At-sea distribution and foraging behaviour of two North Pacific seabirds revealed through GPS tracking

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Ethics Statement

Abstract

Successful conservation of seabirds requires identifying at-sea foraging areas and drivers of habitat use patterns. Here, I used GPS tracking technology to provide insights into the foraging behaviour of Cassin's auklets (*Ptychoramphus aleuticus*) and rhinoceros auklets (*Cerorhinca monocerata*) breeding in British Columbia, Canada. I found that inter-annual variation in Cassin's auklet habitat use (2014, 2015, and 2017) was best explained by sea surface temperature, a dynamic oceanographic feature, while chlorophyll *a* concentrations and bathymetric features were poor predictors of habitat use. I found low spatiotemporal variation in movement patterns of rhinoceros auklets breeding at the Lucy Islands, mirroring stability in surrounding oceanographic conditions and diet composition, but high variability in the movement patterns of rhinoceros auklets at Pine and Triangle Islands. Overall, my results show that oceanographic conditions drive habitat use patterns of both species, and highlights the need to develop dynamic management strategies for successful conservation of at-sea habitat.

Keywords: GPS tracking; habitat use; at-sea distribution; foraging behaviour; Cassin's auklet; rhinoceros auklet

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Chapter 1. General Introduction

Seabird populations worldwide are decreasing, with nearly half of all species undergoing population declines (Croxall et al. 2012, Paleczny et al. 2015). Conservation efforts to date have primarily focused on eliminating threats present on seabird breeding colonies (Croxall et al. 2012, Spatz et al. 2014). Management actions include: banning the direct harvest of adults and eggs (which historically diminished many populations), island habitat restoration, and removal of non-native species (Schreiber and Burger 2001). Ongoing efforts have already eliminated non-native species (e.g. mammalian predators) from 925 breeding islands worldwide (Island Conservation 2018), and both the number and scale of eradication projects continues to increase (Keitt et al. 2011). In contrast, much less has been done to address anthropogenic threats encountered while at sea, such as depleted prey populations, incidental bycatch in fisheries, pollution, and climate change (Croxall et al. 2012, Trathan et al. 2014). To address these at-sea threats to seabirds first requires identifying important marine habitat. This information can then be incorporated into Marine Spatial Planning, such as the establishment of Marine Protected Areas (MPAs), and the identification of critical habitat for species-specific recovery plans (reviewed in Lascelles et al. 2012).

The identification of important at-sea habitat for breeding seabirds, both to inform Marine Spatial Planning and the establishment of MPAs, has been challenging for two reasons. First, identifying important foraging areas has been difficult because of methodological constraints. Methods such as at-sea surveys are limited by ship range and weather, and do not provide information on the birds’ origin or breeding status (reviewed in Lascelles et al. 2012). Furthermore, the first individual-tracking technologies (i.e. satellite and GPS loggers) could only be used to study individual movement patterns of the largest seabird species due to the size and weight of devices. Second, the identification of foraging areas has been difficult because of the dynamic nature of the marine environment. Ocean productivity is driven by the interaction of static (e.g. bathymetry) and dynamic (e.g. currents, winds) processes, which vary over space and time (Mann and Lazier 2006). This results in a spatially and temporally heterogeneous distribution of both environmental conditions (i.e. salinity, temperature) and primary production, which in turn affects the distribution and abundance of prey. Breeding seabirds have several behavioural adaptations to cope with these variable prey fields. For example, seabirds can track distributional shifts of their preferred prey, or they can switch to alternate prey species which may inhabit different marine habitats (Wells et al. 2017). Lastly, seabirds may respond by increasing their foraging effort and expanding their search area to locate enough prey (Horswill et al. 2017). Given that these behavioural changes may only occur under specific environmental conditions, studies investigating seabird habitat use may not capture temporal variation in foraging areas if they are conducted over one or two years.

The reduced size and cost of tracking devices is now allowing researchers to overcome methodological constraints and the challenges associated with environmental variability. Devices can now be used on smaller seabird species to provide a detailed understanding of how individuals of known origin use the marine environment, providing information on foraging paths, time budgets, and the range of habitats visited. The reduced cost now makes it easier to collect multiple years of data, capturing inter-annual variation in movement patterns caused by environmental conditions. Consequently, tracking studies are beginning to be used to delineate and assess boundaries for protected areas surrounding breeding colonies (Ludynia et al. 2012, Ponchon et al. 2017), or to assess spatial overlap between seabirds and anthropogenic activities (e.g. offshore wind farms, Cleasby et al. 2015; fisheries, Waugh et al. 2005, Torres et al. 2011). Furthermore, GPS tracking can be combined with environmental data to develop spatial models of suitable habitat, allowing governments, non-governmental organizations, and industry to better incorporate the habitat needs of seabirds (reviewed in Lascalles et al. 2012, Chivers et al. 2013).

The Canadian federal government is interested in using tracking devices to help deliver on several commitments to protect seabirds from anthropogenic threats encountered at sea, including in the coastal waters of British Columbia. The entire continental shelf region of B.C. is subjected to anthropogenic activity, with particularly high impacts in the Strait of Georgia, Queen Charlotte Strait, and Chatham Sound (Ban et al. 2010). The greatest impacts come from fisheries, run-off from land-based activities, and transportation (Ban et al. 2010), and many of these anthropogenic activities are anticipated to increase in intensity in the future (e.g. transportation; Nuka Research 2013). To better manage the effects of multiple human activities, the government is interested in incorporating seabird distributions into marine zoning and spatial planning.

For example, the federal government’s Oceans Protection Plan aims to incorporate marine wildlife distributions into emergency response planning (e.g. in the event of an oil spill). Furthermore, the federal government is committed to protecting 10% of coastal and marine areas as MPAs by 2020 to meet a global target set by the Convention on Biological Diversity. For example, the government has recently designated a MPA around the Scott Islands, the largest and most diverse seabird colony in B.C., for the purposes of conserving at-sea habitat (Government of Canada 2017a).

To meet these commitments and to effectively manage protected areas, baseline information is needed on the habitat use patterns of B.C.’s seabirds. Alcids, which are pursuit-diving seabirds, are of high interest for several reasons. First, the province supports globally significant populations of several species. It’s estimated that 70% of the world’s Cassin’s auklets (*Ptychoramphus aleuticus*), and 50% of the world’s rhinoceros auklets (*Cerorhinca monocerata*), breed on offshore islands along the coastline (Rodway 1991). The majority of Cassin’s auklets nest on Triangle and Sartine Islands, part of the Scott Islands chain, while major colonies of rhinoceros auklets occur on Pine and Storm Islands, Triangle Island, Sgang Gwaay, and the Lucy Islands (Rodway and Lemon 2011). Second, both species face several threats, despite being numerically abundant. They are susceptible to oil pollution and bycatch in gillnets (Page et al. 1990, Oka and Okuyama 2000, Smith and Morgan 2005, Fox et al. 2016), and they are sensitive to changes in ocean climate that impact the availability and abundance of their prey (Hedd et al. 2006, Hipfner 2008, Borstad et al. 2011). For instance, Cassin’s auklets have been shown to have lower reproductive success and survival during periods of warmer ocean temperatures (i.e. El Niño events; Wolf et al. 2009, 2010, Morrison et al. 2011). Given the projected future increase in ocean temperatures, Cassin’s auklet populations are predicted to decline and they have been assessed as ‘Special Concern’ by the Committee on the Status of Endangered Wildlife in Canada for this reason (COSEWIC 2014). Rhinoceros auklets also have lower reproductive success during unfavourable ocean conditions (Borstad et al 2011), but populations are currently considered stable (Rodway and Lemon 2011).

In this thesis, I build on previous research on Cassin’s and rhinoceros auklets to provide insights into their at-sea foraging behaviour and movements. In Chapter 2, I provide the first description of the fine-scale movements of Cassin’s auklets breeding at Triangle Island, at the center of the Scott Islands Marine National Wildlife Area. Using three years of GPS tracking data, I describe inter-annual patterns in the at-sea distribution of Cassin's auklets, and describe foraging trip characteristics and individual time budgets in relation to the Scott Islands Marine National Wildlife Area. Finally, I assess the relative importance of dynamic and static environmental variables as predictors of Cassin's auklet habitat use using both individual and population level analyses.

In Chapter 3 of this thesis, I assess the foraging behaviour of rhinoceros auklets breeding at three of the major island colonies in British Columbia – Pine, Triangle, and Lucy Islands. I use GPS tracking data collected in 2014, 2016, and 2017 to describe at-sea space use and individual movement patterns. I also assess whether the timing of the spring phytoplankton bloom and breeding phenology is associated with variation in foraging behaviour across colonies and years, and whether variation in foraging behaviour affects diet composition. In Chapter 4, I summarize the previous chapters and place my results in the context of a larger body of research. I also discuss the management implications of my results and suggest areas deserving of further research.

Chapter 2. At-sea distribution and fine-scale habitat use patterns of zooplanktivorous Cassin's auklets during the chick-rearing period

2.1. Abstract

Understanding the fine-scale movements and habitat use patterns of marine predators is critical for identifying important foraging habitat and guiding effective conservation planning. Here, I used GPS loggers to track chick-rearing Cassin's auklets (*Ptychoramphus aleuticus*) at their largest breeding colony, located on Triangle Island, British Columbia, Canada. I conducted analyses at both the individual and population level to assess whether inter-annual variation in habitat use (2014, 2015, and 2017) was related to dynamic oceanographic features, such as sea surface temperature (SST) and chlorophyll *a* concentrations, or static bathymetric features. At both scales of analyses, the foraging behaviour of Cassin's auklets was best explained by SST. At the individual level, birds spent more time foraging in areas with lower SSTs, relative to other areas visited over the course of a foraging trip. At the population level, the at-sea distribution of Cassin's auklets varied across years, with birds using areas northwest of colony in 2014 and areas west of the colony in 2015 and 2017. Furthermore, the probability of foraging across the study area was higher in areas with lower SSTs, suggesting that SST is related to the broad-scale foraging distribution of Cassin's auklets. Identification of the environmental drivers of habitat use across multiple years can be used to help predict suitable at-sea habitat across time, leading to more effective conservation and management.

2.2. Introduction

Many seabird populations are decreasing, and at-sea threats include incidental bycatch in fisheries, pollution, depleted prey populations, and climate change (Croxall et al. 2012; Trathan et al. 2014; Paleczny et al. 2015). The establishment of Marine Protected Areas (MPAs) has emerged as a promising tool to protect seabirds and their foraging habitats from these anthropogenic threats (Pichegru et al. 2010; Ludynia et al. 2012). However, the likelihood that MPAs will successfully protect such highly mobile top predators depends on sound scientific information regarding seabird foraging movements and drivers of habitat use (Green et al. 2015). Marine environments are vast and spatially heterogeneous, and habitats can be characterized in terms of static features (e.g. bathymetry), and dynamic features (e.g. fronts, upwelling plumes) which can vary over space and time (Thomson 1981; Mann and Lazier 2006). Static features can be important predictors of seabird habitat use because they reflect the habitat preferences of their prey (e.g. Watanuki et al. 2008). Additionally, static features can be important because they interact with dynamic features, such as winds and currents, to generate oceanographic conditions that enhance primary productivity (reviewed in Hazen et al. 2013). Generally, ocean productivity increases when cold, nutrient-rich water is brought to the surface, which supports phytoplankton blooms (Mann and Lazier 2006). Phytoplankton blooms, in turn, can support dense aggregations of zooplankton and upper trophic level consumers which then attract top predators (Genin et al. 2004; Ainley et al. 2009; Grecian et al. 2016). However, the spatial and temporal predictability of productivity varies based on underlying oceanographic processes, such that static features may only be important under certain conditions (reviewed in Hazen et al. 2013). Therefore, seabird habitat use may be better explained by dynamic features because they are more closely linked to ocean productivity and potential foraging gains.

Given the complexity of oceanographic processes and the absence of information on the abundance and distribution of prey, conservation biologists require simpler tools to identify habitat for species of interest (Oppel et al. 2012; McGowan et al. 2013). For seabirds, one increasingly common approach is to link tracking data to bathymetric and remotely-sensed environmental characteristics that reflect oceanographic processes. Tracking studies have demonstrated that, for some species, foraging is concentrated near continental shelves, slopes, and seamounts where the complex bathymetry brings cold, nutrient-rich water to the surface (e.g. black petrels *Procellaria parkinson* - Freeman et al. 2010; little auks *Alle alle* - Amélineau et al. 2016). However, the foraging areas of many seabird species are better predicted by dynamic features, such as low sea surface temperatures (SST), high salinity, high chlorophyll *a* concentrations, and high chlorophyll *a* anomalies, which are all signatures of upwelling and primary productivity (Ainley et al. 2009; Paiva et al. 2010; Suryan et al. 2012, Gremillet et al. 2014; Grecian et al. 2016). Similarly, other seabirds have been found to forage in areas with high SST and chlorophyll *a* gradients, suggesting that ocean fronts are an important habitats for these species (Cape gannet *Morus capensis* - Sabarros et al. 2014; northern gannet *Morus bassanus* - Scales et al. 2014). Given the importance of dynamic features to seabirds, the designation of MPAs requires multiyear data to assess the relative stability of foraging areas and identify biologically important candidate regions for protection.

