 2.1 Summary of GLS logger recovery data and deployment effort in each colony-year. While not all recoveries yielded usable data, datasets noted as 'incomplete' include data through 1 January at minimum. No males were tagged in 2014-15.

		No. of datasets		Sex		No.	Recovery
Year	Colony	Complete	Incomplete	F	M	Deployed	rate
2014-15	Triangle	4	0	4	0	30	13%
	Frederick	6	0	6	0	25	24%
2015-16	Triangle	15	1	12	3	30	53%
2016-17	Triangle	8	1	3	6	23	43%

2.4.1 Migratory behavior

During the nonbreeding period, individuals from Triangle Island and Frederick Island ranged in latitude from Baja California to southeast Alaska (Figure 2.1). While these birds primarily utilized nearshore habitats, offshore areas in the southeast Gulf of Alaska were heavily utilized during the post-breeding (summer) period and some Gulf crossings occurred. Individual birds used one of four distinct migratory tactics: 1) migration south of the colony ('South'), 2) migration north of the colony ('North'), 3) migration north followed by migration south ('North-South'), and 4) local migration within British Columbian waters ('Local'). The North-South migratory tactic was the most common, with 50-60% of birds using this tactic each year, followed by the South tactic, the Local tactic, and finally the North tactic used by only two birds (Table 2.2). Proportionally more males used the South tactic while proportionally more females used the North-South tactic, and no males used the Local tactic (Table 2.2).
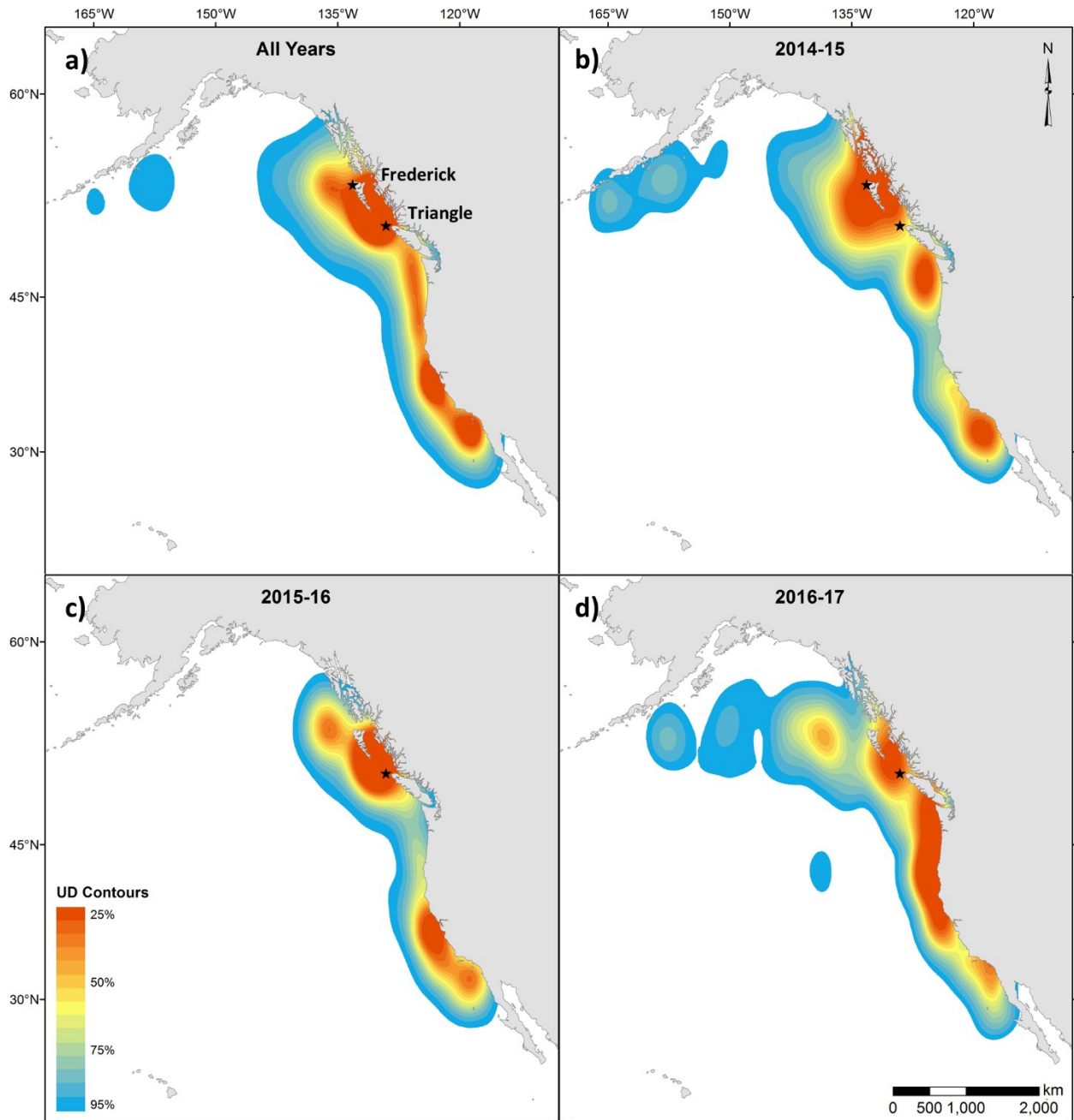
Figure 2.1 Nonbreeding utilization distributions (UDs) of all Cassin's auklets with complete tracking datasets by year. UD contours represent 5% isopleths calculated from the probability density surface and stars indicate the breeding origin of birds represented in each plot. Equinox periods are not represented due to erroneous latitude estimates.

Table 2.2 Proportion of tracked Cassin's auklets using the four migration strategies in each year, overall, and by sex[†]. The number of birds using the Alaska Peninsula within each strategy is indicated in superscript after the proportion.

	Sample	South	North	North-South	Local
2014-15	10	0.10	0.00	0.60 [(2)]	0.30
2015-16	16	0.38	0.06	0.50	0.06
2016-17	9	0.22	0.11 [(1)]	0.56 [(2)]	0.11
All Years	35	0.26	0.06 [(1)]	0.54 [(4)]	0.14
Female	25	0.16	0.04	0.60 [(4)]	0.20
Male	9	0.56	0.11 [(1)]	0.33	0.00

[†]One bird was of unknown sex.

Within this variation in migratory tactics, six recurrent and distinct nonbreeding residency areas were identified, primarily within nearshore waters, around which I defined the following occupancy regions: 1) British Columbia (49-54.3°N), 2) southeast Alaska and the eastern Gulf of Alaska ('east GoA', >54.3°N, <145°W), 3) south of the Alaska Peninsula and the western Gulf of Alaska ('west GoA', >145°W), 4) Washington and Oregon (49-42°N), 5) north and central California (42-35°N), and 6) southern California and Baja ('Southern California Bight', 35-27°N). I will refer to these regions throughout the remainder of this manuscript.

At a general, seasonal level, migrants (excluding the Local tactic) departed the British Columbia region in mid-summer (~July) and occupied the Alaskan and/or Washington/Oregon regions during the late summer and fall (Figure 2.2). Many birds moved south into the California regions in late fall (~Nov-Dec), remaining there through the winter, while others remained in the Washington/Oregon region. Some North-South migrants made stopovers in the British Columbia region on their way south in the late summer and fall. Most birds returned to the colony region in late winter (~Feb-March) and laid in spring (~April) (Figure 2.2). Within this overall pattern, individual birds varied considerably in arrival date, departure date, and duration of residency in each region, resulting in variable utilization intensity (spatiotemporal overlap) across each period

of regional occupancy (Figure 2.2). For additional figures representing the data in Figure 2.2, but emphasizing the number of individuals moving between specific regions, see Appendix C.

Residencies in northern regions ranged from 14-114 days (east GoA median = 88.5 d, west GoA median = 68 d), British Columbia stopovers from 10-70 days (median = 33 d), Washington/Oregon residencies from 12-163 days (median = 73 d), north/central California residencies from 7-102 days (median = 50 d), and Southern California Bight residencies from 25-116 days (median = 67 d). Pre-lay durations were similarly variable (range 28-161 d, median = 51 d), reflecting variable return dates and relatively synchronous laying, with all birds present in the colony region for a period in March prior to laying.
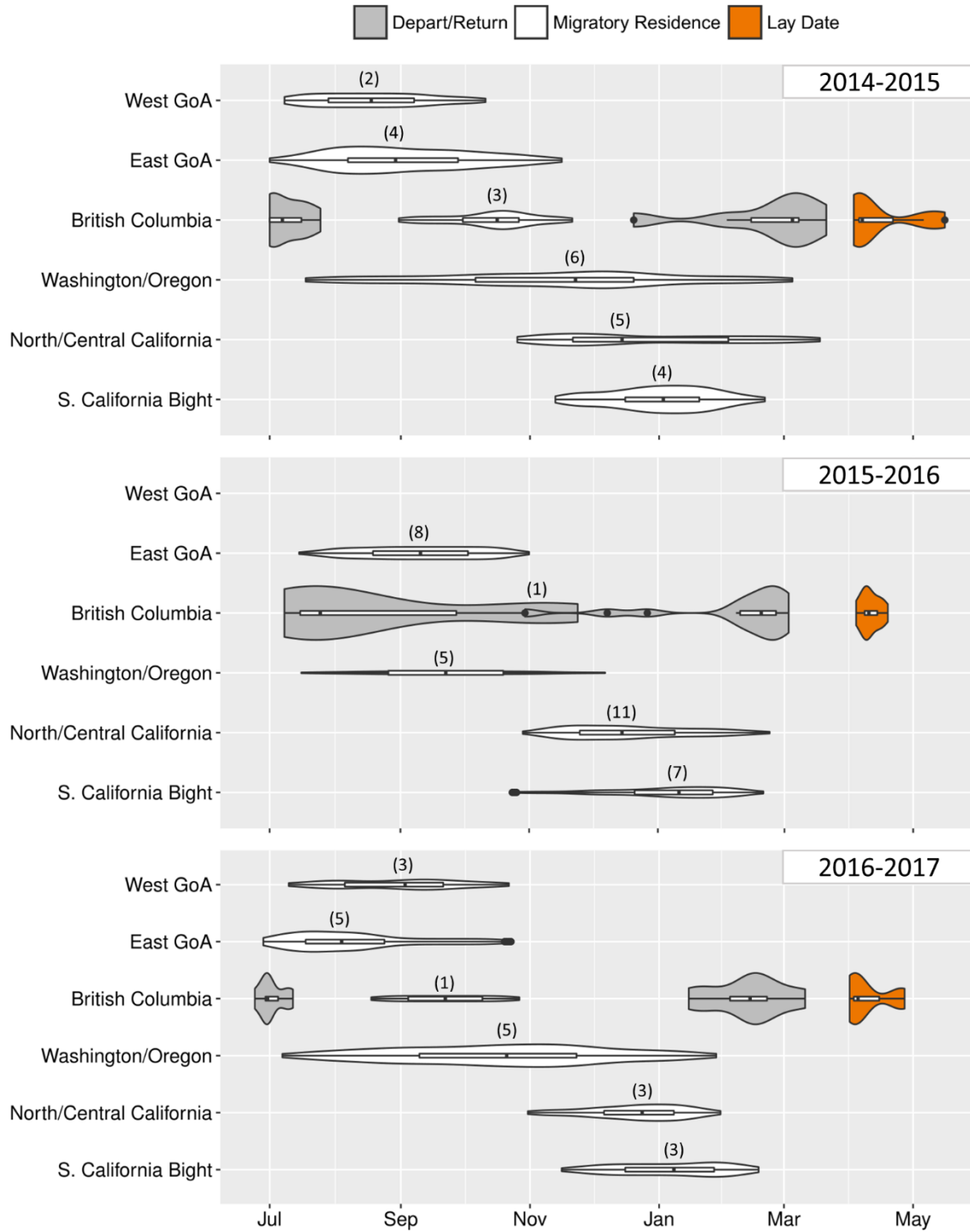
Figure 2.2 Regional occupancy of migratory Cassin's auklets in the six nonbreeding residency areas across each year (white), with distributions of departure and arrival dates from the colony region (grey) and lay dates (orange). Standard box-and-whisker plots are included within each plot and the number of birds utilizing each region is shown above the median. No local migrants or incomplete datasets are included (yearly plots top to bottom: n = 7, n = 14, n = 7).

2.4.2 Drivers of migratory behavior

Migratory tactic was influenced by sex (ANOVA, Likelihood-Ratio (LR) $X^2_{(3, n=35)}$ = 11.42, p = 0.01) but showed little evidence of variation by year (ANOVA, LR $X^2_{(6, n=35)}$ = 10.94, df = 6, p = 0.09), and none by colony (ANOVA, LR $X^2_{(3, n=35)}$ = 5.82, p = 0.12). The North tactic was not used as a reference level due to limited occurrence (n = 2). Sex effects were as follows: The log odds of having a Local tactic rather than a South tactic decreased by 57.04 if a bird was male rather than female (Z-test, Z = -1.80×10^5, p < 0.001) and the log odds of having a North-South tactic rather than a Local tactic increased by 22.86 if a bird was male rather than female (Z-test, Z = 5.10, p < 0.001). Therefore, females may be more likely than males to exhibit a Local tactic.

Migration departure dates were significantly affected by year (ANOVA, LR $X^2_{(2, n=30)}$ = 15.43, p < 0.001) but not by sex, colony, or tactic (ANOVA; sex: LR $X^2_{(1, n=30)}$ = 1.80, p = 0.18; colony: LR $X^2_{(1, n=30)}$ = 0.30, p = 0.59; tactic: LR $X^2_{(2, n=30)}$ = 2.50, p = 0.29). Post-hoc analyses revealed that departures were significantly earlier in 2016-17 than in 2015-16 (pairwise comparisons of estimated marginal means - Tukey's HSD, z-ratio = -3.53, p = 0.001), showed little evidence of being earlier in 2014-15 than 2015-16 (Tukey's HSD, z-ratios = 2.19, p = 0.07), and were not significantly different between 2014-15 and 2016-17 (Tukey's HSD, z-ratio = -0.73, p = 0.75). Mean departure dates (± SEM) were 10 July (± 4 d) in 2014-15, 23 August (± 13 d) in 2015-16, and 3 July (± 2 d) in 2016-17.

Return dates were significantly affected by colony and tactic (ANOVA; colony: LR $X^2_{(1, n=28)}$ = 9.69, p = 0.002; tactic: LR $X^2_{(2, n=28)}$ = 10.09, p = 0.006), but not sex or year (ANOVA; sex: LR $X^2_{(1, n=28)}$ = 0.19, p = 0.66; year: LR $X^2_{(2, n=28)}$ = 1.41, p = 0.49). Birds from Triangle Island (mean ± SEM = 9 February ± 6 d) returned to the colony region significantly earlier than those

from Frederick Island (mean ± SEM = 12 March ± 5 d) (Tukey's HSD, z-ratio = 2.25, p = 0.02).

North migrants (mean ± SEM = 7 December ± 39 d) had significantly earlier return dates than

North-South migrants (mean ± SEM = 19 February ± 5 d) (Tukey's HSD, z-ratio = -3.347, p =

0.002); however, there was no difference between South migrants (mean ± SEM = 12 February ±

10 d) and either of those tactics (Tukey's HSD; North and South: z-ratio = -1.87, p = 0.15; North-

South and South: z-ratio = 1.33, p = 0.38).

Pre-lay duration was significantly affected by migratory tactic (ANOVA, LR $X^2_{(2, \text{n}=28)}$ =

10.90, p = 0.004), but not by sex, year, or colony (ANOVA; sex: LR $X^2_{(1, \text{n}=28)}$ = 0.84, p = 0.36;

year: LR $X^2_{(2, \text{n}=28)}$ = 0.29, p = 0.86; colony: LR $X^2_{(1, \text{n}=28)}$ = 0.93, p = 0.33). Post-hoc analyses

indicated that North migrants (mean ± SEM = 120 ± 42 d) had significantly longer pre-lay

durations than North-South migrants (mean ± SEM = 52 ± 4 d) (Tukey's HSD, z-ratio = -3.70, p

= 0.001), but showed little evidence of being longer for North migrants than South migrants (mean

± SEM = 61 ± 11 d) (Tukey's HSD, z-ratio = -2.20, p = 0.07), and no evidence of a difference

between North-South and South migrants (Tukey's HSD, z-ratio = 1.36, p = 0.36).

2.4.3   Nonbreeding distributions

Cassin's auklets primarily utilized nearshore habitats, with core use areas (50% UD

contours) falling within the 200 m isobath. Across all years, the entire British Columbian and

United States coastline emerged as a core use area for this species (Figure 2.1a), reflecting large-

scale repeatability in nonbreeding distribution. Within this broad core use area, three distinct areas

received particularly high use (25% UD contours) over time: the central and northern coast of

British Columbia, the central California coast (Gulf of the Farallones and Monterey Bay), and the

Southern California Bight (Figure 2.1a). These were regions where core use areas occurred every year, although in 2014-15 the British Columbia core use area was broader, extending north into southeast Alaska and further offshore (Figure 2.1b). Additional, distinct core use areas occurred in the Washington/Oregon region (2015-15; Figure 2.1b) and offshore in the east GoA (2015-16, 2016-17; Figure 2.1c-d), while a continuous coastal core use area, spanning the Washington/Oregon and north/central California regions, occurred in 2016-17 (Figure 2.1d).

2.4.4   Oceanographic context

Plots of mean SST during each period of interest overlaid with 50% and 90% UD contours did not suggest any clear links between this variable and differences in yearly distribution patterns (Figure 2.3). While it may appear that the west GoA region was used only during elevated local SST conditions, sample sizes in this region are too small to infer a correlation. Conversely, birds showed greater utilization of the Washington/Oregon region in summer and fall when SST was lowest there (2015 and 2016, anomalously low SST). Birds migrating south to the north/central California region and the Southern California Bight appeared to track the southerly retreat of ~19°C SST in all years (Fig. 3, green). During the summer, SST within the British Columbia core use area was generally 14-19°C (Figure 2.3, light blue to green). In the winter, as the British Columbia core use area cooled to ~9°C and many birds moved south, the new southern core use area (or the southern extent of this area in 2016-17) occurred over roughly the same SST range observed in British Columbia during the summer. Still, many birds remained in more northern, cooler SST regions throughout the nonbreeding period. Cassin's auklet distributions also did not suggest avoidance of, or attraction to, regions with anomalous SST conditions (Figure 2.4).

My proxy for primary productivity (chl *a*) showed persistent elevation in nearshore waters and was highest in both nearshore and offshore regions during the summer and fall, as well as during the 2014-15 spring equinox period. Winter chl *a* was also highest in that year. Beyond predominantly nearshore distributions and the restriction of northern, offshore movements to productive summer months, variation in Cassin's auklet distributions did not suggest direct links with primary productivity (Figure 2.5). For example, chl *a* was not higher in the Gulf of Alaska or Washington/Oregon regions in years when they were utilized relative to years when they were not, nor was there relatively lower chl *a* in alternative habitats. High utilization intensity in the Southern California Bight was also unaffected by a marked absence of the typical winter increase in chl *a* in 2014-15, which left the region at ~4 mg m^{-3} rather than 12 mg m^{-3} or higher (Figure 2.5; for more years see the NASA Ocean Color Group database at oceancolor.gsfc.nasa.gov).
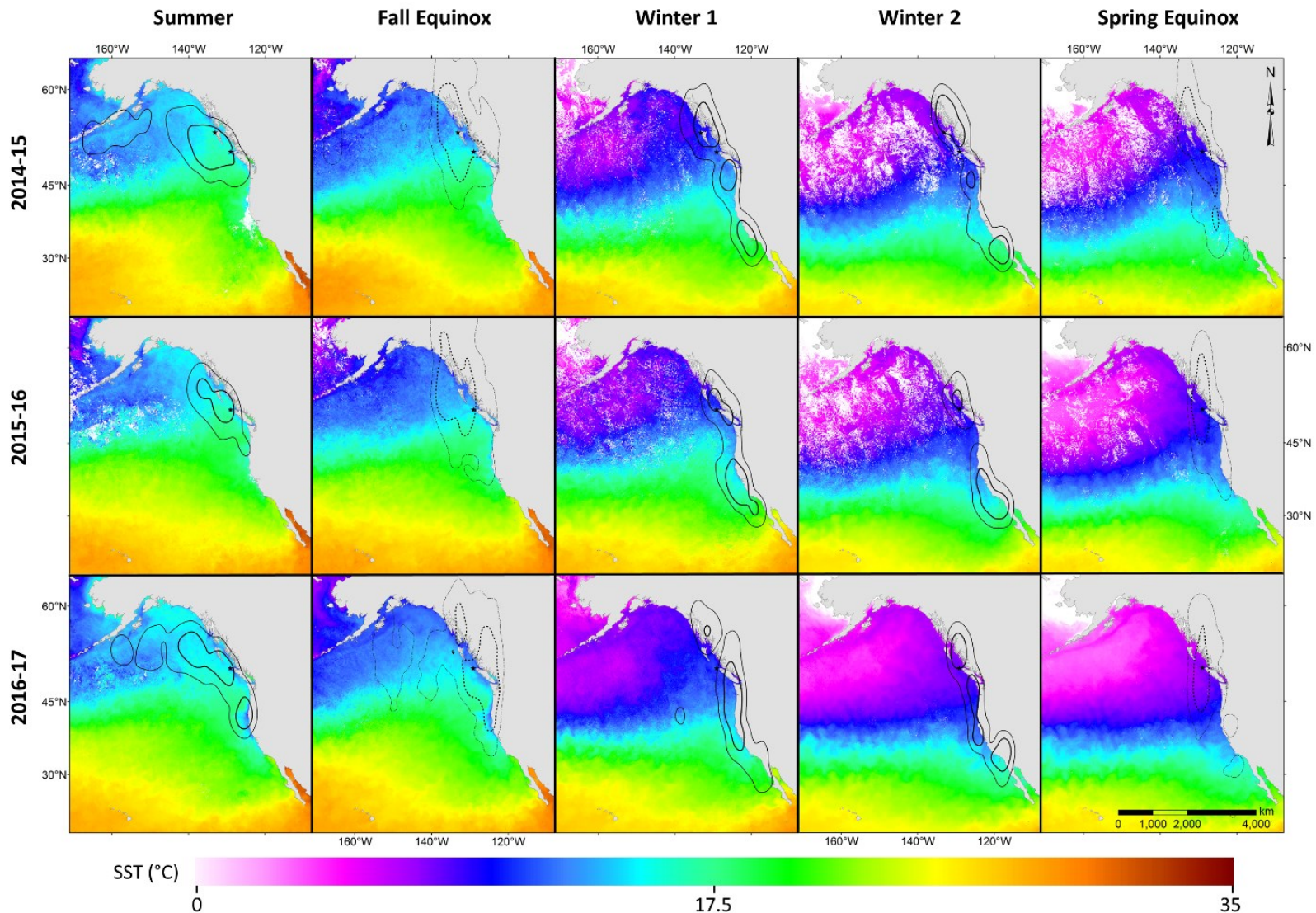
Figure 2.3 Mean sea surface temperature (SST) during each period of interest (columns) in each year (rows), overlaid with 90% (regular) and 50% (bold) utilization distribution (UD) contours derived from all birds tracked during that period. During equinox periods, UD contours are represented by dashed lines to indicate unreliable latitudes.
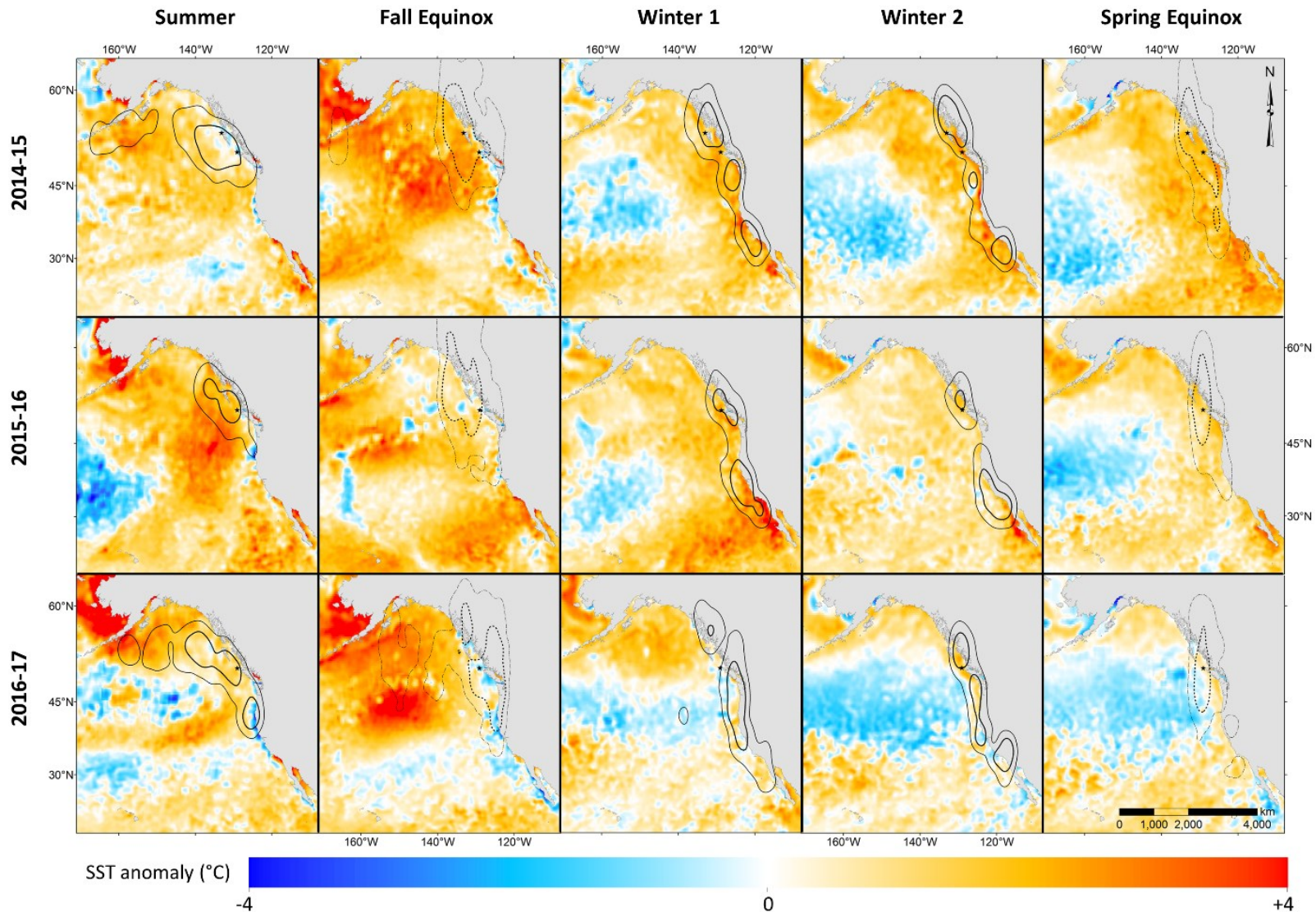
Figure 2.4 Mean sea surface temperature (SST) anomaly during each period of interest (columns) in each year (rows), overlaid with 90% (regular) and 50% (bold) utilization distribution (UD) contours derived from all birds tracked during that period. During equinox periods, UD contours are represented by dashed lines to indicate unreliable latitudes.

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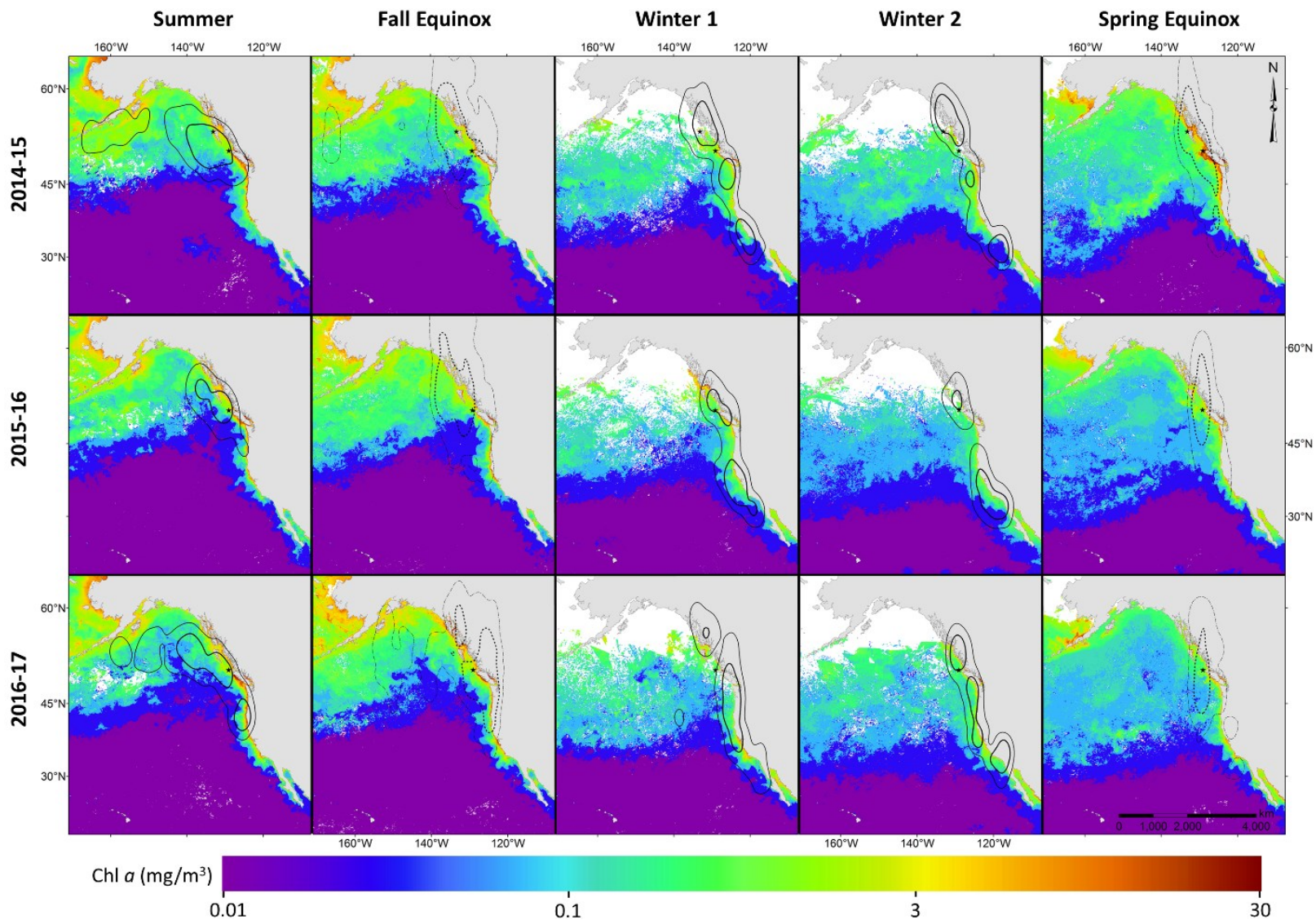
Figure 2.5 Mean chlorophyll *a* (chl *a*) concentration during each period of interest (columns) in each year (rows), overlaid with 90% (regular) and 50% (bold) utilization distribution (UD) contours derived from all birds tracked during that period. During equinox periods, UD contours are represented by dashed lines to indicate unreliable latitudes.