The Cassin's auklet (*Ptychoramphus aleuticus*) is a zooplanktivorous alcid distributed widely throughout the northeastern Pacific Ocean. The marine habitat requirements of Cassin's auklet remain one of the least resolved aspects of its biology and most research to date comes from the southern margins of its breeding distribution. In the southern California Current System (CCS), foraging Cassin's auklets associate with bathymetric features, such as shelf-breaks and seamounts, that promote primary production and dense aggregations of their main prey, *Euphausia pacifica* and *Thysanoessa spinifera* ('euphausiids'; Adams et al. 2004). Birds breeding on the Channel Islands, California have also been found to forage in cool, high chlorophyll waters (Adams et al. 2010). However, little is known about the habitat preferences of Cassin's auklets breeding in British Columbia, Canada, where 75% of the global population nests on just a handful of island colonies (Rodway and Lemon 2011). Here, Cassin's auklets occupy the Transition Zone, an oceanographic domain between the upwelling CCS and the downwelling Alaska Gyre System. In the Transition Zone, foraging Cassin's auklets prey primarily on the subarctic, oceanic copepod species *Neocalanus cristatus*, and reproductive success is lower when they must instead rely on euphausiids (Hedd et al. 2002; Hipfner 2008, 2009). Given these differences in oceanography and diet, it is unknown how the habitat use of Cassin's auklets in the Transition Zone might differ from that of birds breeding in the CCS. Furthermore, Cassin's auklets have been assessed as a species of 'Special Concern' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), making this information critical for conservation efforts in their core breeding range (COSEWIC 2014).

Here, I investigated the habitat use of Cassin's auklets breeding at the world's largest colony of this species, located at Triangle Island in British Columbia, Canada (Rodway 1991). Specifically, I used GPS tracking technology to investigate the habitat use of Cassin's auklets foraging during the chick-rearing period, during which time they are foraging both to feed themselves and to collect prey to deliver back to the nest. My objective was to determine whether static and/or dynamic oceanographic features that are readily available can be related to individual and population level patterns of habitat use. At the individual level, I used a time-in-area approach to look at the influence of oceanographic features on the amount of time individual birds spent in an area, relative to other areas visited over the course of their foraging trip. At the population level, I modelled the influence of oceanographic features on the probability of foraging within a grid cell of the study area, as well as the intensity of grid cell use. I predicted that Cassin's auklets would use deeper waters and sloping bathymetries (e.g. the continental shelf-break) where upwelling is more likely to occur. I also predicted that they would use areas with relatively low SSTs and high chlorophyll *a* concentrations, reflecting both productive, recently upwelled water, and the preferred thermal habitat of the subarctic copepod *N. cristatus* (Mackas et al. 2001).

2.3. Methods

2.3.1. Study Species

Cassin's auklets (*Ptychoramphus aleuticus*) breed on offshore islands from the Aleutian Islands, Alaska to Baja California, Mexico. They have high breeding site fidelity, are socially monogamous, and exhibit nocturnal colony attendance (Ainley et al. 2011). A single-egg clutch is laid in an earthen burrow and the male and female alternate incubation duties every 24 hours (Manuwal 1974a). Chicks are semi-precocial at hatching and require brooding for 3-6 days (Manuwal 1974a). During this period, the male and female alternate between brooding and foraging, exchanging roles each night. Once the chick is capable of thermoregulation, both parents forage at sea during the day. While foraging, Cassin's auklets dive from the surface of the water and propel themselves with their wings in pursuit of prey. They are capable of diving to 40 m, but spend most of their time within the top 10 m of the water column (Burger and Powell 1990, Manugian et al. 2015). Bouts of diving are interspersed with periods of rest, causing extensive spatial overlap between these two behaviours (Thoresen 1964, Manugian et al. 2015). Undigested prey intended for the chick is stored in a sac-like extension of the buccal cavity (the "gular pouch"), and is delivered during a single, nightly visit to the burrow (Manuwal 1974a, Speich and Manuwal 1974).

While still numerically abundant, Cassin's auklets have become a species of conservation concern because they are sensitive to changes in ocean climate that impact the availability and abundance of their zooplankton prey (Wolf et al. 2009, 2010, COSEWIC 2014). Ocean conditions, including large-scale ocean climate events such as El Niño Southern Oscillation, have been linked to decreased adult survival, decreased reproductive success, and mass mortality events (Hipfner 2008, Wolf et al. 2009, 2010, Morrison et al. 2011, Jones et al. 2018). Ocean temperatures and the frequency of extreme climatic events are expected to increase due to climate change (Cai et al. 2014), and population models predict that Cassin's auklets will continue to decrease throughout their range (Wolf et al. 2010).

2.3.2. Study Site

Triangle Island (50° 51' 35" N; 129° 4' 34" W), the outermost island of the Scott Islands archipelago, is located approximately 45 km northwest of Cape Scott, Vancouver Island. The waters surrounding Triangle Island lie in the Transition Domain, where the North Pacific Current bifurcates into the northward Alaska Current and the southward California Current. In the winter, southeasterly winds dominate the region and direct surface currents northward along the coast (Thomson 1981). In the spring, the weakening of the Aleutian Low results in a transition to northwesterly winds and southward surface currents (Thomson 1981). The southward surface currents generate weak upwelling along the coast, which interacts with increasing day length to generate spring phytoplankton blooms. The productivity of the surrounding waters allows Triangle Island to support British Columbia's largest and most diverse seabird colony. Notably, during the last comprehensive survey in 1989, the Cassin's auklet population on Triangle Island was estimated at 500,000 pairs (Rodway 1991). To protect the marine habitat of breeding seabirds on Triangle Island, the Canadian federal government has designating the surrounding waters as the Scott Islands Marine National Wildlife Area.

2.3.3. Field Methods

We deployed GPS loggers on Cassin's auklets nesting in West Bay, Triangle Island in mid-May of 2014, 2015, and 2017. Deployments occurred when chicks were 1-4 days old, during which time they require constant brooding, to maximize the likelihood of retrieving GPS loggers. We first excavated and mapped Cassin's auklet burrows during the incubation period to identify occupied burrows suitable for GPS deployment. We then checked occupied burrows for signs of hatching every 3-4 days. When a chick was encountered, we removed the attending adult from the burrow. We banded the adult with a stainless steel band and measured its wing chord (± 1 mm), bill depth (± 0.1 mm), and mass (± 2 g). We assigned sex based on bill depth, where birds with a bill depth >9.9 mm were classified as male, and birds with a bill depth of <9.5 mm were classified as female; birds with a bill depth between 9.5-9.9 mm were classified as unknown sex (Knechtel 1998). We then attached a URIA 68 GPS-UHF logger (Ecotone Telemetry, Gdynia, Poland) to the mantle feathers using waterproof tape (TESA #4651, TESA, Hamburg, Germany). Finally, we applied a small amount of waterproof superglue to the end of the tape to secure the logger. The combined mass of the GPS logger and tape was 5.0 grams, corresponding to 3.0% of the body mass of the lightest adult. We then returned the adult to the burrow, usually within 15 minutes of capture. The GPS loggers recorded the position and instantaneous speed of the bird every 2-5 minutes for the duration of the bird's subsequent foraging trip. We re-checked the burrow two days later when the bird was expected to have returned. Upon recapture, we removed the GPS logger from the bird and returned it to its burrow, usually within 10 minutes.

2.3.4. Environmental Data

To investigate the relationships between Cassin's auklet habitat use and environmental characteristics, I obtained data on 5 static and 2 dynamic variables for the waters surrounding Triangle Island. Variables were chosen because they were both readily available and have been found to influence the habitat use of seabirds in other studies (e.g. Ainley et al. 2009, Adams et al. 2010, Nur et al. 2011). The static habitat variables included were: distance from the nearest coastline ($DIST_{coast}$), water depth, seafloor slope, distance to the 200 m isobath ($DIST_{200}$), and distance to the 1000 m isobath ($DIST_{1000}$). I calculated $DIST_{coast}$ from coastline data downloaded from the BC Freshwater Atlas (https://catalogue.data.gov.bc.ca/dataset/freshwater-atlas-coastlines). I derived the remaining static variables from water depth data downloaded from the British Columbia Marine Conservation Analysis, provided at a 100x100 m resolution (http://bcmca.ca/datafeatures/eco_physical_bathymetry/). The dynamic habitat variables included were chlorophyll *a* and sea surface temperature (SST). I used chlorophyll *a* data collected by the Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) satellite, downloaded as 8-day composite images with 4x4 km resolution from the NASA Ocean Color website (http://oceancolor.gsfc.nasa.gov/). Persistent cloud cover during the exact period of GPS tracking resulted in incomplete satellite images over the study area, so I used the last complete composite image taken prior to the tracking period. For 2014 and 2015, this was the composite for the 8-day period starting May 1st, and for 2017 this was the composite for the 8-day period starting May 9th. I used SST data from the Multi-scale Ultra-high Resolution Sea Surface Temperature (MUR SST) dataset. MUR SST is a blended dataset produced by the NASA Jet Propulsion Laboratory (https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1) using multiple satellite sensors and in-situ observations. I downloaded daily images at 1 km resolution for May 15-21 in 2014, May 9-15 in 2015, and May 10-22 in 2017 using the Marine Geospatial Ecology Tool (MGET) for ArcGIS 10.3 (Roberts et al. 2010). For each date of tracking, I created a weekly SST composite spanning the seven days up to and including the day of tracking. I created each composite by averaging the SST values over the seven day period. Finally, I resampled all environmental rasters to match the extent and resolution of the chlorophyll a dataset (4x4 km), which had the coarsest resolution.

2.3.5. Track Processing

I conducted all analysis in R Statistical Environment (version 3.4.0, R Core Team 2017). I processed GPS tracks to represent a single foraging trip per individual using the package ‘adehabitatLT’ (Calenge 2006). I first removed positions in close proximity to the colony, where Cassin’s auklets do not forage, by excluding points within 500 meters of West Bay. Next, I interpolated foraging tracks to correct for unequal sampling frequencies between individuals and temporal gaps in the data. Temporal gaps were likely the result of increased diving activity by the birds, since submersion interferes with satellite reception. This could potentially bias the data toward non-foraging locations, so I interpolated a new position every one minute along the GPS track using linear interpolation, increasing the number of points in our dataset from 3,363 to 30,698.

2.3.6. Description of Individual Foraging Trips

For each foraging trip, I calculated the following trip descriptors: maximum distance from the colony (km), total distance travelled (km), trip duration (minutes), and the proportion of time spent in the outer third of the foraging trajectory. I also used path segmentation to describe the number of bouts of flying and foraging/resting during foraging trips (Grémillet et al. 2004, McLeay et al. 2010). To do this, I determined the speed threshold between these two behaviours by examining the frequency distribution of instantaneous flight speeds, which revealed a bimodal distribution separated at ~5 m/s (Appendix Figure A1). The mode consisting of speeds >5 m/s represents flying between feeding areas. The remaining positions represent foraging and/or resting, since Cassin's auklets forage by diving from the surface of the water. I was unable to distinguish between resting locations and foraging locations, but resting and foraging occur in similar areas (Manugian et al. 2015). Using a sliding window, I then identified behavioural change-points between successive relocations when the speed threshold of 5 m/s was crossed (Edelhoff et al. 2016). Resulting path segments were identified as "foraging/resting" if the speeds were below 5 m/s, and as "flying" if the speeds were above 5 m/s. For each foraging trip, I then calculated: the total number of flying bouts, the mean duration of flying bouts, and the mean duration of foraging/resting bouts.

2.3.7. Individual-Based and Population-Based Analyses

I used two approaches to examine the habitat use of Cassin's auklets over the three years. First, I used a time-in-area approach to look at the relationships between environmental variables and the amount of time individual birds (n=24) spent in an area (Warwick-Evans et al. 2015). Given that Cassin's auklets display nocturnal colony attendance, daily foraging trips among individuals were approximately the same duration (mean ± s.d. = 1134 ± 41 min). I therefore modelled the absolute time spent in an area, rather than the proportion of time, which allowed me to include incomplete foraging tracks in my analyses (e.g. the proportion of time spent in an area would be higher for incomplete foraging trips because the length of the data series is shorter, biasing the data). For each individual, I overlaid the interpolated GPS track onto a grid of cells matching the resolution and extent of the environmental data (i.e. 4x4 km). I calculated the number of minutes spent in each visited cell by summing the number of GPS locations falling within it. I then extracted the values of each habitat variable for each of the visited cells. I used Linear Mixed Models (LMMs), with individual as a random effect, to model the log number of minutes spent in a cell as a function of habitat characteristics (candidate models described below) using the R package 'nlme' (Pinheiro et al. 2018). I used a log-transformation of the response variable rather than a negative-binomial Generalized Linear Mixed Model (GLMM) so that I could include a spatial correlation structure using the linear-modelling package 'nlme.' I pooled data between the sexes because there were no significant differences in any of the foraging trip descriptors (t-test, p-values > 0.2). Furthermore, a post-hoc addition of an interaction with sex did not improve habitat selection models.

In my second modelling approach, I pooled foraging locations by year and conducted population-based analyses of habitat use within the study area. I identified likely foraging locations as those points associated with a travel speed <5.0 m/s, and then pooled foraging locations from tracks collected within the same year (n=7, n=8, and n=9 in 2014, 2015, and 2017, respectively). Foraging points from each year were overlaid on a grid of the study area, which I defined as the minimum convex polygon (MCP) encompassing all GPS locations recorded over the three years of the study. Grid cells that contained at least one foraging location were coded as '1' (presence), whereas all other cells were coded as '0' (absence). Of the cells coded as '1', I then calculated the number of minutes of use by summing the total number of interpolated locations falling within it. I then extracted static and dynamic environmental data for each cell in the study area. My first model used binomial GLMMs, with year as a random effect, to model the presence or absence of foraging in relation to environmental variables using the R package 'lme4' (Bates et al. 2015). I included an additional term, the autocovariate, in my models to control for spatial autocorrelation. The autocovariate expresses how much the response variable at any one cell reflects the response value in surrounding cells. I used a second-order neighbourhood (5x5 moving window) to calculate the autocovariate term at each focal cell (Crase et al. 2012). My second modelling approach used LMMs to model the log of the number of minutes of use ('intensity of use') in relation to habitat. I included year as a random effect and a spatial correlation structure following the same protocol outlined in the individual-based analysis.

2.3.8. Candidate Models and Model Selection

For both the individual-based and population-based analyses, environmental variables were first checked for collinearity by calculating all pairwise Pearson's correlation coefficients (Zuur et al. 2007). Significant correlations (r > 0.6) were found between the following pairs: $DIST_{coast}$ and $DIST_{colony}$, and water depth and $DIST_{200}$. I therefore excluded $DIST_{coast}$ and $DIST_{200}$ from subsequent analyses. Finally, environmental variables were standardized by subtracting the mean and dividing by two standard deviations so that the coefficients could be directly compared (Schielzeth 2010). I constructed a set of candidate models a priori to investigate the relative importance of static habitat variables, dynamic variables, and the combination of static and dynamic variables. My candidate model set included every possible combination of the two dynamic variables (i.e. SST, chlorophyll *a*, and SST*chlorophyll *a*), and every possible combination of the three static variables ($DIST_{1000}$, depth, and slope). I also included a model with all five habitat variables. I also hypothesized a priori that central-place foraging would constrain habitat selection, such that birds would prefer areas closer to the colony. I therefore included models with the addition of an interaction term with distance from the colony ($DIST_{colony}$), measured using the coordinates of West Bay, Triangle Island (50° 51' 42.030", -129° 05' 14.316"). A full list of candidate models is shown in Table 2.1. Model selection was based on Akaike's information criterion (AICc) and Akaike weights (w_i) (Burnham and Anderson 2002). I identified the most parsimonious model as the model with the lowest AICc. I then calculated ΔAICc for each model as the difference in AICc between that model and the most parsimonious model.

For the individual-based analysis and the 'intensity of use' population-based analysis, models included a spatial correlation structure. I compared Gaussian, exponential, linear, rational quadratic, and spherical correlation structures in the top model using ΔAICc, and found that the rational quadratic correlation structure provided the best fit. I subsequently added this correlation structure to all candidate models and repeated AICc model selection.

2.3.9. Model Performance

I validated the final models from each analysis by plotting the Pearson's residuals against the predicted values and against each response variable included in the model. To assess model performance, I calculated the marginal R^2, which describes the variance explained by the fixed effects, and the conditional R^2, which describes the variance explained by both the fixed and random effects (Nakagawa and Schielzeth 2013). To facilitate comparison with other studies, I also calculated the percent deviance explained by each model relative to an intercept-only model (eg. $100 \times [(deviance_{null} - deviance_{model})/deviance_{null}]$).

2.4. Results

2.4.1. Description of Individual Foraging Trips

Over the three breeding seasons of the study (i.e. years), I recorded 24 individual foraging trips by Cassin's auklets (*Ptychoramphus aleuticus*), obtained from ten females, eight males, and six birds of unknown sex. The basic trip characteristics for each individual are summarized in Appendix Table A1. All trips proceeded as follows: colony departure occurred on average at 0423h, shortly before sunrise. Upon departure, birds travelled quickly away from the colony, reaching two-thirds of their maximum distance (average maximum distance = 75.0 km) from the colony in just 180 min. They spent about 65% of the trip time in the most distal third of the route. Birds returned on average at 2310h, 107 min after sunset, having been away 1134 min and having travelled on average 189.9 km in an elongated loop. During the trip they made on average 14 landings, alternating 67.3 min on the surface (presumably resting and foraging) with 15.4 min of flying. These attributes did not differ between the sexes nor the three study years, and the summary data for all tracks are presented in Table 2.2. However, the predominant direction of trips varied among the years. In 2014, Cassin's auklets travelled north-northwest of Triangle Island and foraged over the shallower waters of the continental shelf. In contrast, Cassin's auklets in 2015 and 2017 generally travelled westward to the continental shelf-slope and beyond (Figure 2.1). In all three years, Cassin's auklets travelled to areas outside the boundaries of the MPA, particularly when individuals travelled north-northwest of the colony in 2014.

2.4.2. Individual-Based Time-In-Area Approach

Four models in the candidate set examining how much time an individual spent in a 4x4 km cell received strong support (AICc < 2.0; Burnham and Anderson 2002; Table 2.3). The top-ranked model (ΔAICc = 0, w_i = 0.21) included the dynamic variable SST (β = -0.38, 95% CI = -0.71 to -0.05), along with $DIST_{colony}$ (β = 0.48, 95% CI = 0.23 to 0.74), and their interaction ($SST{:}DIST_{colony}$: β = -0.37, 95% CI = -0.84 to 0.10), and received approximately four times the support of the null model (Appendix Table A2). The top model indicated that as SST decreased, Cassin's auklets spent more time in a cell, and that this effect was stronger at greater distances from the colony (Figure 2.2a). At a distance of 50 km, corresponding to two-thirds the maximum distance for an average foraging trip, an increase in SST from 10.2º C to 11.2º C was estimated to decrease the amount of time spent foraging in a cell from 14.7 to 9.1 min. At 75 km (the mean maximum distance), an increase in SST from 10.2º C to 11.2º C was estimated to decrease the amount of time spent in a cell from 21.3 to 9.0 min.

Two of the strongly supported models included the static variable slope (Appendix Table A2). One of these models, which included the variables slope ($\beta = 0.17$, 95% CI = 0.03 to 0.21), $DIST_{colony}$ ($\beta = 0.45$, 95% CI = 0.19 to 0.70), and their interaction ($\beta = 0.12$, 95% CI = -0.34 to 0.57), received almost identical support to the top-ranked model ($\Delta AICc=0.39$, $w_i=0.17$). The model indicated that Cassin's auklets spent more time in cells where the underlying bathymetry had a greater slope, and that the effect was stronger at greater distances from the colony (Figure 2.2b). At 50 km from the colony, as the bathymetry changed from a relatively shallow slope of 4º to a steeper slope of 24º degrees, the amount of time spent in a grid cell increased from 10.9 to 16.9 min. At 75 km from the colony, the amount of time spent in a grid cell increased from 13.5 to 24.3 min over the same temperature range. Lastly, two of the strongly supported models included the static variable $DIST_{1000}$: the model including $DIST_{1000}$, $DIST_{colony}$, and their interaction ($\Delta AICc=1.73$), and the model including $DIST_{1000}$, slope, and their interactions with $DIST_{colony}$ ($\Delta AICc=1.87$). Both models indicated that Cassin's auklets spent more time in cells that were closer to the 1000 m isobath, and that the effect was stronger at greater distances from the colony. However, the two models including the $DIST_{1000}$ variable received considerably less support than the models including the variables SST or slope (w_i = 0.09 and 0.08, respectively).

Unexpectedly, I found a positive effect $DIST_{colony}$ in all supported models. Controlling for other environmental variables, Cassin's auklets spent more time in cells further away from the colony, which could indicate that competition or prior experience is contributing to habitat use. Overall, my results suggest that one dynamic variable – SST, and one static variable – slope, are the most important environmental variables predicting time spent in a cell, but model performance was low. In the top-ranked model, which included SST, $DIST_{colony}$, and their interaction, the conditional R^2 explained 19% and the marginal R^2 explained 7% of the variation. In the second-ranked model, which included slope, $DIST_{colony}$, and their interaction, the corresponding values were 13% and 4%.

2.4.3. Population-Based Analyses

Only one model in the candidate set examining the probability of foraging within a grid cell received strong support (AICc < 2.0, Appendix Table A3). The top-ranked model included the dynamic variable, SST ($\beta = -0.5$, 95% CI = -0.82 to -0.19), $DIST_{colony}$ ($\beta = 0.4$, 95% CI = 0.08 to 0.72), and their interaction ($SST{:}DIST_{colony}$: $\beta = -0.15$, 95% CI = -0.8 to 0.49). This model received over 13 times the support of the null model and over seven times the support of the next ranked model ($w_i = 0.65$, Appendix Table A3). This model indicated that as SST increased, the probability of foraging within a grid cell decreased, and that this effect was stronger at greater distances from the colony (Figure 2.3a). At 50 km from the colony, as SST increased from 10.4º C to 11.4º C, the probability of foraging in a grid cell was predicted to decrease from 8.5% to 4.1%. While at 75 km from the colony, as SST increased from 10.4º C to 11.4º C, the probability of foraging in a grid cell was predicted to decrease from 10.8% to 4.6%. Model performance was moderate; both the marginal and conditional R^2 explained 23.4% of the variation. The probability of foraging in a grid cell, predicted using the top-ranked model and SST values over each tracking period, is shown in Figure 2.4. The degree to which the areas with the highest probability of foraging were protected varied across years. In 2014, when birds travelled north-northwest of the colony, much of the area fell outside the boundary of the MPA, while protection was greater in 2015 and 2017.

Five models in the candidate set examining the intensity of use within a grid cell received strong support (AICc < 2.0). The four highest-ranked models included the dynamic variable SST and indicated that Cassin's auklets spent more time foraging in grid cells with lower SSTs. These models received five to nine times the support of the null model (Appendix Table A4). In the top-ranked model (AICc = 0, $w_i = 0.18$), which only included the variable SST ($\beta = -0.45$, 95% CI = -0.82 to -0.09), an increase in SST from 10.4º C to 11.3º C was predicted to decrease the number of minutes spent foraging in a grid cell from 25.8 to 11.4 min (Figure 2.3b). Two of the five strongly supported models included the dynamic variable chlorophyll *a*, including a model with a similar level of support to the top-ranked model (AICc = 0.5, $w_i = 0.14$). Both models indicated that Cassin's auklets spent more time foraging in grid cells with higher chlorophyll *a* concentrations. Finally, one of the strongly supported models included the static variable $DIST_{1000}$. This model indicated that Cassin's auklets spent more time foraging near the 1000 m isobath, but received less than half the support of the top-ranked model (AICc =

1.6, $w_i = 0.08$). Overall, the model competition suggests that dynamic variables are the most important predictors of intensity of use, with the variable SST receiving the most support. However, model performance was poor; the marginal and conditional R^2 explained 0.5% of the response for the top-ranked model, and 2.7% of the response for the second-ranked model.

2.5. Discussion

Using three years of GPS tracking data, my study provides new insights into the fine-scale movements and habitat use patterns of Cassin's auklets (*Ptychoramphus aleuticus*) breeding at Triangle Island, the world's largest colony of this species. First, I found yearly changes in the spatial distribution of Cassin's auklets, where birds either used areas north-northwest of the colony over the continental shelf (2014), or west of the colony towards the shelf-break (2015 and 2017). Second, I found that Cassin's auklets foraged at considerable distances from Triangle Island, with foraging trips routinely taking them outside the boundaries of the Scott Islands Marine National Wildlife Area. Finally, my analyses, conducted using both individual and population level approaches, indicated that Cassin's auklets use areas with cooler waters. My results therefore suggest that habitat use by Cassin's auklets breeding at Triangle Island is influenced more by dynamic habitat variables than static habitat variables.

2.5.1. Foraging Range and Distribution

In my study, movements of Cassin's auklets mirrored those reported by Boyd et al. (2008), who used aerial radiotelemetry to relocate breeding individuals from Triangle Island while they were foraging at sea. They found that Cassin's auklets used areas westward of the colony in 1999 and 2000, but areas northwest of the colony in 2001. While I verified that these are the main foraging areas, I also found that Cassin's auklets travelled farther from the colony than previously estimated. In the radiotelemetry study, Cassin's auklets were, on average, 55 kilometers away from Triangle Island at the time they were relocated by fixed-wing aircraft (Boyd et al. 2008). However, estimates of foraging range were likely influenced by time of day (i.e. incoming or outgoing locations), survey duration, and aircraft range. In contrast, my fine-scale tracking showed that the mean maximum distance from the colony was 75 km and that Cassin's auklets spent

65% of their time in the most distal third of their foraging trip. This suggests that the extent of the at-sea area used by Cassin's auklets has been previously under-estimated, particularly when considering individual time-budgets. My results also show that birds frequently used habitat outside the boundary of the Scott Islands Marine National Wildlife Area. The foraging trajectories showed that birds routinely left the MPA, and travelled furthest beyond the boundary when using areas north-northwest of the colony (e.g. in 2014). Furthermore, the predicted probability of foraging within a grid cell illustrated that high-use areas occurred outside the MPA in all three years, especially in 2014 (Figure 2.4).