2.5 DISCUSSION

2.5.1 Migratory behavior

I determined that Cassin's auklets from two large breeding colonies in British Columbia, which supports the bulk of the global population, employed four broad migratory tactics. A slight majority (54%) moved north into Alaskan waters following breeding, and then moved south of the colony within United States coastal waters in the late fall and winter. The second most common tactic (26%) involved only southward migration. Between the two tactics, 80% of tracked Cassin's auklets utilized habitats along the United States coast during the fall and winter. Less common tactics included movement into Alaskan waters after breeding, followed by late-fall and winter residency within the colony region (6%), or local migration (14%) where individuals remained in the colony region throughout the year. The existence of this local tactic indicates that Cassin's auklets are partial migrants (Chapman et al., 2011). Similarly large variations in migratory tactic have also been documented in other species of Alcidae (Fayet et al., 2016; Gaston et al., 2017; Lorentsen and May, 2012), including partial migration in Atlantic puffins (*Fratercula arctica*).

During this study, the migratory tactic employed by individual Cassin's auklets was predicted by sex, but not by year or colony of origin. Male birds were significantly more likely than female birds to employ the South tactic or the North-South tactic rather than the Local tactic, indicating that female birds were significantly more likely to be local migrants. Sexual segregation by habitat is common in birds; however, it is usually females that migrate furthest (Catry et al., 2005). While these differences are often attributed to social dominance or size-based characteristics, including competitive exclusion of females by larger males or inherent differences

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in foraging niche (Phillips et al. 2004b, Catry et al. 2005), sexual size dimorphism is only slight in Cassin's auklets (Knechtel, 1998) and unlikely to play a role. However, sex-based differences in foraging niche are not always driven by size and other factors, such as energy or nutrient requirements, could be at play (Lewis et al., 2002). In addition, female Cassin's auklets seem to experience greater reproductive costs than males, showing significantly increased mortality during poor oceanographic conditions (Morrison et al., 2011). Thus, more females than males may forgo long-distance migration due to physiological constraints (Chapman et al., 2011), particularly during anomalous oceanographic conditions such as the warm-water anomalies which prevailed during this study.

All four migratory tactics were utilized within the context generally repeatable phenology, with movements north into Alaskan waters in late summer and fall, south into United States and/or Baja California waters in fall and winter, and back north to the colony region in late winter. There was considerable individual variation within these tactics with respect to the specific locations used and the timing and duration of their use, resulting in different combinations of nonbreeding residency areas and variable spatiotemporal overlap between individuals. Notably, the timing of major migratory decisions - such as dates of departure and return to the colony region, and the duration of pre-laying residency in the colony region - varied with one or more of the factors migratory tactic, sex, year, and colony.

Departures from the colony region occurred in late June or July after breeding was completed. While independent of migratory tactic, sex, and colony, departures were significantly later in 2015 than 2016, and may have been intermediate in 2014 (not significant). At the individual-level, I would expect migratory departure to be correlated with lay date – driven by the same environmental and/or physiologic factors which affect timing of laying – since incubation

and nestling growth periods are relatively fixed in this species (Ainley et al., 2011). However, this interpretive framework cannot be applied to differences in departure dates among years in this study. Yearly, initial lay date data are only available at the colony-level and the relationship between colony-level lay dates and the cessation of reproductive responsibilities is frequently complicated by egg loss, relaying, and/or reproductive failure. In addition, late laying individuals are likely underrepresented in our tracking dataset. Due to these complications, examination of the potential drivers of annual variation in departure dates remains an area for future research.

Returns to the colony region, by contrast, were significantly affected by migratory tactic and colony, but not by sex or year. North migrants were by far the earliest returnees since they were only absent from the colony region during the late summer and fall; however, the only significant difference was with North-South migrants, likely due to small sample sizes and high variance among South migrants. Cassin's auklets also returned earlier to the more southerly colony (Triangle Island) than the more northerly colony (Frederick Island), likely due to seasonally adjusted breeding phenology. Return dates were negatively correlated with pre-lay duration (Pearson's correlation: $r_{(26)} = -0.94$, t = -14.04, $p < 0.001$), reflecting more synchronous lay dates than return dates within each colony-year. Because of this, pre-lay duration was also significantly affected by migratory tactic, such that North migrants had longer pre-lay durations than North-South migrants. All pre-laying residencies were longer than necessary (median = 50 d, range = 28-131 d) to avoid migration-breeding overlap. Egg production in Cassin's auklets takes just 11-13 days, with 8 days for yolk formation and a 3-5 day lag before laying (Astheimer, 1986; Roudybush et al., 1979). Extended pre-laying residencies may allow birds to regain energy stores prior to breeding, reduce potential carryover effects from migration (Crossin et al., 2010), and fine-tune lay dates based on local environmental conditions, a decision affecting nestling survival and

fledging mass (Hipfner, 2008; Hipfner et al., 2010). Pre-laying residency could also be important for burrow selection and maintenance, territory holding, and/or pair formation.

2.5.2 Nonbreeding distributions

During the nonbreeding period, Cassin's auklets from the large colonies at Triangle Island and Frederick Island ranged in latitude from Baja California to southeast Alaska (Figure 2.1). Auklets mainly utilized nearshore habitats within the 200 m isobath (50% UD contours), although offshore areas in the eastern Gulf of Alaska were also used. Across all years, the entire west coast of British Columbia and the continental United States emerged as a core use area for this species (Figure 2.1a), with three distinct areas receiving particularly high use (25% UD contours): British Columbia's central and northern coasts, the central California coast, and the Southern California Bight (Figure 2.1a).

Core use areas were spatially restricted within each of the six recurrent residency areas identified in this study, resulting in a patchy distribution, except during the winter of 2016-17 when the Washington/Oregon and north/central California core use areas merged (Figure 2.1). Of note, these six regions were found to align remarkably well with Marine Ecoregions of the World ('MEOWs'; Spalding et al. 2007): ecologically defined near-coastal regions within the 200 m isobath. Our designations differed only in that I grouped southeast Alaskan habitat with the east GoA region (rather than with British Columbia), considered east and west GoA separately, and included offshore habitat in northern regions. This suggests that regions targeted by Cassin's auklets outside the breeding season are ecologically distinct. Individual variation in migratory

behavior is thus likely to result in unique environmental experiences which, in turn, could generate additional variation in carryover effects among individuals.

The fact that core use areas occurred consistently in space and time (Figure 2.3, columns) suggests that meso- to large-scale distributions of prey may be reasonably predictable to these birds (Block et al., 2011; Weimerskirch, 2007). Post-breeding movements by 60% of migrants into the east GoA region, offshore and to the northwest of the British Columbia core use area (Figure 2.3, columns 1-2), coincided with the summer transition to upwelling favorable winds over the southern Gulf of Alaska (Weingartner, 2005), and a second peak in local zooplankton abundance (NOAA National Marine Fisheries Service, 2017). Core use areas for these birds also coincided with Bowie Seamount Marine Protected Area and regions influenced by Haida eddies (Figure 2.6; Canessa et al., 2003; Whitney and Robert, 2002). Cassin's auklets may target this region to replenish their energy stores after breeding; however, since productivity and occupancy are also high in British Columbia at that time, intra-specific competition and individual quality may also be involved.
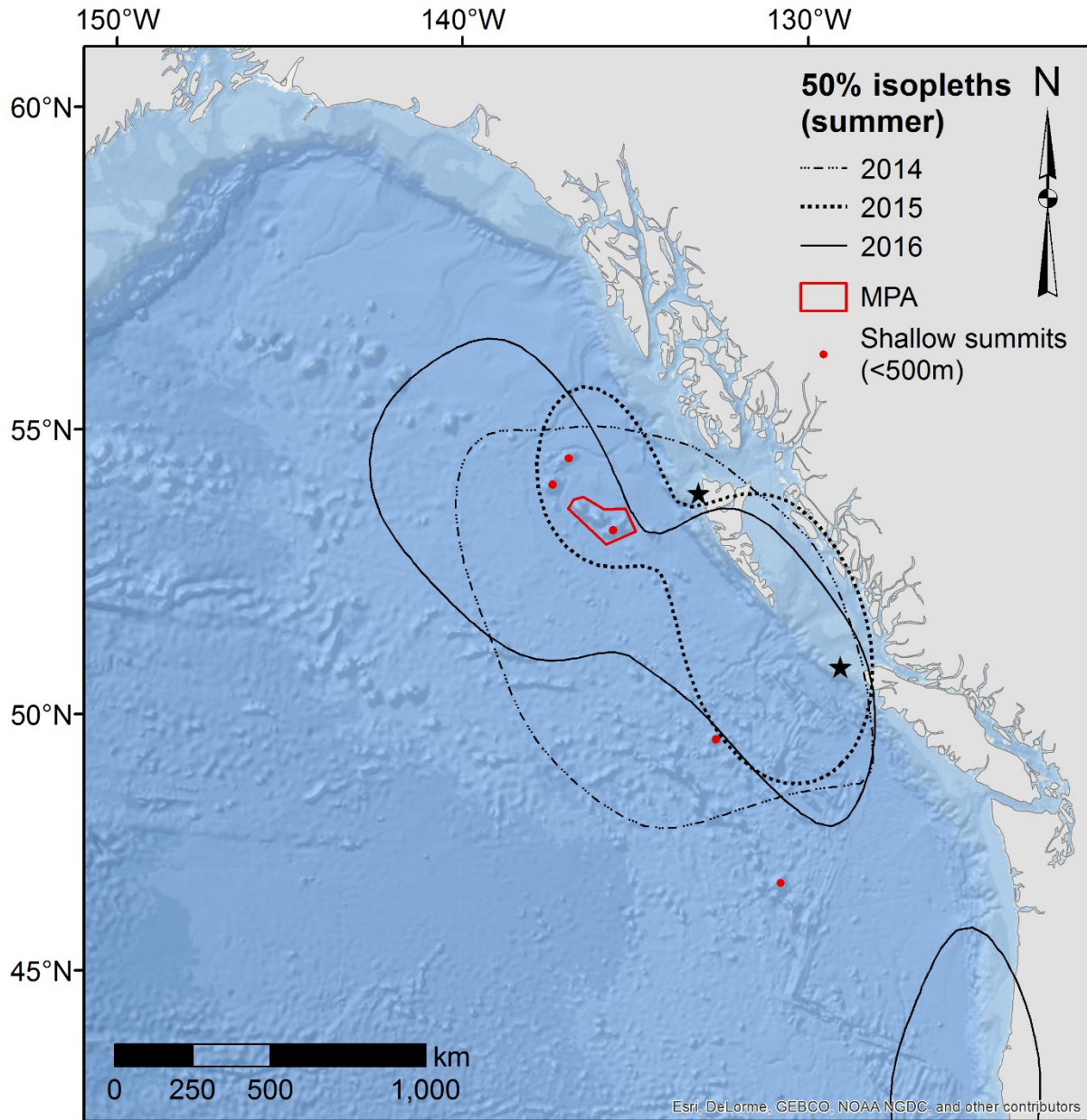
Figure 2.6 Post-breeding, summer core use areas (50% utilization distribution contours) for Cassin's auklets in relation to the Bowie Seamount Marine Protected Area (MPA). All North Pacific seamount summits within 500 m of the surface are indicated in red.

North and North-South migrants departed the east GoA region in late summer and fall, coincident with the return of downwelling-favorable winds (Weingartner, 2005). During fall and winter, birds instead inhabited nearshore waters in British Columbia or migrated south within the

warmer California Current System (CCS) (Figure 2.3, columns 3-4). During spring and summer, Ekman transport and offshore winds generate significant upwelling and productivity in the CCS while upwelling-suppressing countercurrents develop during late fall and winter (Bograd et al., 2010; Hunt, 1995). Most birds moved into this system while productivity was waning; however, winter productivity is not negligible and reduced carrying capacity in the colony region and/or individual differences in dietary niche may drive southern migration at this time (Alerstam et al., 2003; Chapman et al., 2011). While thermal tolerance of birds or their prey can also drive migration, it is unclear whether southward tracking of ~19°C SST was causal or correlational since many birds remained in colder regions with no apparent detriment.

Moving further south, occupancy of the Southern California Bight occurred every year (Figure 2.2) and peaked slightly later than in north/central California (Figure 2.3, columns 3-4). Due to a persistent central eddy which is best developed in winter (Dong et al., 2009; Mantyla et al., 2008), the Bight exhibits conditions favorable for prey aggregation. Interestingly, plankton abundance is at or near its lowest when most birds occupy the region in December and January (Mantyla et al., 2008; NOAA National Marine Fisheries Service, 2017); but larval fish abundance spikes at that time and fish egg abundance is high (NOAA National Marine Fisheries Service, 2017). Cassin's auklets may be exploiting this resource since a similar pattern of prey availability occurs in central California (~1 month earlier with lower peak abundances; NOAA National Marine Fisheries Service 2017), where increased consumption of fish larvae (5.9% → 8.8% by mass) and eggs (0% → 17.5% by mass) has been recorded between the summer and fall/winter periods (Ainley et al., 1996).