2.5.2. Environmental Predictors of Habitat Use

Using modelling approaches at two different scales of analysis, I found that the habitat use patterns of Cassin's auklets were best explained by the dynamic variable SST. The individual-based analysis provided evidence that Cassin's auklets spent more time in areas with lower SSTs, suggesting that SST directly or indirectly influences their decision to forage in an area, relative to other areas encountered over the course of a foraging trip. Furthermore, the population-based analyses provided evidence that foraging was more likely to occur in areas with lower SSTs, suggesting that SST is related to the observed changes in the foraging distribution of Cassin's auklets between years. The mechanism generating the association between Cassin's auklets and cooler SSTs is unknown, but I hypothesize that it is indirectly caused by the effect of SST on the distribution and abundance of their zooplankton prey. Other alcids, which are primarily visual predators, have been found to return to medium-sized patches where prey have previously been encountered, and then use fine-scale search patterns or local enhancement to locate prey aggregations (Regular et al. 2013). I speculate that Cassin's auklet do the same, primarily using experience and memory to return to productive foraging areas.

SST might be related to both the broad- and fine-scale distribution of the Cassin's auklet's prey for two reasons, which are not mutually exclusive. First, temperature may determine the spatial distribution of their ectothermic prey, such as *Neocalanus cristatus*, a subarctic copepod species that is abundant in subarctic water masses (Mackas et al. 2001; Keister et al. 2011). Second, cooler SSTs may also be indicative of recently upwelled, nutrient-rich waters that can support dense aggregations of zooplankton. Previous research has found that aggregations of the three main prey species taken by Cassin's auklets – *N. cristatus*, and the euphausiids *Thysanoessa spinifera*, and *Euphausia pacifica* – are all more likely to be found in areas of upwelling (Mackas et al. 1997; Marinovic et al. 2002; Santora et al. 2011). In support of this second hypothesis, Manugian et al. (2015) found that Cassin's auklets breeding in the CCS foraged in recently upwelled waters, which were also shown to have higher abundances of euphausiids. In addition, I found that the relationship with SST was stronger at greater distances from the colony in both the individual and population level analyses. This result was unexpected, but could be driven by depressed prey populations in proximity to the colony (Ashmole's halo; Ashmole 1963; Lewis et al. 2001). Alternatively, the effect of distance could be an indication that individuals are relying on local enhancement and previous foraging experience to return to productive foraging areas (Irons et al. 1998, Regular et al. 2013).

Cassin's auklet foraging patterns were not explained by the dynamic variable chlorophyll *a*. I predicted that if Cassin's auklets breeding on Triangle Island targeted recently upwelled water, I would find that foraging activity would be higher in areas with lower SSTs and higher chlorophyll *a* concentrations. However, chlorophyll *a* and SST were not correlated, and I only found limited evidence that chlorophyll *a* explained habitat use. Models including chlorophyll *a* received some support in the population-based analysis of the intensity of grid cell use, but no support in the analysis of the probability of grid cell use, nor in the individual-based analysis. This was unexpected, given that research in the CCS has found that Cassin's auklets target areas of enhanced upwelling (Manugian et al. 2015) and primary productivity (Adams et al. 2010). The chlorophyll *a* estimates I obtained may have failed to predict foraging patterns for at least two reasons. First, satellite-derived chlorophyll *a* has several methodological drawbacks: it does not detect potentially important phytoplankton blooms below the surface, data loss due to cloud cover is common, and there can be a lag between phytoplankton and zooplankton blooms (Suryan et al. 2006, 2012; Gregg and Casey 2007). Second, I was unable to obtain chlorophyll *a* over the exact period of GPS tracking, and this temporal discrepancy may have obscured a relationship with Cassin's auklet habitat use.

Contrary to my predictions, I also found that the at-sea habitat use of Cassin's auklets was poorly explained by static features. I found some evidence that seafloor slope influenced habitat use, with individuals spending more time in areas with more sloping bathymetry relative to other areas visited during individual foraging trips. However, when I looked at the characteristics of foraging areas relative to the entire available area (population-based analyses), I found no evidence that seafloor slope, water depth, or $DIST_{1000}$ influenced the likelihood that a given area would be used. My results contrast with previous work in the CCS that have found that seafloor bathymetry is a strong predictor of at-sea densities of Cassin's auklets. For example, Nur et al. (2011) found that the abundance of Cassin's auklets throughout the CCS was best predicted by seafloor slope and distance to the shelf-slope (1000 m isobath). Similarly, studies of Cassin's auklets breeding on the Channel Islands, California, have found that birds used areas close to seamounts and to the shelf-break (Adams et al. 2004, 2010). My contrasting results might be due to differences in the foraging ecology of Cassin's auklets breeding at Triangle Island vs. those in the CCS. At Triangle Island, the population of Cassin's auklets is estimated at 500,000 pairs (vs. 50,000 pairs at the largest colony in the CCS; Manuwal 1974b, Lee et al. 2007), and density-dependent competition might cause foraging birds to disperse over a large area and use less preferable habitats. It is also possible that the wider dietary breadth of Cassin's auklets at Triangle Island, which includes *N. cristatus* (offshore species; Mackas et al. 2001) and euphausiids (shelf species; Mackas et al. 1997) causes them to exploit a wider range of bathymetries. Alternatively, these differences might be due to the more variable oceanographic conditions around Triangle Island compared with the other Cassin's auklet colonies studied in the CCS. In my study region, zooplankton are usually transported seaward of the shelf due to upwelling and westward currents that move over Cook Bank. However, inter-annual variation in local currents, the strength of upwelling, and even individual weather events within a season, can change the rate and direction of transport (Mackas and Coyle 2005). In this case, zooplankton might be transported onto the continental shelf from their preferred habitats in deeper water. This could explain why *N. cristatus* (an oceanic species) was abundant in diet samples in 2014 (Triangle Island Research Station, unpubl. data), even though birds were found foraging shoreward of the shelf-slope.

2.5.3. Model Performance

Predictive habitat modelling is a promising tool for the identification of suitable at-sea habitat, ensuring that key areas are protected (Louzao et al. 2012). I tested whether biologically relevant and widely-available environmental characteristics were related to Cassin’s auklet habitat use. All approaches indicated that SST was the most important variable, but I found that model performance varied among individual-based and population-based approaches. The individual-based analysis evaluating the number of minutes spent in a grid cell had low performance, with the studied environmental variables explaining 7% of the observed variation. Individuals explained a large portion of the observed variation (fixed and random effects explained 19% of the variance), which is unsurprising given our small sample sizes and the structure of the data. In the population-based analysis, I found that the analysis evaluating the probability of foraging within a grid cell explained 23% of the variance, while the analysis evaluating the intensity of grid cell use only explained 0.005% of the variance. One possibility is that my sample size was adequate to detect drivers of broad-scale (presence/absence) habitat use, but was too small to detect relationships with the intensity of grid cell use. Alternatively, there may be different biotic and abiotic factors determining the potential for an area to have prey (i.e. the probability that foraging will occur there), vs. the profitability of an area (i.e. where birds should spend more time). For instance, the location of prey in the water column, the size of the prey patch, and the presence of conspecifics could all influence how actively an area is used. Marginal and conditional R^2 values were identical, showing that year did not affect the observed relationships between foraging and environmental variables. Higher model performance using presence-absence modelling techniques suggests that this type of habitat model could be used to predict the broad-scale distribution of Cassin’s auklets among years. Model performance could nonetheless be improved. This could be achieved by exploring potential temporal lags between physical forcing, primary production, and zooplankton, or by investigating the importance of additional oceanographic processes, such as the location of persistent fronts and eddies.

The extent to which habitat models can be used in seabird conservation depends on their predictive power, and other studies generally report favourable performance (Paiva et al. 2015; Avalos et al. 2017; Ponchon et al. 2017). However, my results are difficult to compare to other studies for two reasons. First, other studies generally model each year of data independently, either due to limitations of the modelling approach or to determine if environmental drivers of habitat use differ among years (e.g. Deppe et al. 2014; Robertson et al. 2014; Avalos et al. 2017). However, such an approach may be less informative for management because predictive habitat modelling requires knowledge of the environmental variables that can reliably predict habitat use across time. Second, there are currently a diversity of performance metrics such as Area Under the Curve (Avalos et al. 2017), percent deviance explained (Scales et al. 2014), and cross-validation (Scales et al. 2016). Among these approaches, cross-validation is one of the most robust methods because it compares model predictions to a subset of withheld data; however, this also makes it difficult to implement in studies like mine that have relatively small sample sizes. Overall, I suggest also that future studies take a multi-year modelling approach to evaluate the robustness of seabird habitat associations across time (i.e. Green et al. 2015; Warwick-Evans et al. 2018), and when possible, assess performance using cross-validation.

2.5.4. Management Implications

In this study, I demonstrate that foraging distributions can vary dramatically over time, highlighting that tracking data needs to be collected over multiple years to effectively inform the establishment of MPA boundaries. Furthermore, my results suggest that habitat use in some seabirds is best predicted by dynamic ocean features such as SST, rather than bathymetric features. The use of remote sensing should therefore be explored as a means of evaluating changes in important habitat. The influence of dynamic ocean features also highlights the potential utility of creating dynamic MPAs using predictive habitat models. While dynamic MPAs have not yet been implemented, advocates suggest that boundaries which track the movement of optimal habitat over time could be more successful at meeting conservation goals (Hooker et al. 2011), especially with projected changes in oceanographic conditions due to climate change.

Table 2.1 Candidate models used to test the influence of static and dynamic environmental variables on the habitat use of Cassin's auklets.

Model Type	Parameters
Excluding $\text{DIST}_{\text{colony}}$	
Dynamic Variables	SST
	chlorophyll
	SST + chlorophyll
Static Variables	depth
	slope
	DIST_{1000}
	depth + slope
	depth + DIST_{1000}
	DIST_{1000} + slope
	depth + DIST_{1000} + slope
Static and Dynamic Variables	SST + chlorophyll + depth + DIST_{1000} + slope
Including $\text{DIST}_{\text{colony}}$	
	$\text{DIST}_{\text{colony}}$
Dynamic Variables	SST*$\text{DIST}_{\text{colony}}$
	chlorophyll*$\text{DIST}_{\text{colony}}$
	(SST + chlorophyll)*$\text{DIST}_{\text{colony}}$
Static Variables	depth*$\text{DIST}_{\text{colony}}$
	slope*$\text{DIST}_{\text{colony}}$
	DIST_{1000}*$\text{DIST}_{\text{colony}}$
	(depth + slope)*$\text{DIST}_{\text{colony}}$
	(depth + DIST_{1000})*$\text{DIST}_{\text{colony}}$
	(DIST_{1000} + slope)* $\text{DIST}_{\text{colony}}$
	(depth + DIST_{1000} + slope)* $\text{DIST}_{\text{colony}}$
Static and Dynamic Variables	(SST + chlorophyll + depth + DIST_{1000} + slope)*$\text{DIST}_{\text{colony}}$

Table 2.2 **Summary data for GPS tracks obtained from 24 individual early chick-rearing Cassin's auklets at Triangle Island, British Columbia (n=7 for 2014, n=8 for 2015, and n=9 for 2017).**

Foraging trip descriptor	Average	SD	Range	N
Departure from colony, local time	0423h	28 min	0339h - 0521h	24
Departure, minutes before sunrise	82	28	32 - 129	24
Maximum distance from colony (km)	75.0	26.1	38.5 - 113.5	24
Minutes to reach 2/3 maximum distance	180	75	69 - 301	17
Percent time in outer 1/3 of distance	65.2	10.6	33.3 - 81.4	17
No. foraging/resting bouts	14.4	4.7	9 - 25	17
Flying bout duration (min)	15.4	8.0	5.6 - 35.2	17
Rest/feeding bout duration (min)	67.3	20.7	29.9 - 111.3	17
Return to colony, local time	2310h	38 min	2241h - 0053h	17
Return, minutes after sunset	107	37	74 - 205	17
Duration of trip (min)	1134 (18.9 hrs)	41	1062 - 1212	17
Total distance travelled (km)	189.9	56.8	93.6 - 285.3	17

Table 2.3 Models of Cassin's auklet habitat use during early chick-rearing at Triangle Island in 2014, 2015, and 2017 using tracking data obtained from 24 individuals. Only strongly supported models (ΔAICc < 2.0) and null models are reported. All models predicting the number of minutes spent in a cell include individual (n=24) as a random effect and a spatial correlation structure. All logistic models predicting the probability of foraging in a cell include a spatial autocovariate and year (n=3) as a random effect. All models predicting the intensity of use include year (n=3) as a random effect and a spatial correlation structure. I report: K = number of parameters estimated, AICc = Akaike's Information Criterion, ΔAICc = the differences between the AICc of each model and the model with the lowest AICc score, wt = likelihood of each model relative to all other models in the candidate set, % dev. = deviance explained relative to the intercept only model, marginal R^2 = marginal pseudo-R^2, and conditional R^2 = conditional pseudo-R^2 (Nakagawa & Schielzeth 2013).

Parameters	K	AICc	ΔAICc	wt	% Dev.	Marginal R^2	Conditional R^2
Number of minutes spent in a cell (Individual-based analysis)							
SST * $\text{DIST}_{\text{colony}}$	8	3476.5	0.0	0.21	4.61	0.07	0.19
slope * $\text{DIST}_{\text{colony}}$	8	3476.9	0.4	0.17	4.60	0.04	0.13
DIST_{1000} * $\text{DIST}_{\text{colony}}$	8	3478.3	1.7	0.09	4.56	0.04	0.09
(DIST_{1000} + slope) * $\text{DIST}_{\text{colony}}$	10	3478.3	1.9	0.08	4.67	0.04	0.10
$\text{DIST}_{\text{colony}}$ (null)	6	3479.3	2.7	0.05	4.42	0.03	0.13
Probability of foraging in a cell (Population-based analysis)							
SST * $\text{DIST}_{\text{colony}}$	6	1338.2	0	0.65	44.7	0.23	0.23
$\text{DIST}_{\text{colony}}$ (null)	4	1343.3	5.16	0.05	44.5	0.18	0.18
Intensity of use (Population-based analysis)							
SST	6	1415.2	0.0	0.18	3.28	0.005	0.005
(SST + chlorophyll) * $\text{DIST}_{\text{colony}}$	10	1415.4	0.5	0.14	3.82	0.027	0.027
SST + chlorophyll	7	1416.3	1.1	0.10	3.35	0.003	0.003
SST * $\text{DIST}_{\text{colony}}$	8	1416.2	1.1	0.10	3.49	0.004	0.004
DIST_{1000} * $\text{DIST}_{\text{colony}}$	8	1416.7	1.6	0.08	3.46	0.016	0.016
$\text{DIST}_{\text{colony}}$ (null)	6	1420.1	4.8	0.02	2.95	0.007	0.007

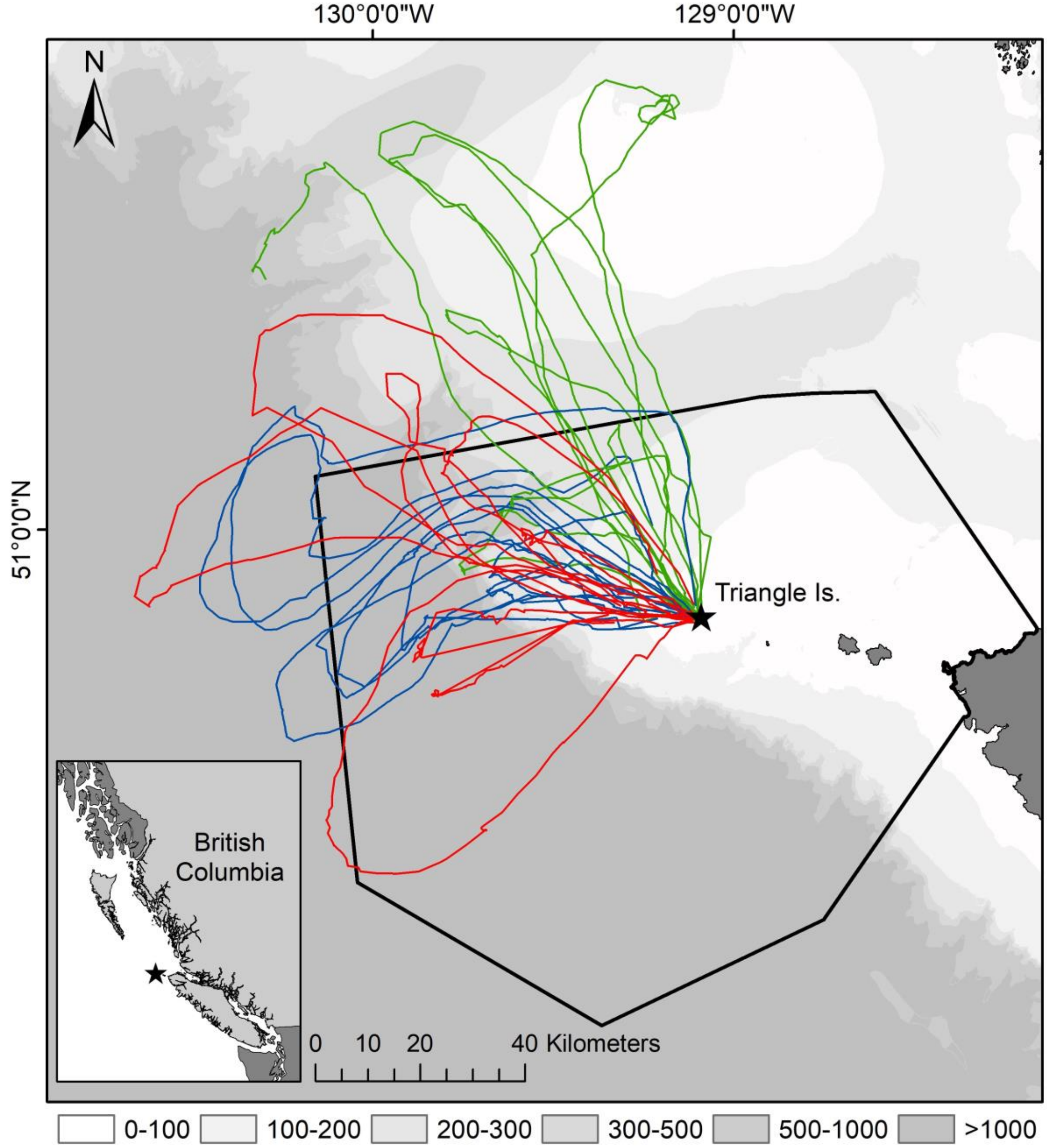

Figure 2.1 Foraging trips of chick-rearing Cassin's auklets in 2014 (*green*, n=7), 2015 (*blue*, n=8), and 2017 (*red*, n=9) recorded via GPS logger. Boundary of the proposed Scott Islands Marine National Wildlife Area is outlined in *black*, and depth contours (m) are shown in *greyscale*.

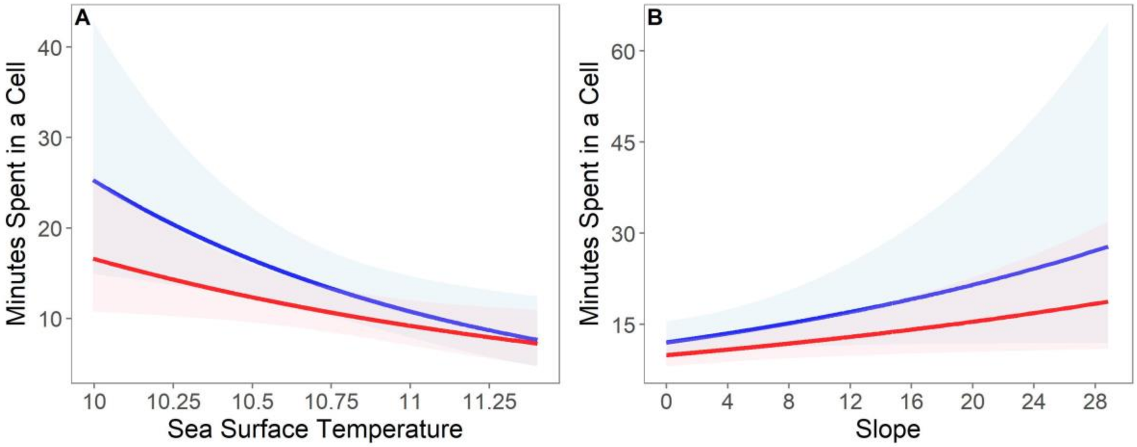

Figure 2.2 Conditional relationships between (A) sea surface temperature, and (B) seafloor slope, and the predicted number of minutes spent in a cell using the two best-supported models. *Red* line shows the relationship when $\text{DIST}_{\text{colony}}$ is held constant at 50 km, *blue* line shows the relationship when $\text{DIST}_{\text{colony}}$ is held constant at 75 km. Bands indicate the 95% confidence interval.

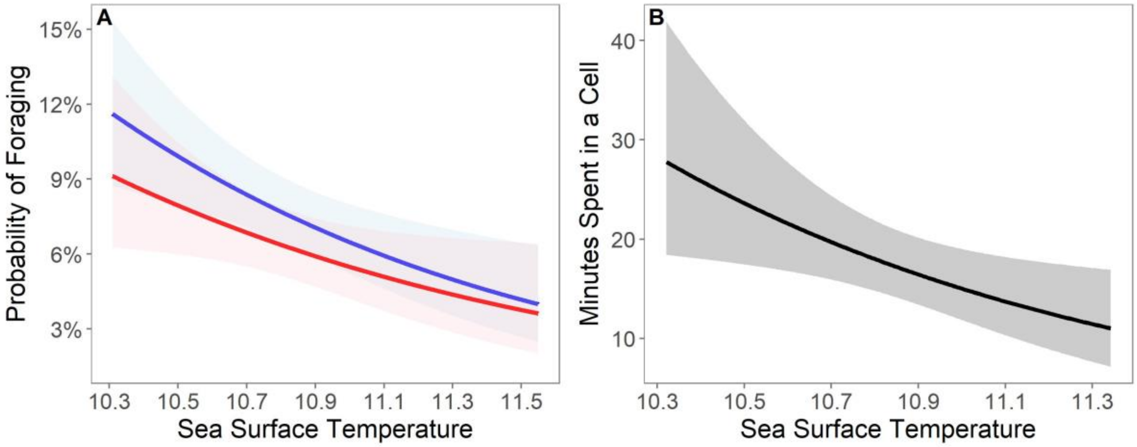

Figure 2.3 Conditional relationships between sea surface temperature and (A) the predicted probability of foraging in a grid cell, and (B) the predicted number of minutes spent foraging in a grid cell using the top-ranked model from each population-based analysis, respectively. In (A), the *red* line shows the relationship when DIST$_{colony}$ is held constant at 50 km, and the *blue* line shows the relationship when DIST$_{colony}$ is held constant at 75 km. Bands indicates the 95% confidence interval.

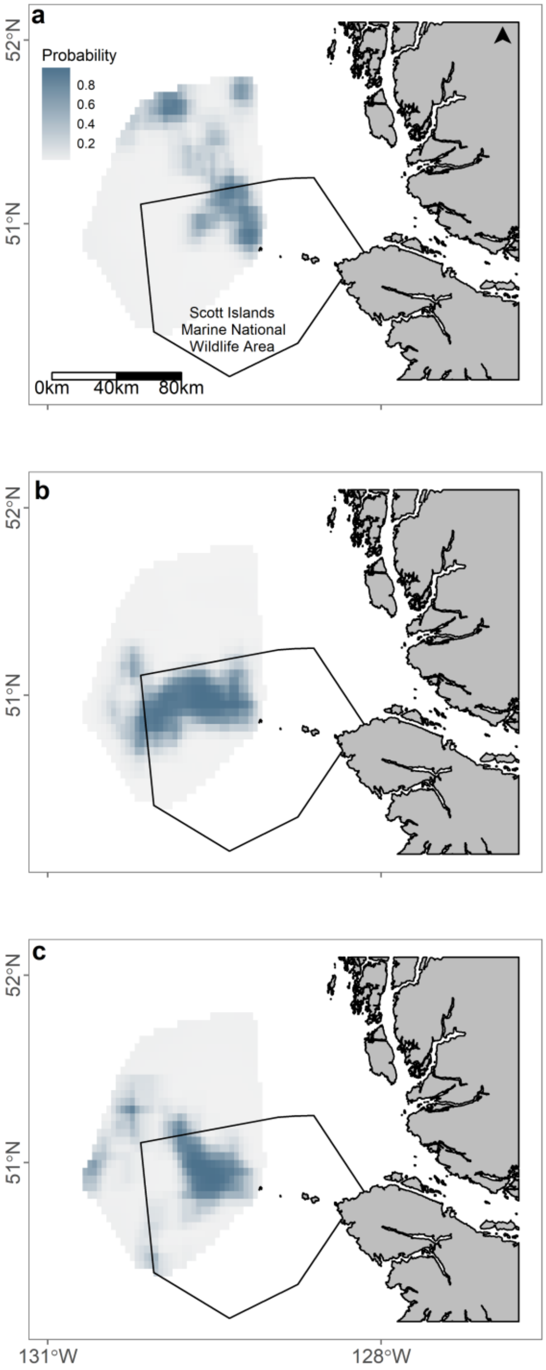

Figure 2.4 The predicted probability of foraging in a grid cell of the study area in relation to the Scott Islands Marine National Wildlife Area (outlined in *black*) in (A) 2014, (B) 2015, and (C) 2017. The study area (*shaded*) was defined as the minimum convex polygon (MCP) encompassing all GPS locations recorded over the three years of the study. The probability of foraging was predicted using the top-ranked model from the population-based analysis (Table 2.3).