While directed migration to reasonably predictable habitats can save energy, behavioral flexibility may be important for CCS migrants since the system exhibits particularly strong intra-

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and inter-seasonal variations in productivity due to changes in upwelling, the El Niño Southern Oscillation, and decadal-scale climate forcing (Bograd et al., 2010). Our data suggest that Cassin's auklet distributions may be refined by both resource predictability (memory) and behavioral responses to local conditions. The Washington/Oregon region and the Gulf of the Farallones, featuring the only major, nutrient-providing estuaries in the CCS (Bograd et al., 2010), were each targeted in two years, and the Southern California Bight was used consistently despite anomalously low productivity in 2014-2015 – suggesting memory effects and potentially fixed behavior for some individuals. Behavioral flexibility was also suggested since core use areas in the CCS north of Point Conception and habitat use in the Gulf of Alaska clearly varied across years. However, it is important to note that such apparent distributional 'responses' could be generated by mortality of tracked birds using seemingly unoccupied regions.

2.5.3   Oceanographic context

Warm water phenomena (the Blob, El Niño, positive PDO phase) had profound ecosystem effects during this study, altering the physiochemical structure of the water column and reducing primary production and biomass available to upper trophic levels in the CCS (Gómez-Ocampo et al., 2017; Whitney, 2015). These changes undoubtedly affected the predictability and suitability of nonbreeding habitat for Cassin's auklets. During the alongshore phase of the Blob (fall 2014 - spring 2015), the biomass of relatively lipid-poor 'southern' copepod species was anomalously high while that of 'northern' species was anomalously low (Leising et al., 2015; Peterson et al., 2016b), effecting prey quality in addition to abundance. Euphausiid abundance was anomalously

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low in the central and southern CCS; however, juvenile rockfish abundance was anomalously high throughout the system (Leising et al., 2015).

Despite anomalous conditions during this study, I found little evidence that Cassin's auklets utilized or avoided habitats with specific SSTs or strong SST anomalies (Figure 2.3, Figure 2.4), or sought out areas with particularly elevated chl *a* within the coastal region (Figure 2.5). Analyses of coastal transect surveys off southern British Columbia from 1996-2004 also found that Cassin's auklet distributions were not associated with SST anomalies (O'Hara et al., 2006). This may be further evidence of relatively fixed individual migratory tactics; however, the validity of the assumptions that these parameters indicate relative prey availability (Grémillet et al., 2008) and, if they do, that regions of particularly high prey density represent absolutely better foraging habitat for Cassin's auklets (Lovvorn, 2010), are in question. Competitive or energetic effects could also be involved. For example, resting metabolic rate is much higher for Cassin's auklets on water than in air due to thermoregulatory costs, with a linear increase in resting metabolic rate observed with water temperatures below 21°C (Richman and Lovvorn, 2011). In some marine birds, resting on water can be the greatest contributor to daily energy expenditure (Lovvorn et al., 2009). This suggests that the apparent tracking of ~19°C SST by southern migrants could be driven by individual energetic state, with individuals in poorer condition choosing to migrate within warmer waters to reduce energetic costs, even if such movements coincided with reduced prey availability. Whether Cassin's auklets can adjust their distributions in response to environmental cues, particularly in the context of potential tradeoffs between prey quality, availability, and energetic costs, is relevant to conservation in an increasingly variable ocean and should be the subject of future studies.

A Cassin's auklet die-off of unprecedented scale occurred along the continental United States during the 2014-15 nonbreeding period, with deposition rates peaking in December and January in the Washington/Oregon region (>100 times baseline rates; Jones et al., 2018). Starvation due to shortages of lipid-rich planktonic prey and spatial compression into nearshore habitats is the prevailing theory, with an emphasis on increased likelihood of deposition (Jones et al., 2018). My data indicate that the Washington/Oregon region was a core use area for auklets from British Columbia during the peak of the mortality event, supporting the hypothesis of Jones et al. that affected birds were predominantly of northern origin. Northern auklets may also have been affected in central California since our data indicate a core use area there when peak anomalous deposition rates were recorded in November and December; however, the majority of these mortalities were hatch year birds (Jones et al., 2018).

The distributional data for Cassin's auklets used in Jones et al. (2018) was derived from at-sea surveys which were limited to southern California during peak deposition periods, restricting their habitat compression analyses to this region (south of 39.4°N). I cannot confirm habitat compression in the Washington/Oregon region immediately preceding or during the mortality event as Jones et al. suggest – tracked birds showed core use areas in this region during the winters of 2014 and 2016 but the former distribution does not appear notably more compressed toward nearshore habitats than the latter (Fig. 3, column 3). However, distributional data from my study do provide some support for habitat compression on a broader spatial scale since the total winter core use area utilized by southern migrants (Cylindrical Equal Area projection) was smallest in 2014-15 (414,181 km^2) and increased as oceanographic conditions improved through 2015-16 (550,262 km^2) and 2016-17 (678,234 km^2). I reiterate that that these data only indicate the distributions of surviving, adult birds.

2.6 CONCLUSION

I determined that nonbreeding Cassin's auklets from British Columbia employ one of four migratory tactics, utilizing northern, southern, and/or locally restricted habitats. Within these tactics there is additional variation in migratory phenology and regional use which likely generates differences in nonbreeding experience and potential carryover effects within these populations. Some of this variability is attributable to sex, year, and colony; however, many other factors may be involved. Despite anomalous and variable oceanographic conditions, birds did not appear to target or avoid regions based on SST or chl *a* at the population level. Future studies should pursue nonbreeding habitat modelling to help predict population-level responses to increasing oceanographic variability; however, increased tracking effort will be required to generate within-tactic sample sizes large enough to support such analyses. In addition, I recommend recording SST and pressure along with light intensity during future nonbreeding tracking studies. This would enable the use of robust, individual-level movement models and assessments of both finer-scale habitat associations and behaviors. Studies to determine the repeatability of migratory behaviors, and the ability (or inability) of individuals to respond to environmental conditions, will also be crucial for predicting population resilience to oceanographic change.

CHAPTER 3: CARRYOVER EFFECTS OF PRE-BREEDING CORTICOSTERONE AND DIET ON EGG SIZE

3.1 ABSTRACT

The measurement of corticosterone levels in feathers (fCort) is gaining recognition as an effective means for describing links between stages of the annual cycle in birds. Many seabirds are especially good models for exploring these links, or carryover effects, due to their migratory behavior and reproductive investment in a single-egg clutch. Here, I measure fCort in Cassin's auklet (*Ptychoramphus aleuticus*) breast feathers at two colonies in British Columbia during 2011, a year of favorable oceanographic conditions, and examine its relationship with egg size. These feathers are grown at sea during the late winter period, 1-2 months prior to egg laying. Assuming that fCort provides some measure of nutritional stress and hypothalamic-pituitary-adrenal axis activity during feather growth, I predicted that fCort would be positively correlated with egg size via increased support for foraging activity during the nutritionally demanding molt stage. I also analyzed the δ^{13}C and δ^{15}N stable isotope content of breast feathers, measures commonly used to characterize seabird diet composition. Contrary to prediction, neither fCort nor stable isotope ratios were good predictors of egg size. Our results appear to conflict with two previous studies on alcids in which fCort and stable isotopes showed clear links with egg size; however, both studies were conducted in years when oceanographic and foraging conditions were poor. Under these conditions, upregulation of corticosterone may be needed to mediate the energetic tradeoffs between self-maintenance and reproduction, supporting increased foraging effort and thus increasing both the likelihood of reproduction and large egg size. However, when foraging

conditions are favorable, I suggest that such tradeoffs and associated physiological constraints are minimized and regulation of egg size may be effectively independent of circulating corticosterone levels and diet type.

3.2 INTRODUCTION

Many contributors to lifetime fitness and population level processes, including variation in breeding propensity, reproductive success, and survivorship, can be influenced by carryover effects: features of an organism's current performance that are explained by its past experience (O'Connor et al., 2014). These effects can act across a variety of temporal and spatial scales and have been documented in many marine species, including seabirds (e.g. Harrison et al., 2011). The most commonly identified carryover effects on reproduction stem from non-breeding or pre-breeding body condition (Crossin et al., 2013b, 2012a; Harrison et al., 2011; Salton et al., 2015), winter habitat quality (Norris et al., 2004; Sedinger et al., 2011), diet (Inger et al., 2010; Sorensen et al., 2009), and physiologic state (Crossin et al., 2013b, 2012a, 2010; Kouwenberg et al., 2013). Each of these factors has been implicated in effects on breeding, including the decision to breed, reproductive phenology, and success, as well as levels of investment such as egg size and chick provisioning.

Since many carryover effects from the non-breeding period appear to be driven by environmental experience and nutritional stressors, physiologic state and diet are likely to be important indicators of these effects. Glucocorticoid hormones, including corticosterone (Cort), act as metabolic regulators of physiological and behavioral responses to unpredictable stressors (Hau et al., 2010; Wingfield et al., 1998), helping to regain positive energy balance in situations

of allostatic overload (McEwen and Wingfield, 2003). These hormones are thus important components of pre-breeding physiologic state and have been identified as key mediators of many carryover effects.

For seabirds, the measurement of Cort in feathers (fCort) has been a particularly useful way to examine longer term, cumulative Cort dynamics during the non-breeding period when most birds molt and grow new feathers (Bortolotti et al., 2009, 2008; Fairhurst et al., 2013). Similarly, feathers can be used to obtain integrated information on diet during the non-breeding period via stable isotope composition (Inger and Bearhop, 2008); 15-nitrogen is enriched in consumer tissues as trophic level increases (increasing δ^{15}N) and 13-carbon exhibits an enrichment gradient from offshore to inshore prey sources and from pelagic to benthic prey sources (increasing δ^{13}C) (Bond and Jones, 2009; Hobson et al., 1994; Kelly, 2000). Increases in fCort can be regarded as a direct physiological indicator of increased nutritional stress during periods of low food availability (Kitaysky et al., 2007; Will et al., 2015, 2014; but see opposite relationship in Patterson et al., 2015), and have also been linked to enhanced foraging effort, with positive effects on foraging success and reproductive investment (Crossin et al., 2012c; Kouwenberg et al., 2013). Feather Cort, δ^{15}N, and δ^{13}C each provide unique information about non-breeding foraging experience and are useful tools for assessing the potential mechanisms governing carryover effects, particularly when examined together.

Seabirds share a suite of life-history traits across species, including high survival rates and low reproductive rates (Lack, 1968). Recent studies of these species have linked elevated pre-breeding fCort and diet quality to key fitness traits such as earlier laying and larger egg sizes (Kouwenberg et al., 2013; Sorensen et al., 2009), and have also demonstrated that elevated fCort can be associated with increases in foraging activity required to support successful reproduction

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(Angelier et al., 2008; Crossin et al., 2013a, 2012c). If Cort is elevated to stress-induced levels, however, anti-gonadotropic effects can ensue (Salvante and Williams, 2003; Sapolsky et al., 2000), possibly by altering protein and lipid metabolism to favor self-maintenance over reproduction (Wingfield et al., 1998) and by suppressing the release of luteinizing hormone (LH) and subsequent estrogenic pathways (Brann and Mahesh, 1991; Etches et al., 1984; Goutte et al., 2010). Elevated fCort has thus been linked to negative reproductive effects, including later arrival at the breeding colony, poorer body condition at arrival, and reduced reproductive success (Harms et al., 2015), as well as breeding deferral (Crossin et al., 2013a; Hansen et al., 2016). Although such effects are detrimental to current reproduction, they may benefit lifetime fitness by helping balance reproductive demands with maternal quality and nutritional state (similar to Love and Williams, 2008).

Here, I test the hypothesis that the pre-breeding physiologic state and diet of a sentinel seabird, the Cassin's auklet (*Ptychoramphus aleuticus*), as represented by feather Cort and stable isotope content, will carry over to affect breeding investment and performance in the form of egg size. Our study took place in a year with favorable oceanographic conditions, thus I did not anticipate any chronic elevations in Cort sufficient to inhibit reproduction. Using the single-egg clutch of the Cassin's auklet as a model, I predicted (1) that higher fCort levels and (2) lower $\delta^{15}N$ would be linked to larger egg size, due to increased physiological support for foraging activities during the nutritionally demanding molt stage and preferred, lower trophic level diet, respectively. Cassin's auklet mouth parts are adapted for zooplanktivory (Bédard, 1969) and, though non-breeding diet is not well understood, known prey items include copepods and euphausiids, as well as larval fish, crab, and squid (Ainley et al., 2011). I assume a lower trophic level preference partly because nestling growth is higher with lower trophic level, higher energy density diets (Hedd et

al., 2002; Vermeer and Cullen, 1982). Shifts in adult diet from higher to lower trophic levels have also been documented between the pre- and post-laying period when zooplankton biomass is increasing off the southern coast of British Columbia (Hipfner et al., 2014; Mackas, 1992), suggesting that adult auklets may preferentially select energy dense, lower trophic level prey when it is available. In addition, I predicted (3) that higher $\delta^{13}C$ would be linked to larger egg size, reflecting easily accessed nearshore prey rather than potentially more energetically demanding offshore prey types. Potential effects of colony of origin were also considered.

3.3   METHODS

All research protocols were approved by Simon Fraser University Animal Care Services (974B-94), and carried out under additional permits from Environment Canada (banding permit 10667F, and Migratory Birds scientific permit BC-11-0016).

3.3.1   Field methods

Cassin's auklets nest in burrows on offshore islands along the west coast of North America (Ainley et al., 2011), and typically lay their single egg from late March to early May at British Columbian colonies (Hipfner et al., 2010). Breast feathers were collected from breeding birds at two colonies, Triangle Island (n = 14, 50º 52' N, 129º 05' W) and Rankine Island (n = 16, 52º 15' N, 131º 03' W) (Figure *1.1*), in April of 2011. Cassin's auklets undergo body molt to replace these feathers during the late wintering, spring migration, and pre-laying residency periods, with peak replacement occurring in February and March (Ainley et al., 2011; Pyle, 2009) while most

birds are arriving back at the colony (see Chapter 2:), thus our samples represent an integrated measure of circulating Cort levels and diet at that time. Adult auklets were removed from their incubation chambers and up to eight feathers were sampled by putting pressure at the base of the calamus and giving a quick tug in the natural direction of the feather. Samples were stored in envelopes in a dark dry place until processing and analysis. Egg length and breadth, adult morphometrics, and sex based on bill depth (Knechtel, 1998) were also recorded (measurements within 0.05mm and 0.5g). Only female birds were used in this study.

3.3.2   Hormone analysis

Feather corticosterone was determined using an established radioimmunoassay protocol (see Crossin et al., 2013a). Prior to analysis, each sample was prepared according to a protocol adapted from Bortolotti et al. (2008) and modified by Lattin et al. (2011). In short, the calamus was removed from each feather and the samples were standardized by mass to 0.0090 ± 0.0002g (Mettler Toledo, New Classic MF, model ML204/03, $d = 0.1$ mg) to minimize any potential mass bias. The total length of feathers in each sample was then recorded for use in standardizing the fCort measurement (pg/mm). Final samples included material from 4-7 feathers. These samples were placed into vials, minced, and heat treated at 74°C for at least 30 min, as per United States of America import regulations, before being sent to Tufts University (Medford, MA) for fCort extraction and analysis.