Chapter 3. Spatiotemporal variation in the foraging behaviour of chick-rearing rhinoceros auklets in two marine ecosystems

3.1. Abstract

Understanding how spatiotemporal variation in oceanographic conditions affects the foraging behaviour and at-sea distribution of seabirds is critical for effective marine spatial planning. I compared the foraging behaviour of rhinoceros auklets (*Cerorhinca monocerata*) breeding on three colonies: Lucy, Pine, and Triangle Islands. For 2-3 (2014, 2016, 2017) years at each colony, I equipped chick-rearing rhinoceros auklets with GPS loggers and simultaneously recorded nestling diet. I found that rhinoceros auklets breeding on the Lucy Islands showed little inter-annual variation in their movement patterns across years, and consistently fed chicks meals composed of their primary prey, Pacific sand lance (*Ammodytes personatus*). Unsurprisingly, I also found that oceanographic conditions were stable across the three years. In contrast, I found that the movement patterns of birds from Pine and Triangle Islands were variable, apparently in response to oceanographic variability. When the spring phytoplankton bloom occurred in late-March/early April, rhinoceros auklets fed chicks more Pacific sand lance and foraged in nearshore habitats. When the spring bloom was delayed, rhinoceros auklets provisioned their chicks with secondary prey species and used alternate foraging areas, including pelagic, offshore waters. My results suggest that inter-annual variation in foraging movements is influenced by early spring conditions. My results also highlight that effective seabird conservation will require dynamic management strategies, particularly for seabirds that inhabit marine ecosystems that experience greater ocean climate variability.

3.2. Introduction

Movement ecology of seabirds has become an active area of research in recent years, as conservation efforts move towards the identification of at-sea habitat for incorporation into Marine Spatial Planning (Ludynia et al. 2012, Meier et al. 2015). Marine Spatial Planning aims to integrate the management of multiple human activities to promote sustainable use of marine resources (Douvere 2008). Within this framework, protection of the marine environment is achieved by ensuring that human activities occur in areas and in such a way that the effects on the ecosystem are minimized, and by protecting ecologically sensitive areas as Marine Protected Areas (MPAs; Douvere 2008). For vulnerable wildlife such as seabirds, Marine Spatial Planning has become a promising tool to limit anthropogenic threats, such as pollution, incidental bycatch, and competition with fisheries, in important habitat (Croxall et al. 2012, O'Brien et al. 2012). For example, MPAs are beginning to be used to protect at-sea habitat during the breeding season, when seabirds are central-place foragers and face the highest energetic demands. To determine the foraging range of breeding seabirds, and to collect other movement data relevant to Marine Spatial Planning, bio-logging technologies (e.g. GPS and satellite loggers) are being increasingly employed (e.g. Ludynia et al. 2012). However, tracking data are often collected over one or two years, and if these years only represent a narrow set of environmental conditions, then the resulting conservation efforts may fail to protect seabirds over the long term (Bogdanova et al. 2014). Therefore, for Marine Spatial Planning to be successful, conservation biologists must consider any temporal and spatial variation in seabird foraging behaviour.

Spatial and temporal variation in seabird foraging behaviour is driven by the availability and distribution of their prey, which is affected by highly dynamic oceanographic processes. Both regional processes (e.g. currents, strength of upwelling events) and basin-wide climate phenomena (e.g. El Niño Southern Oscillation, Pacific Decadal Oscillation) cause changes in abiotic conditions and marine productivity (McGowan et al. 1998). Marine productivity, in turn, affects the abundance and distribution of prey species available to seabirds (Schreiber and Burger 2001, Frederiksen et al. 2006, Wells et al. 2017). Seabirds can respond to these changes by tracking the distributional shifts of their primary prey (Green et al. 2015), or by switching to secondary prey species (Montevecchi et al. 2009). For example, common murres (*Uria aalge*) typically forage offshore for their primary prey, young-of-year rockfish (*Sebastes spp*.; Wells et al. 2017). However, in years when rockfish are not as abundant, common murres shift to inshore areas where they switch to foraging on northern anchovy (*Engraulis mordax*; Wells et al. 2017). Variation in marine productivity can also cause changes to the foraging behaviour of seabirds if they are forced to increase their foraging effort or search more widely for prey. For many species of seabirds, this has been measured as increases in the foraging home range, the duration and distance travelled during foraging trips, and increased diving effort (Horswill et al. 2017). Finally, foraging movements of breeding seabirds are not only influenced by the spatial distribution of prey, but also by the need to return to the nest at regular intervals (Ydenberg & Davies 2010). This limits the area over which seabirds can forage, and constrains seabirds to select prey that are not only suitable for provisioning chicks but also within foraging range.

The rhinoceros auklet (*Cerorhinca monocerata*) is a medium-sized (~500 g), pursuit-diving alcid found throughout the temperate North Pacific from Japan to California (Gaston & Dechesne 1996). The core of their distribution is in British Columbia, (B.C.), Canada, where 50% of the global population breeds on island colonies along the coastline (Rodway et al. 2018). Across B.C., breeding rhinoceros auklets primarily provision their offspring with Pacific sand lance (*Ammodytes personatus*) – a small forage fish associated with shallow water and sandy substrates (Bertram & Kaiser 1993, Haynes et al. 2007, Robinson et al. 2013). Sand lance is considered the primary prey because bill loads comprised of sand lance have, on average, more calories than bill loads comprised of other forage fish (Pearson et al. in prep). Furthermore, chick growth and fledging success is highly correlated to the prevalence of sand lance (Bertram et al. 1991, Hedd et al. 2006, Borstad et al. 2011), while similar relationships have not been detected with the other prey species commonly found in chick diets (Hedd et al. 2006).

The availability of sand lance is affected by regional and basin-wide ocean climate that control the onset of the spring phytoplankton boom (Hedd et al. 2006, Borstad et al. 2011). When the spring phytoplankton bloom coincides with the emergence of larval sand lance (early – mid April), survival of sand lance is thought to be higher and they are more abundant in the diets of rhinoceros auklets later in the summer (Borstad et al. 2011). In years when sand lance is uncommon in chick diets, provisioning rhinoceros auklets rely on a diversity of secondary prey, including both inshore species (e.g. Pacific herring – *Clupea pallasi* and juvenile salmon – *Oncorhynchus spp*.) and offshore species (e.g. Pacific saury – *Cololabis saira*, juvenile rockfish – *Sebastes spp*.; Vermeer 1980, Bertram et al. 1991, Bertram and Kaiser 1993, Hedd et al. 2006, Thayer et al. 2008, Borstad et al. 2011).

Little is known about the effect of spatiotemporal variation in oceanographic conditions on the at-sea distribution and foraging behaviour of rhinoceros auklets (but see Fox et al. 2017). Variation in productivity, and therefore the abundance of sand lance, may generate differences in the foraging behaviour of birds breeding on different colonies. Here, I used GPS loggers to examine the foraging behaviour of rhinoceros auklets breeding at three colonies in B.C.: Lucy, Pine, and Triangle Islands. The Lucy Islands are located nearshore within Chatham Sound. This area experiences greater oceanographic stability because productivity is mainly driven by freshwater inputs and estuarine processes, leading to more stable levels of primary production from year to year (McGowan et al. 1998, Ware & Thomson 2005). I therefore hypothesized that rhinoceros auklets would show lower variability in their foraging behaviour and in chick diet composition across years, and to exploit shallow areas where sand lance are more likely to be abundant. In contrast, productivity around Pine and Triangle Islands, which have greater exposure to the Pacific Ocean, is instead driven by currents and northwesterly winds that generate coastal upwelling. The onset and intensity of these northwesterly winds can vary each spring, causing substantial inter-annual variation in the timing and magnitude of the spring phytoplankton bloom (Bylhouwer et al. 2013). I therefore hypothesized that foraging movements and diet composition would differ between years. I also expected that the secondary prey selected by rhinoceros auklets would differ for Pine and Triangle Islands, based on their proximity to nearshore and offshore habitats. I hypothesized that rhinoceros auklets from Pine Island would continue to forage inshore because of the local abundance of juvenile salmon and herring in Queen Charlotte Sound (Clarke and Jamieson 2006). In contrast, I hypothesized rhinoceros auklets from Triangle Island would modify their foraging behaviour due to their proximity to the continental shelf-break.

3.3. Methods

3.3.1. Study Species

Rhinoceros auklets (*Cerorhinca monocerata*) are socially monogamous and exhibit nocturnal colony attendance (Gaston & Dechesne 1996). A single-egg clutch is laid in an earthen burrow, and the male and female alternate incubation duties every 24 hours. Chicks are semi-precocial, and are only brooded for 2-4 days (Wilson & Manuwal

1986). During this time, one member of the pair remains in the burrow during the day while the other forages at sea for itself and the chick. Once the chick is capable of thermoregulation, it is left unattended while both adults forage at sea during daylight hours. Adults return to the colony at night to provision their young with small forage fish carried crosswise in their bill (called a ‘bill load’), and often spend a few hours in the nest chamber before departing the colony before dawn.

3.3.2. Field Methods

GPS tracking and diet sampling of rhinoceros auklets was conducted at the Lucy Islands (54° 17’ 42" N; 130° 37' 6" W), Pine Island (50° 58' 40" N; 127° 43' 44" W), and Triangle Island, B.C. (50° 51' 35" N; 129° 4' 34" W) in 2014, 2016, and 2017 (Figure 3.1). Sampling dates and sample sizes for each colony-year of the study are presented in the supplementary materials (Appendix Table B1). To deploy GPS loggers on chick-rearing rhinoceros auklets, we first excavated burrows during daylight hours to confirm the presence of a chick. For each chick found, we measured its wing chord (± 1mm) and calculated its hatch date using the known relationship between wing length and chick age (unpubl. data, Triangle Island Research Station). Chicks were usually found unattended in the nest chamber, but many were still being brooded by an attending adult on Triangle Island in 2017. For these burrows only, we returned on the subsequent day to deploy GPS loggers during daylight hours. This ensured that the adult receiving the GPS logger was not the same bird that was attending the chick during burrow excavation, a precaution taken to minimize stress to the birds. For all other deployments, we returned to the burrows at night and trapped adults either by hand inside the nest chamber, or using purse nets or noose mats placed at the burrow entrance.

We banded each adult with a stainless steel band and measured its wing chord (± 1mm), horn (± 0.1mm), bill depth (± 0.1mm), and mass (± 5g). We then attached a GPS logger (Ecotone Uria 68 or Uria 60, Ecotone Telemetry, Gdynia, Poland) to the mantle feathers using waterproof tape (TESA #4651, Hamburg, Germany). Finally, we applied a small amount of waterproof superglue to the end of the tape to secure the attachment. The combined mass of the GPS logger and tape was either 5.0 or 6.0 grams, corresponding to <1.6% of the body mass of the lightest adult. We then returned the bird to its burrow, usually within 10 minutes of capture, or released it on the surface of the colony if it was caught during the departure period. GPS loggers recorded position and instantaneous speed every 2 minutes in 2014 and 2016, and every 5 minutes in 2017, for the duration of the bird's subsequent foraging trip. If the battery became depleted, GPS loggers switched to recording a position every 60 minutes, ensuring that a complete trajectory was recorded. Upon the birds' return to the colony, data from the GPS loggers were automatically downloaded to a base station. We were unable to retrieve most loggers, but recapture of a few individuals suggests that loggers were shed within 3-5 days.

To examine nestling diet, we collected bill loads of fish from a random sample of provisioning rhinoceros auklets as they returned to the colony after dusk. We caught birds either by hand or using pheasant nets, placed the contents of the bill load in a Whirl-Pak® bag, and immediately released the bird. The fish in each bill load were later identified to genus, and when possible, to species.

3.3.3. GPS Track Processing

I conducted all track processing in R Statistical Environment (version 3.4.0, R Core Team 2017). First, I removed all GPS locations occurring prior to the foraging trip start time, defined by the first at-sea location recorded after deployment, and all GPS locations occurring after the foraging trip end time, defined by the first colony-based position recorded upon the birds' return. In many instances, the foraging trip end time was unavailable because the GPS loggers did not record a position when they were within range of the base station. In these cases, I used the timestamp associated with the last at-sea location recorded on the return flight to the colony.

3.3.4. Fine-scale Movements

To describe spatial differences (i.e. differences among colonies) in the fine-scale foraging behaviour of rhinoceros auklets, I used path segmentation to compare time allocated to flying vs. foraging/resting based on the birds' travel speed. I was unable to test for differences between years because of a potential bias associated with the different sampling frequencies used in 2014/2016 vs 2017 (2 min vs 5 min, respectively). I also restricted my analyses to complete, one-day foraging trips because high temporal resolution is required to accurately identify behavioural change-points. First, I determined the speed threshold between these two behaviours by examining the frequency distribution of instantaneous flight speeds, which revealed a bimodal distribution separated at ~5 m/s (Appendix Figure B1; Gremillet et al. 2004, McLeay et al. 2010). The mode consisting of speeds >5 m/s represents flying between feeding areas, and is in accordance with other estimates of rhinoceros auklet flight speeds (Kikuchi et al. 2015). The remaining positions represent foraging and/or resting, since rhinoceros auklets forage by diving from the surface of the water (Kikuchi et al. 2015). I was unable to distinguish between resting locations and foraging locations, but there is high spatial overlap between these two behaviours (Kato et al. 2003). Next, I estimated a new position every 30 seconds along the GPS track using linear interpolation. Using a sliding window, I then identified behavioural change-points between successive relocations when the speed threshold of 5 m/s was crossed (Edelhoff et al. 2016). Resulting path segments were identified as “foraging/resting” if the speeds were below 5 m/s, and as “flying” if the speeds were above 5 m/s. For each segment, I then calculated the total distance travelled (the sum of the displacements between each successive location) and the duration. For each foraging trip, I then calculated: (1) the total number of flying bouts, (2) the mean distance travelled during flying bouts, (3) the mean duration of flying bouts, (4) and the total distance flown. I used one-way ANOVAs, followed by post hoc multiple comparisons, to test for differences among colonies. Due to small sample sizes in 2014 (n=1 for Lucy Island), I was only able to compare flying bout characteristics for 2016 (Lucy Islands vs Pine Island) and for 2017 (all three islands).