The minced feather samples were mixed with 7 mL of methanol, placed in a sonicating bath for 30 min, and incubated overnight in a 50°C shaking water bath. A vacuum filtration system was used to separate out feather fragments and the methanol extracts were dried under nitrogen

gas in a 50˚C water bath. Samples were reconstituted with Tris-HCl buffer (0.05 M, pH 8.0) and run in duplicate through a standard radioimmunoassay (Wingfield et al., 1992) using a Sigma-Aldrich anti-corticosterone antibody (C8784, Saint Loui, MO, USA). Samples were processed in two assays with a mean intra-assay coefficient of variation (CV) of 2.77% and an inter-assay (CV) of 8.56%. Finally, these fCort data were plotted against sample mass to test for any potential bias; no relationship was found between these variables (linear regression: $F_{1,89} = 1.52$, $p = 0.22$, adjusted $R^2 = 0.01$).

3.3.3   Stable isotope analysis

Stable isotope composition was determined using one feather selected at random from each individual. Each feather was soaked in 2:1 chloroform:methanol solution for 24 h to remove surface oils, rinsed twice with fresh solution, and air dried in a fume hood for at least another 24 h. These feathers were then packaged in individual envelopes and sent to the University of Windsor Great Lakes Institute for Environmental Research (Windsor, ON) for analyses. There, the calami were removed and the remaining feather material was freeze-dried, minced to a fine consistency, subsampled, weighed, and run through an Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS) to determine $\delta^{15}N$ and $\delta^{13}C$ using standard procedures. Results are reported in parts per thousand (‰) using delta notation (δ) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X denotes the heavy isotope of the element of interest (e.g. ^{15}N) and R is the ratio of the heavy isotope to the lighter isotope of that element (e.g. $^{15}N/^{14}N$). $R_{standard}$ for ^{15}N is that of atmospheric N_2 air and for ^{13}C is that of Pee Dee Belemnite (PDB). Precision was determined

using standards with n = 19. For $\delta^{15}N$, standard deviation was ± 0.10‰ for both internal standard tilapia and NIST standard bovine liver and for $\delta^{13}C$, standard deviation was ± 0.13‰ for tilapia and ± 0.20‰ for bovine liver. Additionally, 17 samples were run in duplicate, resulting in median error estimates of ± 0.06‰ (3.14% error) for $\delta^{15}N$ and ± 0.09‰ (4.50% error) for $\delta^{13}C$. Duplicate samples were averaged to yield single values prior to analysis.

3.3.4   Statistical analysis

All statistics were run in R version 3.4.1 (R Core Team, 2017). To assess the potential effects of fCort, $\delta^{15}N$, and $\delta^{13}C$ on egg size in Cassin's auklets, I built a candidate set of *a priori* models including all possible combinations of these variables and the two-way interactions among them (Table 3.1), representing all biologically plausible parameters while omitting more complex interactions with unclear biological implications. This candidate set was assessed separately for each colony since many seabirds, including auks, exhibit local adaptation in morphology and behavior between colonies of the same or closely related species (e.g., Catry et al., 2011; Friesen et al., 2007; Ibarguchi et al., 2011; Sausner et al., 2016; Wiley et al., 2012). This approach was favored over assessing a single candidate set with additional parameters for colony and all biologically plausible interactions, which likely would result in over-parameterization – especially given limited sample size. There was no multicollinearity in these variables at either colony as indicated by variance-inflation factors below a threshold of 3 (Fox and Monette, 1992). Egg volume index (EVI) was used as a standardized response variable, calculated as length x breadth^2 x 0.51 (cm^3) (Hoyt, 1979). The distribution of the dependent variable (EVI) at both colonies most

closely resembled a Gamma distribution, therefore I used Gamma family generalized linear models

with inverse link functions ('glm', package 'car').

Table 3.1 Candidate models used to assess
potential predictors of egg volume in
Cassin's auklets at each colony.

Parameters
~ 1 (null model)
fCort
$\delta^{15}N$
$\delta^{13}C$
fCort + $\delta^{15}N$
fCort + $\delta^{13}C$
$\delta^{15}N + \delta^{13}C$
fCort + $\delta^{15}N + \delta^{13}C$
fCort*$\delta^{15}N$
fCort*$\delta^{13}C$
$\delta^{15}N*\delta^{13}C$
fCort*$\delta^{15}N + \delta^{13}C$
fCort*$\delta^{13}C + \delta^{15}N$
fCort + $\delta^{15}N*\delta^{13}C$
fCort*$\delta^{15}N$ + fCort*$\delta^{13}C$
fCort*$\delta^{15}N + \delta^{15}N*\delta^{13}C$
fCort*$\delta^{13}C + \delta^{15}N*\delta^{13}C$
fCort*$\delta^{15}N$ + fCort*$\delta^{13}C + \delta^{15}N*\delta^{13}C$

To allow meaningful comparisons between effects in the presence of interactions and to

improve interpretability, I centered (mean = 0) and scaled (SD = 1) all variables prior to model

selection (Schielzeth, 2010). Comparisons of models in each candidate set were performed using

Akaike Information Criteria corrected for finite sample size (AIC$_c$; Burnham and Anderson, 2004;

Sugiura, 1978; 'AICc', package 'AICcmodav') and normalized evidence weights (AIC$_w$; 'aicw',

package 'geiger'). Models with $\Delta AIC_c < 2$ were considered to have the most substantial support

(Burnham, 2002; Burnham and Anderson, 1998). In addition, I calculated percent increase in

explained deviance relative to the null model ($100 \times [(\text{deviance}_{\text{null}} - \text{deviance}_{\text{model}})/\text{deviance}_{\text{null}}]$) and McFadden's pseudo-$R^2$ for each candidate model to further assess goodness-of-fit.

For the most complex initial model and the best supported models ($\Delta \text{AIC}_c < 2$) at each colony, assumptions of homogeneity, normality of residuals, and independence were examined and found to be reasonable. Explanatory variables were assumed to be functionally deterministic. There was no indication that the relationship between the response and the predictors were non-linear. Multi-collinearity was also assessed for the best candidate models and confirmed absent.

3.4 RESULTS

Average values of all variables were similar between Triangle Island and Rankine Island (Table 3.2). No variables were correlated at either colony (Pearson's correlations: $p > 0.05$; Appendix D, Table D1). Model comparison by AIC_c indicated that the best model to explain variation in EVI at Triangle Island included only the parameter $\delta^{13}\text{C}$; however, three other models received substantial support ($\Delta \text{AIC}_c < 2$), including the null model, the model including $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and the model including only $\delta^{15}\text{N}$ (Table 3.3). The normalized evidence weight (AIC_w) was also highest for the model including only $\delta^{13}\text{C}$ (0.342) but that of the null model (0.188) was similar relative to differences in the rest of the candidate set, suggesting like the several small ΔAIC_c values that the top model was not distinctly the best (Table 3.3). Similarly, percent deviance explained (38.10%) and pseudo-R^2 (still fairly low, 0.11) indicated that the third-best supported model by AIC_c ($\delta^{15}\text{N} + \delta^{13}\text{C}$) had the best fit among the candidate set. Several other models received some support, with 12 of the 18 models having $\Delta \text{AIC}_c < 10$ (Appendix D, Table D2). For Rankine Island, model comparison by AIC_c indicated that the best model to explain variation in

EVI was the null model. One other model, including only the variable $\delta^{15}N$, received substantial support ($\Delta AIC_c < 2$) and had a similar AIC_w to the null model (0.274 and 0.315, respectively; Table 3.3). Percent deviance explained by the second-best model over the null model was 16.03% and pseudo-R^2 was very low at 0.04. Thirteen of the 18 Rankine Island models had $\Delta AIC_c < 10$ (Appendix D, Table D3).

Table 3.2 Unscaled mean fCort, $\delta^{13}C$, $\delta^{15}N$, egg volume index (EVI), and egg measurements $\pm$ SD for Cassin's auklets at each study site and overall in 2011 (Triangle n = 14; Rankine n = 16).

	fCort (pg/mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	EVI	Length (mm)	Breadth (mm)
Triangle	2.4 ± 0.7	-18.50 ± 1.11	15.45 ± 0.80	28.3 ± 2.2	47.1 ± 1.3	34.3 ± 1.1
Rankine	2.6 ± 0.7	-18.50 ± 1.22	15.01 ± 0.93	27.8 ± 2.3	46.7 ± 1.4	34.1 ± 1.2
Overall	2.5 ± 0.7	-18.50 ± 1.15	15.22 ± 0.89	28.0 ± 2.2	46.9 ± 1.4	34.2 ± 1.1

Table 3.3 Best supported ($AIC_c < 2$) generalized linear models (Gamma distribution) predicting variation in egg volume index for Cassin's auklets at Triangle Island and Rankine Island in 2011. All combinations of the variables fCort, $\delta^{15}N$, $\delta^{13}C$, and their pairwise interactions were represented in the original candidate set. For each model below, K is the number of estimable parameters, AIC_w is Akaike model weight, % Deviance Explained is the percent increase in explained deviance relative to the null model, and McFadden's pseudo-R^2 is a goodness-of-fit measure appropriate for generalized linear models.

Parameters	K	AIC_c	ΔAIC_c	AIC_w	% Deviance Explained	McFadden's pseudo-R^2
Triangle Island						
$\delta^{13}C$	3	63.40	0.00	0.342	27.53	0.08
~ 1 (null model)	2	64.61	1.20	0.188	0.00	0.00
$\delta^{15}N + \delta^{13}C$	4	65.24	1.84	0.137	38.10	0.11
$\delta^{15}N$	3	65.36	1.96	0.128	16.65	0.04
Rankine Island						
~ 1 (null model)	2	74.70	0.00	0.315	0.00	0.00
$\delta^{15}N$	3	74.98	0.28	0.274	16.03	0.04

Standardized effect sizes for parameters in the best supported models were on the order of 10^{-2} or smaller at both Triangle Island and Rankine Island (Table 3.4). These scaled estimates

indicate that an increase in one population standard deviation of the independent variable results in a change of X population standard deviations in the dependent variable, EVI, where X is the estimate shown in Table 3.4. For example, an increase of one population standard deviation in $\delta^{13}C$ at Triangle Island (1.11‰, see Table 3.2) is estimated to decrease EVI by 1.35×10^{-3} population standard deviations, or 2.96×10^{-3} cm^3 ($1.35\times10^{-3} \times 2.2$ cm^3). Similarly, an increase of 0.93‰ in $\delta^{15}N$ at Rankine Island corresponds to an increase of 2.70×10^{-3} cm^3 in EVI. In addition to the small magnitude of these effects, the 95% confidence intervals (CIs) overlap zero for all variable estimates except for that of $\delta^{13}C$ in the best supported model at Triangle Island (Table 3.4). This was also the only variable to show significance at the α=0.05 level when each best supported model was examined (ANOVA, type III sum of squares, LR $X^2_{(1,\,n=14)} = 4.42$, $p = 0.035$).

Table 3.4 Model parameter estimates, errors, and confidence intervals (95% CI) for the best supported (AIC$_c$ < 2) generalized linear models (Gamma distribution) predicting variation in egg volume index for Cassin's auklets at Triangle Island and Rankine Island in 2011. The effect of $\delta^{13}C$ on EVI in Triangle Island Model 1 is significant at the α=0.05 level (*).

Rank (AIC$_c$)	Parameter	Estimate	Std. Error	95% CI	
Triangle Is.					
Model 1	$\delta^{13}C$*	-1.35×10^{-3}	6.32×10^{-4}	-2.57×10^{-3}	-9.26×10^{-5}
	Intercept	3.54×10^{-2}	6.36×10^{-4}	3.42×10^{-2}	3.67×10^{-2}
Model 2	Intercept (null model)	3.54×10^{-2}	7.28×10^{-4}	3.40×10^{-2}	3.68×10^{-2}
Model 3	$\delta^{15}N$	-8.89×10^{-4}	6.60×10^{-4}	-2.19×10^{-3}	4.03×10^{-4}
	$\delta^{13}C$	-1.22×10^{-3}	6.27×10^{-4}	-2.43×10^{-3}	2.57×10^{-5}
	Intercept	3.55×10^{-2}	6.15×10^{-4}	3.43×10^{-2}	3.67×10^{-2}
Model 4	$\delta^{15}N$	-1.09×10^{-3}	7.28×10^{-4}	-2.52×10^{-3}	3.34×10^{-4}
	Intercept	3.54×10^{-2}	6.94×10^{-4}	3.41×10^{-2}	3.68×10^{-2}
Rankine Is.					
Model 1	Intercept (null model)	3.60×10^{-2}	7.39×10^{-4}	3.46×10^{-2}	3.75×10^{-2}
Model 2	$\delta^{15}N$	1.17×10^{-3}	7.43×10^{-4}	-2.69×10^{-4}	2.64×10^{-3}
	Intercept	3.61×10^{-2}	7.03×10^{-4}	3.47×10^{-2}	3.75×10^{-2}

Plots of each single-term variable against EVI revealed no clear relationships overall, consistent with small effect sizes and strong support for the null model at both colonies (Figure 3.1). However, Figure 3.1c suggests a slight positive relationship between $\delta^{15}N$ and EVI at Triangle Island and a slight negative relationship at Rankine Island, consistent with the presence of the variable among the top models at both colonies and the signs of the estimates reported in Table 3.4. I further assessed this relationship at each colony using the original, unscaled datasets and simple linear regression (Gaussian) to enable direct comparison of these effects with previous work at Triangle Island. While Sorensen et al. (2009) reported a negative and significant effect of $\delta^{15}N$ on EVI at this colony in 2007 ($\beta = -2.81$, $p = 0.03$, $R^2 = 0.36$, n = 13), the equivalent regression using 2011 data yielded a slope which was instead positive and nonsignificant ($\beta = 1.07$, $F_{1,12} = 2.20$, $p = 0.16$, $R^2 = 0.16$, n = 14). The effect of $\delta^{15}N$ on EVI at Rankine Island in 2011 was approximately opposite that at Triangle Island in the same year but was also nonsignificant ($\beta = -0.95$, $F_{1,14} = 2.46$, $p = 0.14$, $R^2 = 0.15$, n = 16).
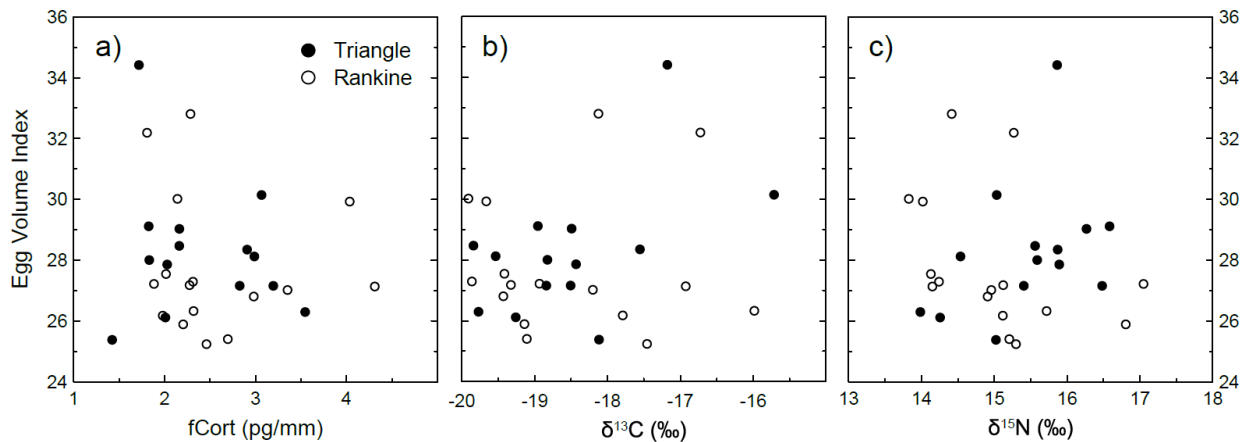

Figure 3.1 Plots of each single term variable (fCort, $\delta^{13}C$, $\delta^{15}N$) against Egg Volume Index (EVI). No clear relationships are evident, with the possible exception of a slight positive association between EVI and $\delta^{15}N$ at Triangle Island and a slight negative association between the same variables at Rankine Island.