3.3.5. Broad-scale Movements

I investigated temporal changes (i.e. differences among years) in the broad-scale movements of birds from each colony by comparing the maximum distance from the colony and total distance travelled. Using the processed GPS tracks, I calculated both of these foraging trip characteristics using the R package ‘move’ (Kranstauber et al. 2017). Because maximum distance travelled and total distance travelled were strongly correlated (Pearson’s r=0.7), I only conducted statistical comparisons using maximum distance from the colony. I used a one-way ANOVA, followed by post hoc multiple comparisons, to test for differences among years. P-values were adjusted for multiple comparisons using Holm’s method. To avoid pseudo-replication, I restricted my analyses to the first foraging trip completed by each bird. I also included foraging trips with low temporal resolution to ensure that the results would not be biased towards shorter foraging trips, which were less likely to experience battery depletion.

I also used kernel density estimates to compare the location and size of each colony's foraging range across years. I first removed all GPS locations identified as 'flying' (speed > 5 m/s). From the remaining subset of locations, I then selected 100 locations from each complete foraging track to reduce biases in the kernel density estimates. For Pine Island, tracking sample sizes were unequal between the two years (n=5 for 2016, n=7 for 2017), so I randomly selected 5 tracks from 2017. Kernel density estimates were generated using the 'Kernel Interpolation with Barriers' tool in ArcGIS 10.3, which allowed me to exclude landmasses from estimates of suitable habitat (MacLeod 2014). The three user-specified parameters, kernel function, grid cell size, and bandwidth, were kept constant between the colony-years. I used a Gaussian kernel function and a grid cell size of 200 x 200 m, which was small enough to retain information on the shape of the coastline. I used a bandwidth of 7000, which was chosen ad hoc following the methodology of Passadore et al. (2018). Using the resulting kernel density estimates, I used the R package 'spatialEco' (Evans 2017) to estimate the core foraging area and home range as the 50% and 95% volume contours, respectively.

3.3.6. Diet Composition

To compare nestling diet across colony-years, I calculated the percent composition by number of the main prey types, Pacific sand lance (*Ammodytes personatus*), Pacific herring (*Clupea pallasi*), juvenile salmon (*Oncorhynchus spp.*), juvenile rockfish (*Sebastes spp*.), Pacific saury (*Cololabis saira*), and slender barracudina (*Lestidiops ringens*), in each bill load (Thayer et al. 2008). I grouped all other fish and squid species as 'other.' To compare diet composition among colony-years, I implemented a nonmetric multidimensional scaling (NMDS) ordination with a Bray-Curtis distance matrix using the R package 'vegan' (Oksanen et al. 2018). For statistical tests, I used a permutational MANOVA (PERMANOVA, 'adonis' function in 'vegan'), followed by pairwise comparisons using the 'pairwise.perm.manova' function in the R package 'RVAideMemoire' (Hervé 2018). P-values were adjusted for multiple comparisons using Holm's method. Furthermore, I separately examined the prevalence of sand lance because it is highly correlated to rhinoceros auklet breeding success in the study region (Bertram et al. 1991, Bertram & Kaiser 1993, Hedd et al. 2006). Given the bimodal distribution of the data (58% of bill loads contained zero sand lance, while 21% of bill loads contained exclusively sand lance), I coded each diet sample as containing at least one sand lance (“1”), or containing no sand lance (“0”). I then used a binomial logistic regression with a logit link to test for differences among colony-years.

3.3.7. Oceanographic Conditions and Breeding Phenology

To evaluate my expectations that oceanographic conditions are more stable from year to year around the Lucy Islands, but variable around Pine and Triangle Islands, I estimated both the timing of the spring phytoplankton bloom and breeding phenology for each colony-year. In the study system, young-of-year sand lance are more common in chick diets when the spring phytoplankton bloom begins in early April, and these years are also associated higher fledgling production (Borstad et al. 2011). Furthermore, these years are also associated with earlier breeding phenology, which is believed to be caused by favourable foraging conditions during the pre-laying period created by an early spring bloom (Hipfner et al. 2010, G. Crossin unpubl. data). I estimated the onset and magnitude of the spring phytoplankton bloom using mean global chlorophyll *a* concentrations derived from the Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) satellite. I downloaded rolling 32 day composites at 4 km resolution from the NASA Ocean Color website (http://oceancolor.gsfc.nasa.gov/) for the following available start dates: February 26, March 6, March 14, March 22, March 30, April 7, April 15, and April 23 of each study year. Following the methods of Borstad et al. (2011), I then calculated the mean chlorophyll a concentration (mg/m^3) over a 45 km radius circle centered on each colony for each period. I estimated the onset of the phytoplankton bloom as the period during which chlorophyll concentrations first exceeded 2mg/m^3, which is considered significantly different from winter concentrations (<1 mg/m^3, Jackson et al. 2015). Finally, I used mean hatch date as an indication of breeding phenology for each colony-year.

3.4. Results

3.4.1. Fine-scale Movements

Over the three breeding seasons of the study (i.e. years), I recorded at least one foraging trip from 39 of the 69 rhinoceros auklets carrying GPS loggers, summarized in

Appendix Table B2. Of these, 21 GPS loggers collected data for two to three foraging trips. For the subset of birds that were tracked for more than one foraging trip, the direction travelled and the maximum distance from the colony was correlated between the first and second foraging trip (bearing: Pearson's r=0.57, N=21 p=0.007; maximum distance from the colony: Pearson's r=0.6, N=21, p=0.004). Successive foraging trips differed by an average of 21.3 km, but one bird tracked on Pine Island in 2017 showed successive foraging trips differing by 93.3 km.

Rhinoceros auklets departed the colony at 0344h ± 46 min, and spent one, and sometimes two days, foraging at sea. Birds spent 57% of their trip time in the most distal third of their route, though this was highly variable among individuals at the same colony and between colony-years (range: 6 – 87%, Appendix Figure B2). Foraging trips consisted of short bouts of flying, followed by longer bouts of foraging and/or resting. Periods of foraging and/or resting were, on average, 131.6 ± 70.0 minutes (range: 40.9-361.8). Birds undertook 11 ± 5 (range: 4-25) flying bouts per foraging trip, with flying bouts lasting 16.8 ± 11.3 minutes (range 3.1-61.5) and covering 12.9 ± 10.0 km (range: 1 – 50.6). While I was unable to compare characteristics of flying bouts between years because of differences in sampling frequencies (2 min in 2014 and 2016, 5 min in 2017), comparisons between colonies within years showed that birds breeding on Pine Island in 2016 differed in their foraging behaviour. In 2016, birds from Pine Island undertook significantly fewer flying bouts (Welch's t-test: $t_{4.88}$=2.67, p=0.045, N=9), and spent a smaller proportion of their time flying (t-test: $t_{6.23}$=1.89, p=0.11, N=9) than birds from the Lucy Islands (Table 3.1). However, there were no significant differences (Student's t-test, all p-values > 0.1) in the distance covered during flying bouts (7.5 ± 5.2 km, range: 1.0 – 17.7 km), nor their duration (11 ± 6 min, range: 3 – 24 min). In 2017, birds from Lucy, Pine, and Triangle Islands did not differ in flying bout descriptors (ANOVA, all p-values > 0.37). During foraging trips in 2017, rhinoceros auklets undertook 11 ± 4 flying bouts (range: 4 – 18). Bouts of flying lasted 20 ± 13 min (range: 10 – 62 min), and covered 14.5 ± 11.5 km (range: 6.3 – 50.5 km).

3.4.2. Broad-scale Movements

I found that inter-annual consistency in foraging movements, both in terms of maximum distance travelled and at-sea distributions, varied between the colonies. First, maximum distance from the colony varied between colony-years (ANOVA, $F_{(6, 32)}$=3.8, p=0.006; Figure 3.2), and post hoc multiple comparisons showed that birds from Pine Island tended to travel shorter distances in 2016 than in 2017 ($F_{(1,10)}$=7.19, p=0.069). In 2016, rhinoceros auklets travelled a mean maximum distance of 25.3 ± 22.9 km (mean ± sd, n=5), while in 2017, this increased to 67.1 ± 28.8 km (n=7). In contrast, I found no annual differences (all p-values > 0.34) at Triangle Island or the Lucy Islands. At Triangle Island and the Lucy Islands, birds travelled 87.2 ± 17.8 km (n=9) and 64.0 ± 25.6 km (n=18), respectively.

Second, I found that inter-annual consistency in the at-sea distributions of rhinoceros auklets also varied between the three island colonies. Rhinoceros auklets breeding on the Lucy Islands foraged in three areas in all three years: coastal habitat within Chatham Sound, Dogfish Bank, and Rose Spit in western Hecate Strait (Figure 3.3 A-C, Appendix Figure B3). However, more birds foraging near Dogfish Bank in 2017, corresponding with increases in both the core foraging range (433.6 km^2 to 800.0 km^2), and the home range (1761.1 km^2 to 3055.8 km^2; Figure 3.4).

Rhinoceros auklets breeding on Pine Island used different areas in each year of tracking. In 2016, rhinoceros auklets stayed near the colony, using areas north of Hope and Nigei Islands (Figure 3.3 D-E). In 2017, rhinoceros auklets continued to use these areas, but also travelled further west to areas along northern Vancouver Island. Three of the seven birds tracked in 2017 also continued southwest from Cape Scott, travelling to oceanic waters beyond the continental shelf-break. As a result, the core foraging range increased from 167.4 km^2 in 2016 to 384.0 km^2 in 2017, and the home range increased from 627.4 to 1445.4 km^2 (Figure 3.4).

Rhinoceros auklets breeding on Triangle Island used similar areas during both years of tracking (2014 and 2017), travelling south or southwest of the colony to areas beyond the continental shelf-break (Figure 3.3 F). Small sample sizes in 2014 precluded kernel density estimates, but in 2017 the core foraging range was 692.3 km^2, and the home range was 2686.0 km^2 (Figure 3.4).

3.4.3. Nestling Diet and Prevalence of Sand Lance

Nestling diets were consistent on the Lucy Islands, but differed from year to year on Pine and Triangle Islands (Figure 3.5). Pairwise comparisons using PERMANOVA indicated that diet composition at the Lucy Islands did not vary among the three years (Figure 3.6; all p-values > 0.18). Bill loads were comprised of herring or sand lance, with juvenile salmon making up a small proportion of the diet. In contrast, diet composition at Pine and Triangle Islands during each year of study were significantly different from each other, and from diet composition at the Lucy Islands (Figure 3.6; p-values = 0.021). In order of percent composition by number, chick diets at Pine Island in 2016 primarily consisted of juvenile rockfish, sand lance, and herring. In contrast, diets in 2017 consisted of herring, with lesser amounts of sand lance, juvenile salmon, juvenile rockfish, saury, and slender barracudina. At Triangle Island in 2014, chick diets were made up of sand lance, juvenile rockfish, and saury, while rockfish, and to a lesser extent slender barracudina, dominated the diets in 2017.

Sand lance was common in nestling diets in all three years at the Lucy Islands. By percent composition by number, sand lance comprised approximately 40% of diet in all years. However, the probability of a bill load containing sand lance was significantly higher in 2016, at 72%, than in 2014 and 2017 (48% and 46%, respectively; Figure 3.7). At Pine and Triangle Islands, the amount of sand lance also varied significantly between years. At Pine Island, the probability of a bill load containing sand lance decreased from 42% in 2016 to 21% in 2017, and at Triangle Island, the probability of a bill load containing sand lance decreased from 48% in 2014 to 10% in 2017 (Figure 3.7). The secondary prey species consumed by rhinoceros auklets chicks were inshore species at Lucy Islands, and both inshore and offshore species at Pine and Triangle Islands. At the Lucy Islands, herring, along with lesser amounts of juvenile salmon, were the secondary prey found in nestling diets in all three years. At Pine Island, secondary prey including herring and juvenile salmon, and offshore species such as juvenile rockfish, saury, and slender barracudina. At Triangle Island, secondary prey mainly consisted of offshore species, such as juvenile rockfish and saury in 2014, and juvenile rockfish and slender barracudina in 2017. Inshore secondary prey were uncommon; herring was never found during chick diet sampling, and salmon only made up a small proportion of the diet (6.6%) in 2014.

3.4.4. Oceanographic Conditions and Breeding Phenology

I found that the timing of the spring bloom was more consistent from year to year at the Lucy Islands and at Triangle Island, but differed between years at Pine Island

(Figure 3.8). At the Lucy Islands, the phenology and magnitude of the spring phytoplankton bloom was similar across all three years, but chlorophyll *a* concentrations became elevated slightly earlier in 2016. At Triangle Island, the timing of the spring phytoplankton bloom was similar during both years of GPS tracking (2014 and 2017), and occurred much later than at the Lucy Islands despite its more southerly latitude. At Pine Island in 2016, chlorophyll *a* concentrations were elevated above 2 mg/m^3 from the beginning of the time series (composite of February 26-March 30), indicating an early and strong spring bloom. In contrast, chlorophyll *a* concentrations in 2017 did not become consistently elevated above 2 mg/m^3 until the April 15-May 16 composite.