3.5 DISCUSSION

Based on previous studies of carryover effects in seabirds, I predicted that fCort and isotopes would explain variation in egg size, supporting a mechanistic link between overwinter experience and reproductive investment. However, independent of colony, there was very little support for effects of pre-breeding fCort, $\delta^{15}N$, or $\delta^{13}C$ on Cassin's auklet egg size during our study and, if these effects were indeed present, they were remarkably small such that most 95% confidence intervals (CIs) on the order of 10^{-3} and 10^{-5} overlapped zero. The only parameter estimate for which CIs did not overlap zero was that for $\delta^{13}C$ in the best supported model at Triangle Island (Table 3.4), suggesting that diets composed of more inshore prey types (higher $\delta^{13}C$) corresponded to smaller EVI; however, this effect was extremely small with a 1.11‰ increase in $\delta^{13}C$ corresponding to a 2.96×10^{-3} cm^3 decrease in EVI.

Failure to reject the null hypothesis in this study does not necessarily contradict evidence that pre-breeding physiologic state and diet can carry over to affect reproductive investment. Inherent uncertainty in the timing of feather growth, the complex role of Cort in mediating nutritional stress and reproductive investment, and the potential for variation in isotopic baselines among individuals due to distributional differences during molt could have affected the results of this study, as well as those of previous works (although most Cassin's auklets breeding in British Columbia return to the colony region before March; see Chapter 2). If I assume these factors had minimal effects, failure to reject the null hypothesis in this study could suggest that the relationship between pre-breeding Cort, diet, and reproductive investment may differ greatly based on the oceanographic conditions and food resources present in any given year. Many studies that identified physiologic or dietary carryover effects on egg size were conducted in resource-limited

years where unfavorable oceanographic and/or foraging conditions prevailed. However, our study took place during a favorable year for Cassin's auklets, which may explain the apparent incongruity between our results and those of similar studies.

Cassin's auklets breeding in British Columbia in 2011 experienced moderate La Niña conditions, persisting since June of the previous year, and a negative (cool) phase of the North Pacific Oscillation (NPO) (minimum Oceanographic Niño Index = -1.4; National Oceanographic and Atmospheric Administration, 2016a, 2016b). Such conditions are highly favorable, marked by cold sea surface temperatures, high ocean productivity (Ainley and Hyrenbach, 2010; Mackas et al., 2007), and high reproductive success. Thus, the lack of support for relationships between fCort, diet, and egg size (absent or very small effect sizes, presence of the null model among the best supported models at each colony) suggests that these auklets had little trouble acquiring the resources needed to produce eggs at either Triangle or Rankine Island. In contrast, a similar study with Atlantic puffins (*Fratercula arctica*) found positive relationships between these variables (positive 95% CIs for effects, strong top model support by AIC$_c$), but took place when birds were experiencing generally poor environmental conditions and low abundance of their preferred prey (capelin, *Mallotus villosus*) during the pre-breeding period (Kouwenberg et al., 2013). In that context, up-regulation of Cort may have supported increased foraging effort (i.e., the Cort-adaptation hypothesis – Bonier et al., 2009; see also Angelier et al., 2008; Crossin et al., 2012c; Doody et al., 2008), enabling puffins to intensify searching behaviors for preferred prey (thus also elevating $\delta^{15}N$) and/or alternate prey types (Kouwenberg et al., 2013). The positive relationship between pre-breeding fCort and egg size in this potentially food limited context points to the role of Cort in mediating foraging success and reproductive investment. However, as I show here – when conditions are favorable, this relationship between fCort, diet quality, and egg size appears

to decouple, or be reduced to the extent that the null model was among the best supported models at each colony and non-zero effect sizes could not be supported for most variables using our dataset, possibly because these birds were under little nutritional constraint.

To illustrate this point further, Sorensen et al. (2009) studied carryover effects in Cassin's auklets at Triangle Island during poor oceanographic conditions and, like Kouwenberg et al. (2013), identified links between diet quality (feather $\delta^{15}N$) and egg size. The pre-breeding period represented in Sorensen et al. (2009) followed six months of unfavorable, weak El Niño conditions, and was characterized by a fairly neutral phase of the NPO (maximum Oceanographic Niño Index = 0.9; National Oceanographic and Atmospheric Administration, 2016a, 2016b). The top models at both colonies in my study did include the variable $\delta^{15}N$, but the CIs for each estimate overlapped zero and no effects were significant (Table 3.4). For comparative purposes I also replicated the regression analysis in Sorensen et al. (2009) at Triangle Island and Rankine Island (each had equivalent sample size to that in Sorensen et al. 2009). Neither showed a significant effect, again suggesting that a detectable effect of diet quality on EVI may only exist under unfavorable conditions, notwithstanding possibility of Type I errors in previous work or Type II errors in this study due to limited sample sizes or variation in the timing and location of feather growth within or among individuals.

Despite very different oceanographic conditions between our study and Sorensen et al. (2009), egg sizes at Triangle Island were similar in 2007 and 2011 (mean EVI ± SD: 28.8 ± 2.2 cm^3 and 28.3 ± 2.2 cm^3, respectively; two-tailed t-test: t_{25} = 0.63, p = 0.53). This suggests that, for Cassin's auklets, egg size may be somewhat buffered from environmental variation. While one might expect mean egg size to be greater and variability to be lower in years when resources are plentiful and egg size is not related to variation in Cort or diet quality, these effects could be

masked by the presence of many more, potentially less experienced birds in the laying population that could reduce mean egg size and increase variance to levels similar to those found under unfavorable conditions with fewer, more experienced breeders. In poor years, only these 'higher quality' females with superior ability to mediate the inhibitory effects of chronic Cort elevation may initiate breeding, even though breeding may be delayed in order to do so (Salvante and Williams, 2003). In fact, variation in oceanographic and foraging conditions might have their greatest impact at this breeding decision stage, via a body condition threshold for the initiation of laying (Crossin et al., 2016, 2013b, 2012a; Salvante and Williams, 2003) and/or via laying date (Hipfner et al., 2010, 2008). Indeed, despite substantial variation among individuals, egg size has been found to be a relatively fixed individual trait in many bird species. That is, egg size is generally heritable with a high degree of consistency between breeding attempts and often little variation attributable to pre-breeding environmental conditions (Christians, 2002); however, this has not yet been assessed for Cassin's auklets.

In summary, this work highlights several cautions for the study and interpretation of carryover effects acting on reproduction, particularly in relation to egg size. First, it illustrates the potential importance of understanding the specific environmental contexts during pre-breeding and breeding and how these can influence the endocrinological and/or physiological processes governing reproductive investment. Our study suggests that during favorable oceanographic conditions, up-regulation of Cort to facilitate increased foraging behavior during the pre-breeding period and the acquisition of preferred prey types may not be necessary for egg production in Cassin's auklets and has very little, if any, effect on egg size. Second, the similarity in egg volume (both mean and variation) between this study and Sorensen et al. (2009) suggests the possibility that egg size could be a relatively fixed individual trait in this species. Additional studies of this

population using larger sample sizes, standardized approaches, and broader coverage of environmental conditions across years would help determine whether carryover effects on egg size are present and how they may vary, or whether Type I or Type II errors may be present in the literature. Future studies may also consider sampling back or head feathers (which may be more extensively replaced than breast feathers; Pyle, 2009), adding lay date as a fitness proxy, and combining physiological sampling with year-round tracking in order to control for potential differences in isotopic baselines due to variation in pre-breeding distributions.

CHAPTER 4: DISCUSSION

This work had two primary objectives: 1) to gain insight into the nonbreeding distributions and migratory behavior of Cassin's auklets breeding in British Columbia and 2) to assess whether resulting nonbreeding experiences may drive carryover effects onto the breeding season. To address the first objective, I obtained nonbreeding positional data from 35 individual Cassin's auklets using GLS loggers, characterized nonbreeding distributions and migratory behavior, compared distributions to satellite-derived environmental data and previously identified habitat characteristics, and tested several potential drivers of migratory behavior. To address the second objective, I measured indicators of pre-breeding physiologic state (fCort) and diet (δ^{15}N, δ^{13}C) using feather samples from female birds and assessed whether these variables predicted reproductive investment in the form of egg size. Given the need to understand how population-level processes and ecosystem dynamics may change in response to rapidly changing and increasingly variable oceanographic conditions, I assessed the first objective across three nonbreeding seasons (2014-2017) and compared the outcomes of the second objective (one nonbreeding season, 2010-2011) with two similar studies conducted during markedly different oceanographic contexts. The main results of this work are summarized below, followed by a brief discussion of their implications, an overview of methodological limitations, and recommendations for future work.

4.1   SUMMARY AND SYNTHESIS

Nonbreeding Cassin's auklets from colonies in British Columbia routinely occupied waters as far north as the Gulf of Alaska and as far south as Baja California (Chapter 2). Northern habitats were utilized in summer and fall, when local productivity may be particularly high, and southern habitats along the coast of the United States and Mexico were utilized in fall and winter. All birds exhibited pre-laying residencies ($\geq$28 d) in the colony region during early spring, prior to the seasonal return of local productivity. Within this general spatial and temporal framework, individual Cassin's auklets exhibited substantial variability in finer-scale migratory phenology and choice of residency areas. At the most general level, this variability could be summarized into four migratory tactics based on the directionality of outward movements relative to the colony of origin: North, South, North-South, and Local. Some of this variability was explained by sex, year, and colony of origin. In addition, Cassin's auklets appeared to target distinct, ecologically differentiated regions within their nonbreeding range which may have, or be expected to have, good quality habitat. Since utilization of some target regions varied across years, migratory behavior in this species may be somewhat flexible; however, fixed tactics were also suggested by consistent utilization of the Southern California Bight despite very low productivity in one year.

Contrary to previous studies of female Cassin's auklets (Sorensen et al., 2009) and Atlantic puffins (Kouwenberg et al., 2013), neither pre-breeding physiologic state (fCort) nor diet (δ^{15}N, δ^{13}C) predicted egg size at either British Columbian colony sampled in 2011 (Chapter 3). The most likely explanation for the marked difference in results between this work and previous studies is nonbreeding environmental context. Carryover effects were identified during poor oceanographic conditions (previous studies) while no detectable effects were identified during favorable

conditions (this work). During poor conditions, upregulation of corticosterone may be needed to mediate the energetic tradeoffs between self-maintenance and reproduction, supporting increased foraging effort and thus increasing both the likelihood of reproduction and large egg size. However, when foraging conditions are favorable, such tradeoffs and associated physiological constraints are likely minimized and regulation of egg size may become effectively independent of circulating corticosterone levels and diet type.

Overall, the research in this thesis revealed considerable variability in nonbreeding behavior, experience, and the occurrence of carryover effects for Cassin's auklets breeding in British Columbia. The results of Chapter 2 expanded previous estimates of nonbreeding range, most notably to include Alaskan habitat, and refuted the hypothesis of simple southerly migration for this species. This diverse use of habitats likely generates variability in nonbreeding experience (e.g. environmental conditions, diet, migratory and foraging effort) which in turn may drive high individual variability in the occurrence and strength of carryover effects. Unfortunately, this diversity in migratory behavior also suggests that relationships between some carryover effect indicators and reproductive parameters may not be consistent across individuals each year. For example, isotopically similar diets from different latitudes or ecoregions could represent substantially different diet qualities. Similarly, circulating Cort levels prior to, or during, return migration could have different effects on upcoming reproduction than equivalent levels expressed following return to the colony region. Since Cassin's auklets typically spent over a month in the colony region before laying, and this period overlaps with at least half of peak body feather replacement (March), potential differences in indicator-effect relationships among individuals were likely minimized in my work and in the similar pre-breeding analyses of Sorensen et al. (2009). However, such complications are likely more prevalent during the rest of the nonbreeding

period, due to greater diversity in migratory behavior, and could have contributed to the lack of relationships between indicators of fall diet quality (primary feather $\delta^{15}N$, $\delta^{13}C$), lay date, and egg size at Triangle Island in 2006-2007 (Sorensen et al., 2009). Combining the tracking and sampling techniques employed in this thesis would enable future studies of carryover effects to control for differences in regional occupancy or behavioral state during feather growth.

This work also suggests that interannual variation in nonbreeding environmental conditions is an important factor influencing reproductive investment in Cassin's auklets. When broad-scale oceanographic conditions are favorable during nonbreeding, it may be easy for Cassin's auklets to obtain the resources required to produce their optimal egg size – regardless of their choice of residency areas or migratory routes (Chapter 3). However, when broad-scale oceanographic conditions are unfavorable and sufficient resources are generally difficult to obtain, nonbreeding distribution and behavior may become of much greater importance, with consequences for nonbreeding experience and carryover effects onto reproduction (Kouwenberg et al., 2013; Sorensen et al., 2009). Again, because of extended spring pre-laying residencies in the colony region, I would expect variation in carryover effects due to distributional differences to be most common from the fall and winter periods. It is important to note, however, that the relative likelihood and importance of carryover effects from different phases of the nonbreeding period have yet to be studied and spring could be the key time when experience carries over to affect investment.

If individual Cassin's auklets cannot alter their primary nonbreeding residency areas by predicting or perceiving local conditions and behaviorally responding to them, or if some birds are restricted to specific residency areas by individual quality and/or competition, such individuals would be particularly vulnerable to nonbreeding carryover effects. As oceanographic change

continues to advance and climatic variability continues to increase, my work suggests that such individuals may face negative selection pressure. Unfortunately, this work was not designed to test the existence or relative prevalence of fixed and flexible migratory phenotypes and thus can only highlight their importance for further study.

4.2 STUDY LIMITATIONS

In this thesis, there were several methodological limitations which may have affected the results of this study. In Chapter 2, individuals tracked using GLS loggers were primarily selected and tagged while raising a nestling (their reproductive attempt had not failed at the egg or hatchling stage), thus the resulting distributional and behavioral data may only be representative of 'higher quality', or more experienced, individuals. This deployment protocol was a trade-off to maximize the likelihood of tag recovery (sample size) by minimizing the risk of abandonment and maximizing the chances of nonbreeding survival and repeat burrow use. Similarly, only being able to obtain data from birds which survived the nonbreeding period means these results are not necessarily representative of population-level nonbreeding behaviors and outcomes. The error in GLS-derived locations (~ 169 km, Phillips et al., 2004a) was not a major limitation since our distributional and large-scale movement objectives did not require fine-scale movement data; however, these positional errors may have reduced the accuracy of some regional arrival and departure date estimates. In addition, behavioral estimates were based only on longitudinal data during equinox periods, wherein latitudes are unreliable. Despite these limitations, GLS loggers were the best option to query nonbreeding distributions and behavior in Cassin's auklets due to the species' small size, high wing-loading, and marine diving behavior. Logger effects on

individual nonbreeding distribution and behavior could be present; however, it is nearly impossible to identify or account for such effects using untagged individuals. This could potentially be explored using stable isotope techniques (Rubenstein and Hobson, 2004; Steenweg et al., 2017) to identify overwinter locations for control birds.

In Chapter 3, there was inherent uncertainty in the exact timing of sampled feather growth. Such variability likely presents an analytical problem only in species with protracted, asynchronous molts rather than in species with synchronous molts (Carravieri et al., 2014). While the definitive prealternate molt in Cassin's auklets may be somewhat protracted (range: January - early April), this estimate was based on museum specimens and represents a species-wide generalization, likely encompassing substantial variation associated with factors such as latitude and resource availability (Pyle, 2009). Since peak body feather replacement is recognized as occurring in February and March (Ainley et al., 2011), it is fairly safe to assume that a sample of several feathers from any given bird at our northern colonies generally represents late winter and early spring nonbreeding experience in that year; however, accidental sampling of older feathers is possible since body feather molt is partial (Pyle, 2009). As mentioned previously, potential variability in molting location (and thus isotopic baselines) as well as inherent complexity in the relationships between pre-breeding corticosterone, diet, and future reproductive investment are also potential limitations in my work.

In addition, egg size is perhaps an imperfect proxy for 'current success' since, although a good measure of maternal investment in Cassin's auklets (Knechtel, 1998), its implications for reproductive performance in this species are unconfirmed. Unfortunately, logistical constraints prevented me from assessing additional reproductive parameters such as hatching success, nestling size, or fledging success. Sample size was also relatively small in Chapter 3 (n = 30), which may

have reduced my ability to detect effects of nonbreeding experience on egg size. However, since my methodologies were very similar to those in two studies which did identify such effects (n = 12, Kouwenberg et al., 2013; n = 16, Sorensen et al., 2009), I feel reasonably confident suggesting that Chapter 3 may indicate a notable reduction or elimination of these effects (barring any previous type I errors), likely due to differences in oceanographic context between these studies.

Overall, this thesis is somewhat limited with respect to sample sizes, diversity of oceanographic contexts (within chapters), and the potential to inform population-level hypotheses. This research was primarily focused at Triangle Island, British Columbia; however, I also studied two other colonies in the province – Frederick Island and Rankine Island. While it is reasonable to assume that my results are generally representative of Cassin's auklets breeding within British Columbia, potential differences between nearby colonies are well within the realm of possibility and even suggested by this work. Among-colony variability across the broad latitudinal range of Cassin's auklet breeding colonies is likely to be substantial. In addition, neither chapter encompasses a full range of anomalously warm to anomalously cool oceanographic conditions, thus my results likely underestimate natural variability in nonbreeding behaviors and/or carryover effects. Oceanographic variability was high across years in Chapter 2, but all years were influenced (to some extent) by the warm-water Blob phenomenon. While Chapter 3 took place in just one year with anomalously cool oceanographic conditions, I was able to compare my results with a similar study in British Columbia during anomalously warm oceanographic conditions (Sorensen et al., 2009). Finally, I was unable to study individuals across years due to concerns regarding GLS logger life-span and recovery rates, thus questions regarding the repeatability of nonbreeding behavior and carryover effects were not addressed. Although the bulk of this work took place at

the world's largest breeding colony of Cassin's auklets, care should be taken not to over-generalize these results for use in population-level or climate change applications.

4.3 FUTURE WORK

More comprehensive, repeated, colony-specific studies for Cassin's auklets will be important for predicting population-level responses to increasing oceanographic variability experienced outside the breeding season. Studies which determine (or further examine) the fixed or flexible nature of individual migratory behavior, intrinsic and extrinsic drivers of behavioral variability, characteristics of preferred nonbreeding habitat, and environmentally-driven carryover effects would all be particularly informative. At a very general level, such studies would benefit from increased sample sizes and more balanced sex ratios within colony-years than those presented here, as well as from increased monitoring and/or sampling effort immediately before and after the nonbreeding period. Given limited resources, I recommend such studies be focused at single colonies since my data suggest some aspects of migratory phenology, and potentially nonbreeding strategy, are colony-specific, thus sample sizes sufficient for desired analyses must be achieved at the colony level.

Due to the substantial differences in environmental conditions experienced by birds using different migratory tactics and small within-tactic sample sizes, my dataset was unable to support appropriate and robust habitat modelling at the level of colony or tactic. Future studies should increase the number of tracked individuals with the specific aim of characterizing within-tactic habitat preferences (and/or environmental experiences) during different phases of the nonbreeding period, comparing these variables between tactics, and relating them to potential carryover effects.

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Since most Intigeo C65 loggers (in range 4, mode 6) had sufficient battery to record light intensity data throughout the nonbreeding period, I highly recommend adding SST to these logs to enable the use of sophisticated individual movement models. Similarly, I recommend the addition of a pressure sensor to gain insight into three-dimensional habitat use and energetics in this species, ideally in conjunction with individual movement data and without total device load exceeding ~1% of auklet body mass. With increased sample sizes and finer-scale individual movement data it is possible that migratory tactics could be further refined beyond the four basic tactics reported here. Given the similarity of our 'high-use regions' to MEOW designations, this may be best explored using the cluster-analysis approach pioneered in Krietsch et al. (2017). However, if this procedure results in the identification of many groupings composed of very few individuals, then migratory 'tactic' may be a misnomer. Variability within 'tactics' in this work is already high. Such a result could suggest that Cassin's auklets move relatively freely (although likely still with respect to individual optima) within the general framework of the nonbreeding range and regional phenology identified in Chapter 2, without significant consequences for nonbreeding survival or future reproduction – although the latter would remain to be confirmed. The adaptive or non-adaptive (though not likely maladaptive) nature of these individually variable migratory patterns could also be a very interesting topic for future research.

As mentioned previously, studies to determine the repeatability of migratory behaviors will be crucial for predicting population resilience to climatic and oceanographic change in this species. Fixed individual migrations – driven by genetic, cultural, or memory effects – can force prolonged exposures to potentially unfavorable nonbreeding conditions with implications for fitness as environmental change progresses and variability increases. Alternatively, the ability of individuals to behaviorally respond to biotic and abiotic environmental stimuli (e.g. temperature, winds,

resource availability, competition) can enable them to optimize nonbreeding experience and fitness to some extent, altering migratory routes and residency areas among years (e.g. Dias et al., 2011). If increased tracking effort reveals such flexible migratory behavior in Cassin's auklets, they may be less affected by environmental changes than species which exhibit fixed behaviors – or vice versa. However, understanding the drivers of this flexibility would also be important since differences in movement patterns do not always occur in response to differences in environmental suitability, nor are they necessarily adaptive. Unfortunately, individual environmental experience is difficult to quantify using GLS loggers due to inherently large error in positional data. If pursuing such work, potential 'decisions' regarding habitat use and resulting environmental experiences might be best explored at the scale of nonbreeding residency periods rather than days.

The extensive individual variability in migratory behavior documented in Chapter 2 makes Cassin's auklets ideal for the study of carryover effects. Future studies should continue to examine indicators of potential nonbreeding carryover effects on future reproduction, behavior, or survival using post-migratory tissue samples to acquire information on nonbreeding experience (Bortolotti et al., 2009; Inger and Bearhop, 2008), as in Chapter 3. If possible, monitoring at the colony should be expanded to include measures of reproductive phenology (particularly lay-date, which may have the greatest influence on reproductive success), investment, and success for sampled birds since seasonal carryover effects on these parameters have been identified in many taxa (Harrison et al., 2011). More accurate data on colony-region departure and return dates would also be beneficial to these aims. Further, I recommend sampling back or head feathers to reduce the chance of accidentally sampling feathers which do not represent the most recent pre-breeding period (Pyle, 2009). Future studies should also assess how carryover effects from breeding may drive variation in subsequent migratory behavior, including intrinsic factors such as reproductive outcome and

post-breeding physiologic state (e.g. Bogdanova et al., 2011). Finally, since comparisons of Chapter 3 with other studies suggest carryover effect occurrence, effect sizes, and/or the mechanisms by which they operate may vary among years with different oceanographic conditions, I recommend explicitly testing for such variability or including multiple years of data in any study of carryover effects.

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APPENDIX A: CHAPTER 2, DETERMINATION OF MAXIMUM DAILY FLIGHT DURATION

Intigeo-C65 geolocation loggers (Migrate Technology Ltd) record wet-dry immersion data in addition to light intensity data. In mode 6, these loggers test every 30 seconds for conductivity and record the total number of 'wet' counts every 10 minutes. Since logger immersion could indicate either resting on water or foraging in this species, I could only obtain reliable information on flight activity. To develop the most appropriate maximum distance filter to use during the quality control steps of geolocation data processing, I used these immersion datasets to determine the maximum time spent in flight per day during the nonbreeding season across all tracked auklets.

I cropped each immersion dataset to the nonbreeding period (1 July – 31 March) and then converted wet counts to dry counts (20 - wet counts) for each 10-minute period. Assuming each dry count represented 30 seconds in flight, I converted these counts to estimates of time spent in flight during each 10-minute period. These periods have time stamps which, along with Intiproc-defined daily sunrise times (threshold 2 lux) for each bird on each day, enabled me to calculate the duration of flight per day for each bird throughout the nonbreeding period, and subsequently to find the maximum of these durations. Across all birds in this study, the maximum flight duration for a single day was 17 hours.

APPENDIX B: CHAPTER 2, DETERMINATION OF EQUINOX PERIODS

Ranges within which latitudinal data were unreliable were determined using our dataset rather than by applying arbitrary date ranges around each equinox. Positional data for each bird were visualized in Google Earth Pro using the timeline function and, around each equinox, the first and last date for which the estimated positions showed clearly erroneous latitudes (latitudinal 'spreading') were recorded. These four dates (equinox period start and end for both fall and spring) were identified for each bird in our study.

Plots of these start and end dates revealed several outliers. These values were removed, resulting in sample sizes of 34 (start) and 33 (end) for fall equinox period estimation and 30 (start) and 28 (end) for spring equinox period estimation. Because these distributions were still quite broad and excluded reliable data from many tags, I used the date at the 85th percentile of each group to generate reasonaly inclusive date ranges for each equinox period. If the index value fell between dates, I took the date resulting in the broader equinox range. All potentially erroneous latitudes remaining in the non-equinox dataset were subjected to the filtering steps described in section 2.3.3. Since reasonable latitudes did occur within these date distributions, particularly at the tails, these methods allowed us to differentiate unreliable periods of positional data while also retaining as much reliable data as possible, with results uniquely appropriate to our dataset.

This procedure resulted in equinox period designations including approximately one month on the winter side of each equinox and two weeks on the summer side of each equinox. Specifically, the fall equinox period ranged from 8 Sept – 25 Oct (14 days pre- and 33 days post-equinox) and the spring equinox period ranged from 14 Feb – 31 March (36 days pre- and 9 days post-equinox). Such winter-weighted effect periods are common, although many publications still apply symmetrical exclusion periods.
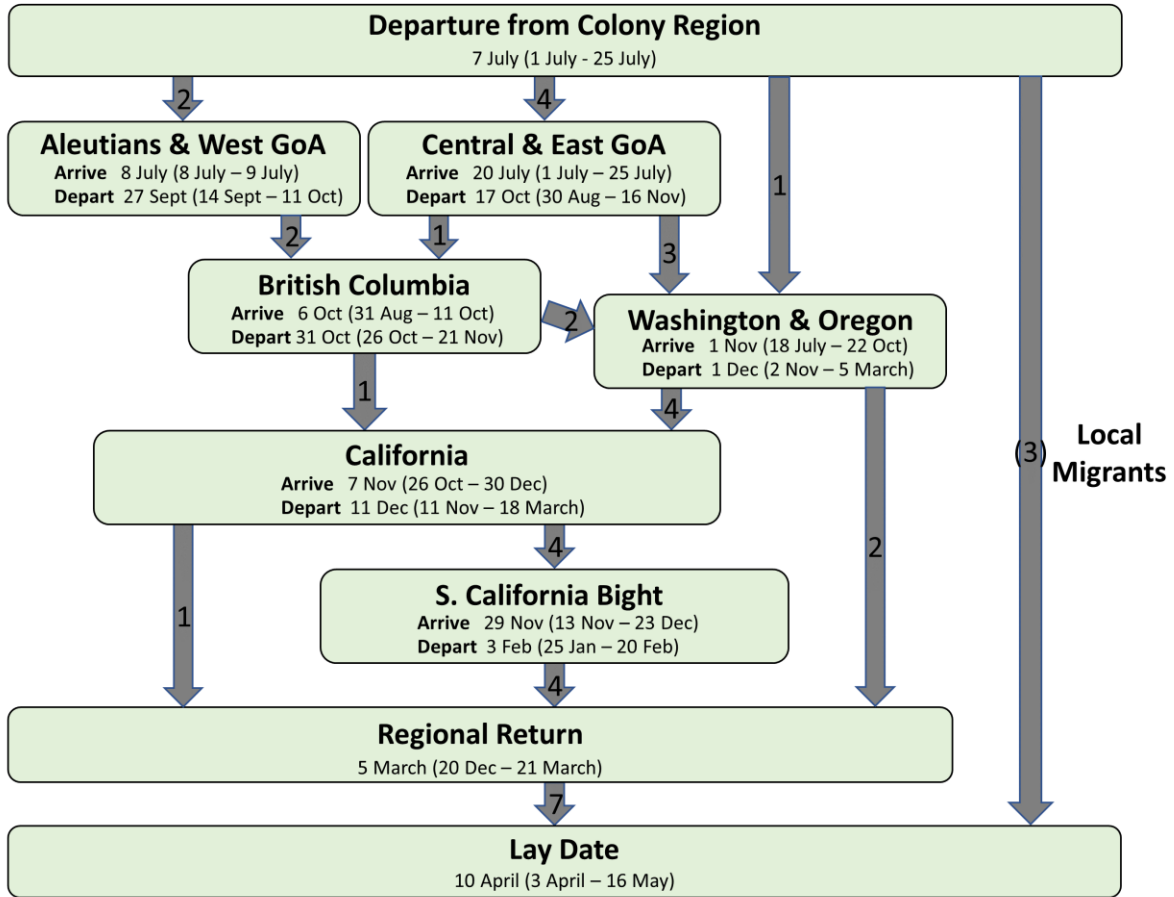
Figure C1. Movements of individual Cassin's auklets during the 2014-2015 nonbreeding period, indicating phenology and regional occupancy. Dates within each category, or region, are indicated as MEDIAN (RANGE). Numbers within arrows represent the number of birds moving between (or remaining within) regions.

Figure C2. Movements of individual Cassin's auklets during the 2015-2016 nonbreeding period, indicating phenology and regional occupancy. Dates within each category, or region, are indicated as MEDIAN (RANGE). Numbers within arrows represent the number of birds moving between (or remaining within) regions. One bird with incomplete tracking data is not shown.
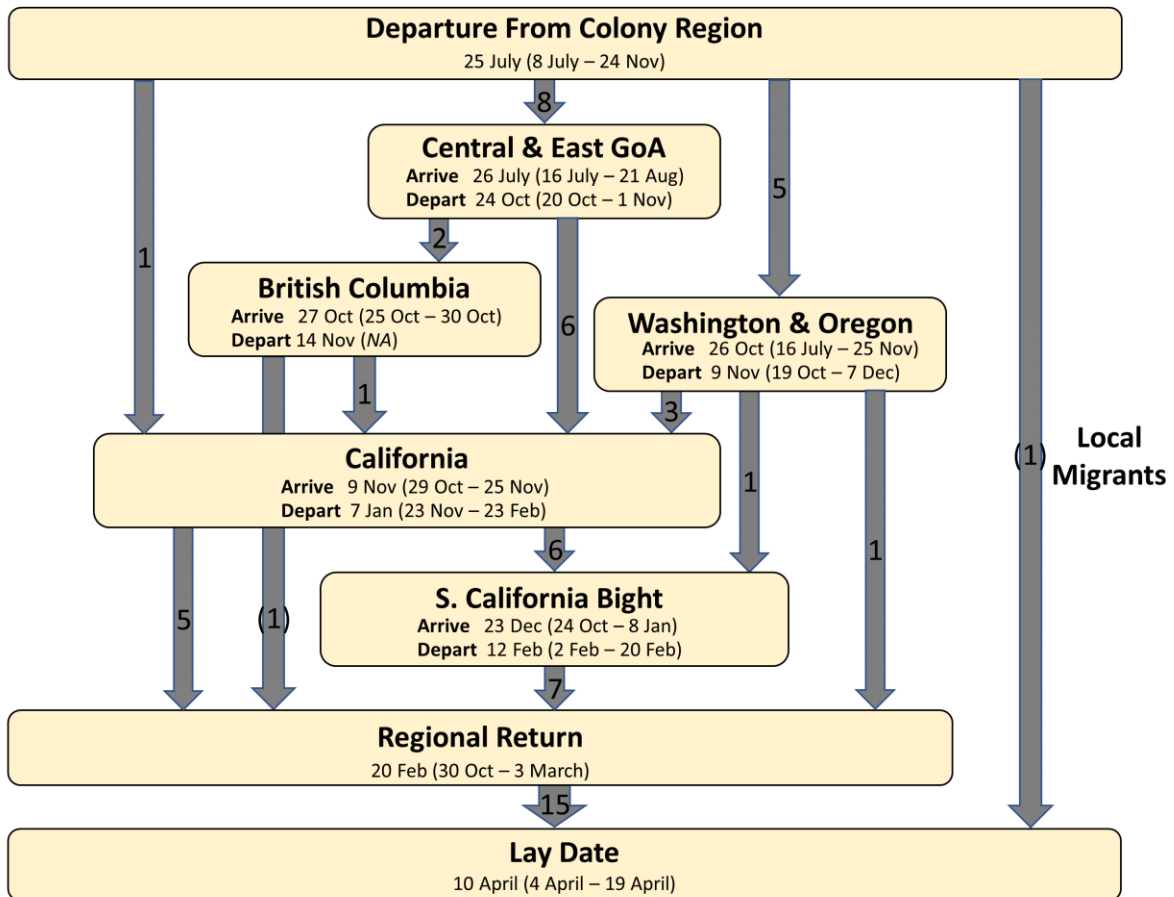
Figure C3. Movements of individual Cassin's auklets during the 2016-2017 nonbreeding period, indicating phenology and regional occupancy. Dates within each category, or region, are indicated as MEDIAN (RANGE). Numbers within arrows represent the number of birds moving between (or remaining within) regions. One bird with incomplete tracking data is not shown.
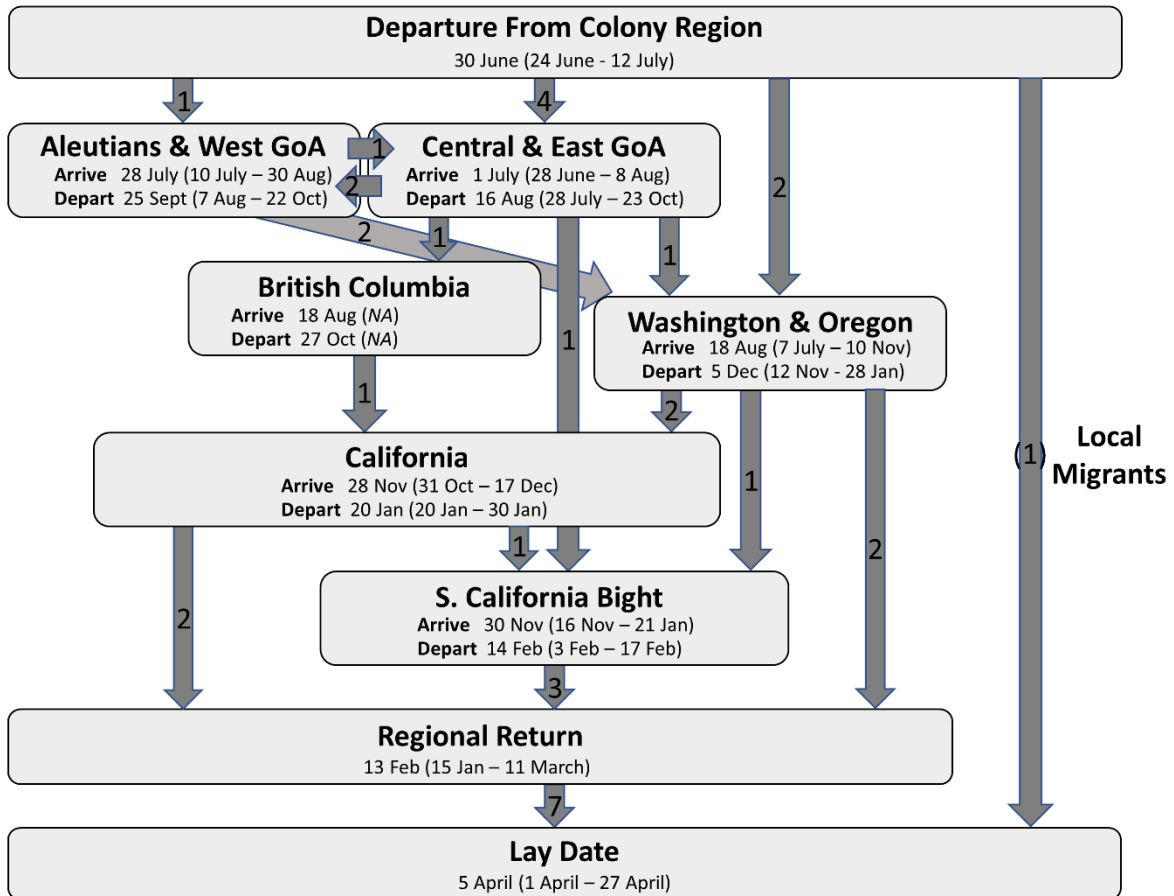
APPENDIX D: CHAPTER 3, SUPPLEMENTARY TABLES

Table D1. Pearson's correlations for all variables in the initial model predicting Egg Volume Index (EVI) in Cassin's auklets at two British Columbian colonies in 2001 (Triangle Island df=12, Rankine Island df=14).

Colony	Variable 1	Variable 2	Correlation	t-value	p-value
Triangle Island	EVI	fCort	-0.18	-0.64	0.54
	EVI	$\delta^{13}C$	0.52	2.08	0.06
	EVI	$\delta^{15}N$	0.39	1.48	0.16
	fCort	$\delta^{13}C$	-0.02	-0.08	0.93
	fCort	$\delta^{15}N$	-0.29	-1.05	0.31
	$\delta^{13}C$	$\delta^{15}N$	0.20	0.70	0.50
Rankine Island	EVI	fCort	-0.08	-0.30	0.77
	EVI	$\delta^{13}C$	0.01	0.05	0.96
	EVI	$\delta^{15}N$	-0.39	-1.57	0.14
	fCort	$\delta^{13}C$	0.03	0.11	0.91
	fCort	$\delta^{15}N$	-0.41	-1.66	0.12
	$\delta^{13}C$	$\delta^{15}N$	0.21	0.80	0.44

Table D2. Performance of generalized linear models (Gamma distribution) predicting variation in egg volume index for Cassin's auklets at Triangle Island in 2011. Models represent all possible combinations of the variables fCort, $\delta^{15}N$, $\delta^{13}C$, and their pairwise interactions and are presented from most to least support by AIC_c. The first four models are best supported ($AIC_c < 2$). For each model below, K is the number of estimable parameters, AIC_w is Akaike model weight, % Deviance Explained is the percent increase in explained deviance relative to the null model, and McFadden's pseudo-R^2 is a goodness-of-fit measure appropriate for generalized linear models.

Parameters	K	AIC_c	ΔAIC_c	AIC_w	% Deviance Explained	pseudo-R^2
$\delta^{13}C$	3	63.40	0.00	0.342	27.53	0.08
~ 1 (null model)	2	64.61	1.20	0.188	0.00	0.00
$\delta^{15}N + \delta^{13}C$	4	65.24	1.84	0.137	38.10	0.11
$\delta^{15}N$	3	65.36	1.96	0.128	16.65	0.04
fCort $+ \delta^{13}C$	4	66.76	3.36	0.064	31.00	0.09
fCort	3	67.42	4.01	0.046	3.49	0.01
$\delta^{15}N*\delta^{13}C$	5	67.52	4.12	0.044	49.23	0.16
fCort $+ \delta^{15}N$	4	69.31	5.91	0.018	17.22	0.04
fCort $+ \delta^{15}N + \delta^{13}C$	5	70.07	6.67	0.012	39.08	0.12
fCort*$\delta^{13}C$	5	70.58	7.18	0.009	36.81	0.11
fCort*$\delta^{15}N + \delta^{13}C$	6	72.18	8.78	0.004	55.47	0.19
fCort*$\delta^{15}N$	5	72.30	8.90	0.004	28.56	0.08
fCort $+ \delta^{15}N*\delta^{13}C$	6	73.54	10.14	0.002	50.93	0.17
fCort*$\delta^{13}C + \delta^{15}N$	6	74.79	11.39	0.001	46.36	0.15
fCort*$\delta^{15}N + \delta^{15}N*\delta^{13}C$	7	78.92	15.52	0.000	61.19	0.22
fCort*$\delta^{15}N + $ fCort*$\delta^{13}C$	7	80.00	16.60	0.000	58.07	0.20
fCort*$\delta^{13}C + \delta^{13}C*\delta^{15}N$	7	82.20	18.80	0.000	50.95	0.17
fCort*$\delta^{15}N + $ fCort*$\delta^{13}C + \delta^{15}N*\delta^{13}C$	8	91.03	27.63	0.000	61.27	0.22

Table D3. Performance of generalized linear models (Gamma distribution) predicting variation in egg volume index for Cassin's auklets at Rankine Island in 2011. Models represent all possible combinations of the variables fCort, $\delta^{15}N$, $\delta^{13}C$, and their pairwise interactions and are presented from most to least support by AIC_c. The first two models are best supported ($AIC_c < 2$). For each model below, K is the number of estimable parameters, AIC_w is Akaike model weight, % Deviance Explained is the percent increase in explained deviance relative to the null model, and McFadden's pseudo-R^2 is a goodness-of-fit measure appropriate for generalized linear models.

Parameters	K	AIC_c	ΔAIC_c	AIC_w	% Deviance Explained	pseudo-R^2
~ 1 (null model)	2	74.70	0.00	0.315	0.00	0.00
$\delta^{15}N$	3	74.98	0.28	0.274	16.03	0.04
fCort*$\delta^{15}N$	5	77.25	2.55	0.088	41.28	0.12
fCort + $\delta^{15}N$	4	77.26	2.56	0.088	22.85	0.06
fCort	3	77.67	2.97	0.071	0.67	0.00
$\delta^{13}C$	3	77.77	3.07	0.068	0.02	0.00
$\delta^{15}N + \delta^{13}C$	4	78.40	3.70	0.050	17.15	0.04
fCort + $\delta^{15}N + \delta^{13}C$	5	81.18	6.48	0.012	24.95	0.07
fCort + $\delta^{13}C$	4	81.30	6.60	0.012	0.69	0.00
fCort*$\delta^{15}N + \delta^{13}C$	6	82.02	7.33	0.008	43.29	0.13
$\delta^{15}N*\delta^{13}C$	5	82.71	8.02	0.006	17.40	0.04
fCort*$\delta^{13}C$	5	84.29	9.59	0.003	8.85	0.02
fCort*$\delta^{13}C + \delta^{15}N$	6	84.32	9.62	0.003	34.54	0.10
fCort*$\delta^{15}N$ + fCort*$\delta^{13}C$	7	86.18	11.48	0.001	51.54	0.17
fCort + $\delta^{15}N*\delta^{13}C$	6	86.35	11.65	0.001	25.71	0.07
fCort*$\delta^{13}C + \delta^{15}N*\delta^{13}C$	7	88.18	13.49	0.000	45.06	0.14
fCort*$\delta^{15}N + \delta^{15}N*\delta^{13}C$	7	88.63	13.94	0.000	43.49	0.13
fCort*$\delta^{15}N$ + fCort*$\delta^{13}C + \delta^{15}N*\delta^{13}C$	8	92.17	17.47	0.000	58.75	0.20