Similarly, breeding phenology was significantly different between colony-years (Welch's ANOVA, $F_{(6, 40.86)}$=11.26, p<0.001, N=160; Figure 3.9). Post hoc comparisons show that the timing of hatch did not differ between years at the Lucy Islands (Welch's ANOVA, $F_{(2, 23.4)}$=1.45, p=0.26). In contrast, hatch date was significantly earlier in 2016 than in 2017 at Pine Island (ANOVA, $F_{(1, 19)}$=20.49, p<0.001), and significantly earlier in 2014 than in 2017 at Triangle Island (Welch's ANOVA, $F_{(1, 50)}$=13, p=0.001).

3.5. Discussion

Seabirds may respond to variation in oceanographic conditions that alter the abundance and distribution of their prey by tracking distributional shifts in their primary prey or by relying on alternate prey species, both of which may be accompanied by increases in foraging effort. I found that rhinoceros auklets breeding on the Lucy Islands, which experiences more stable oceanographic conditions, showed predictable foraging movements between years. Here, chick diet composition also consistently contained a high proportion of sand lance. In contrast, I found that rhinoceros auklets breeding on Triangle and Pine Islands showed more variable movement patterns and diets between years. My results provide baseline data on the spatial distribution of rhinoceros auklets in B.C. More broadly, the observed spatiotemporal variation in foraging behaviour also has important implications for conservation and management.

As predicted, I found that rhinoceros auklets breeding at the Lucy Islands, located nearshore within Chatham Sound, exhibited little inter-annual variation in foraging behaviour. GPS tracking revealed that birds travelled similar distances across years and consistently exploited several distinct foraging areas: coastal areas of

Chatham Sound, and Rose Spit and Dogfish Bank in western Hecate Strait (Figure 3.3 A-C). All three of these areas comprise shallow, sandy habitats that are likely to support abundant sand lance (C. Robertson, pers. comm.). Corroborating the results of Bertram and Kaiser (1993), I found that nestling diets were invariable and consisted of sand lance (~40% each year), along with juvenile salmon and herring. Finally, I showed that the timing of spring phytoplankton bloom and average hatch dates were consistent across the three years of the study, confirming that oceanographic conditions around the Lucy Islands were relatively stable. Taken together, my data suggests that rhinoceros auklets breeding on the Lucy Islands show consistent foraging movements because they can maintain diets of sand lance owing to the oceanographic stability of the region. However, the three main foraging areas were not used equally across years. In 2017, more individuals foraged on Dogfish Bank, which was apparent by the increase in the size of core foraging range and home range.

I found that rhinoceros auklets breeding on Pine and Triangle Islands altered their foraging behaviour between years, apparently in response to oceanographic variability. In 2016, birds from Pine Island foraged in shallow areas close to the colony, and sand lance were a common component of nestling diets. In 2017, a year when the spring phytoplankton bloom around Pine Island was delayed, rhinoceros auklets altered their foraging behaviour. They travelled greater distances during their foraging trips, and the size of the core foraging area and home range increased as their distribution shifted westward into oceanic waters. In that same year, forage fish trawls conducted by the Department of Fisheries and Oceans (DFO) found virtually no sand lance around Pine Island and Triangle Island (Jackie King, pers. comm.). This suggests that oceanographic conditions in 2017 led to poor sand lance recruitment, causing a shift in rhinoceros auklet foraging behaviour. At Triangle Island, rhinoceros auklets used oceanic waters beyond the continental shelf-break in both 2014 and 2017. These two years were also characterized by low amounts of sand lance in nestling diets and delayed spring phytoplankton blooms (relative to other colonies studied in the same years). This is contrast to conditions experienced in 2002, when rhinoceros auklets from Triangle Island were found to be foraging on the continental shelf. In that year, a radiotelemetry study relocated provisioning rhinoceros auklets over the shallow waters of Cook Bank and Goose Island Bank (McFarlane Tranquilla et al. 2005). Diets were 76% sand lance (% composition by number, Triangle Island Research Station, unpubl. data), and the spring phytoplankton bloom was early (Borstad et al. 2011). Overall these results are consistent with the hypothesis that high primary production in early spring plays an important role in determining the availability of sand lance later in the summer. They also suggest that in years of poor sand lance recruitment, rhinoceros auklets breeding on Pine and Triangle Islands rely more on oceanic habitat and must increase their foraging effort.

However, sand lance was not especially uncommon on Triangle in 2014, and I therefore would have expected to find at least some birds in nearshore, shallow habitat. First, it’s possible that, given my small sample sizes in 2014 (n=3), I didn’t track individuals that delivered sand lance simply by chance. Alternatively, it’s possible that sand lance was not abundant enough in 2014 to allow rhinoceros auklets to forage exclusively on Cook Bank. Instead, birds may have predominantly relied on oceanic prey, while some individuals were then able to ‘top up’ their bill loads with sand lance on the return flight to the colony (Burger et al. 1993). To resolve these discrepancies would require additional tracking data during years of more favourable conditions around Triangle Island. In a year of high sand lance availability, I would expect birds to travel to the east to Cook Bank or northeast to Goose Island Bank (McFarlane Tranquilla et al. 2005). While in an intermediate year, it is uncertain if birds would use a ‘topping up with sand lance’ strategy after returning from oceanic waters, or if there is individual variation in movements (e.g. some bird forage in oceanic habitats to the west while others forage on the shelf to the east and northeast).

In years when rhinoceros auklets relied on secondary prey, birds from nearshore Pine Island responded differently from birds from offshore Triangle Island. Birds from Pine Island in 2017 showed two movement patterns; approximately half of the individuals foraging on the continental shelf along northern Vancouver Island, while the other half travelled to oceanic waters beyond the continental shelf break. As suggested by these two movement patterns, nestling diet composition was comprised of both inshore secondary prey species (juvenile salmon and herring), as well as species associated with the continental shelf-break and slope (juvenile rockfish and Pacific saury). At Triangle Island, there was very little variability in movement patterns, and all birds travelled to oceanic waters beyond the continental shelf-break. In both years, rhinoceros auklets returned with offshore secondary prey species, including Pacific saury in 2014, and rockfish and slender barracudina in 2017. This is consistent with previous studies that have inferred from the analysis of nestling diets that birds from

Triangle Island often use oceanic habitats (Vermeer 1980, Bertram & Kaiser 1993, Hedd et al. 2006). However, this result is somewhat surprising given that Cook Bank, where some of the birds from Pine Island foraged in the same year (2017), is closer. One possibility is that, during years of low sand lance abundance, birds from Triangle Island avoid Cook Bank due to intraspecific competition.

Spatial segregation of seabirds from neighbouring colonies has been documented in Adélie penguins (*Pygoscelis adeliae*), Cape gannets (*Morus capensis*) and Northern gannets (*Morus bassanus*; Ainley et al. 2004, Gremillet et al. 2004, Wakefield et al. 2013). Models predict that spatial segregation results when individuals of the smaller colony avoid the foraging range of the larger colony because of higher density-dependent competition (Wakefield et al. 2013). In this case, birds from the smaller Triangle Island colony (42,000 pairs) may be avoiding the foraging areas of birds breeding on Pine and neighboring Storm Island (150,000 pairs). Alternatively, offshore prey species may be preferable to nearshore prey species (e.g. for nutritional content or energetic density; Vermeer and Devito 1986, Beaubier and Hipfner 2013), but the cost of travelling to offshore areas may be an impediment to birds from Pine Island. However, further work is needed to distinguish between these two possibilities. Overall, my results show that rhinoceros auklet are highly flexible generalists predators, using both inshore and offshore habitats and prey species when sand lance are not available. This contrasts with the general notion that rhinoceros auklets in B.C. are a neritic species (Burger et al. 1993), but is similar to the habitat use patterns documented in other parts of their range. For example, rhinoceros auklets breeding in Southern California, where the forage fish community does not include Pacific sand lance, also primarily forage near the continental shelf-break (Wilkinson et al. 2018).

3.5.1. Management Implications

I anticipate that my results will inform ongoing Marine Spatial Planning projects along British Columbia’s coastline. Specifically, this study has identified several important foraging areas that should be considered during marine zoning under the the Pacific North Coast Integrated Management Area (PNCIMA) Plan and efforts to improve emergency response readiness under the Oceans Protection Plan. First, my work on the Lucy Islands supports earlier research that has identified important foraging habitat on Dogfish Bank, an area that is seldom surveyed for seabirds because ships-ofopportunity cannot cross the shallow waters of the bank (Government of Canada 2017b, but see LGL et a. 2009, Fox et al. 2017). This research therefore fills an important knowledge gap, and should be considered when reviewing proposals to develop offshore windfarms in western Hecate Strait (LGL et al. 2009). Second, my results support previous ship-based surveys that have identified Chatham Sound and Queen Charlotte Sound as important foraging areas for rhinoceros auklets breeding on the Lucy Islands and Pine Island, respectively (Fox et al. 2016). Both of these areas experience high shipping traffic and chronic oil pollution (Williams & O'Hara 2010, Fox et al. 2016), and should be priority sites for emergency response planning. More broadly, my results should guide the design of future studies aiming to collect baseline information on the marine distribution of seabirds. Specifically, I recommend that studies should be conducted over several years in order to capture year to year variation in movements driven by ocean climate variability.

3.5.2. Conclusions and Future Directions

In this study, I demonstrate that rhinoceros auklets have highly flexible foraging behaviour, and that inter-annual variation in foraging movements reflects ocean climate variability. My results highlight that effective conservation of seabirds requires multiple years of tracking data, particularly for marine ecosystems that experience higher variability. Failure to incorporate inter-annual variation could lead to ineffective marine planning and risk assessment. For this reason, I suggest that further tracking should be conducted at Pine and Triangle Islands, which I hope will capture additional variation in oceanographic conditions and foraging behaviour.

Table 3.1 **Summary data for breeding phenology, diet composition, foraging trip characteristics, and spatial distribution of chick-rearing rhinoceros auklets. For breeding phenology and individual trip characteristics, values are the mean ± sd (range: minimum – maximum). For diet, values are the probability of a bill load containing sand lance (with the 95% confidence intervals) predicted from logistic regression.**

	Lucy Islands			**Pine Island**		**Triangle Island**	
	2014	**2016**	**2017**	**2016**	**2017**	**2014**	**2017**
Breeding Phenology							
N chicks	53	24	10	10	11	44	8
Est. hatch	June 24 ± 5.8	June 21 ± 7.6	June 23 ± 5.7	June 17 ± 3.9	June 25 ± 4.6	June 16 ± 6.4	June 19 ± 1.1
date	(June 16 – July 12)	(June 11 - July 5)	(July 16 – July 3)	(June 11 - 22)	(June 19 - July 2)	(June 7 - 27)	(June 18 - 21)
Diet							
N bill loads	99	46	61	31	100	61	20
Prob. of	0.48	0.72	0.46	0.42	0.21	0.48	0.10
containing S.L.	(0.39 - 0.58)	(0.57 - 0.83)	(0.34 - 0.58)	(0.26 - 0.6)	(0.14 - 0.3)	(0.35 - 0.6)	(0.03 - 0.32)
Individual Trip Characteristics							
N tracks [*]	2 [1]	8 [5]	8 [5]	5 [4]	7 [5]	3 [3]	6 [4]
Max. Dist. (km)	-	54.3 ± 23.5	73 ± 27	25.3 ± 22.9	67.1 ± 28.8	88 ± 26.6	86.8 ± 14.9
	(47.4 - 86.1)	(32.2 - 87.2)	(32.2 - 110)	(5.8 - 62.8)	(30.8 - 107.6)	(59.6 - 112.5)	(63.2 - 106.6)
Tot. Dist. (km)	-	178.1 ± 95.6	221.2 ± 75.9	73.5 ± 59.4	220.4 ± 74.9	197.9 ± 56.9	191.5 ± 34.5
	(220.8 - 280.8)	(94.8 - 378.2)	(109.8 - 348.7)	(25.8 - 174.6)	(113 - 298.1)	(137.4 - 250.4)	(137.3 - 233)
Sampling freq.	2	2	5	2	5	2	5
# flying bouts	14	16 ± 7.1	10 ± 2.6	7 ± 2.2	9.8 ± 4.2	7.3 ± 2.9	13 ± 3.6
	-	(7 - 25)	(7 - 14)	(5 - 10)	(4 - 14)	(4 - 9)	(10 - 18)
Avg. duration of	14.1	11.1 ± 3.7	18.9 ± 8.4	10.2 ± 9.2	23.1 ± 21.6	21.7 ± 2.5	16.6 ± 6.4
flying bouts (min)	-	(7.3 - 16.1)	(10.7 - 31.6)	(3.1 - 23.6)	(11.7 - 61.5)	(18.9 - 23.5)	(10.1 - 24)
Dist. flown during	11.5	8.1 ± 3.4	13.3 ± 7	6.9 ± 7.4	18.2 ± 18.3	21.4 ± 3.7	11.5 ± 5
flying bouts (km)	-	(4.5 - 12.8)	(6.3 - 24.1)	(1 - 17.7)	(7.7 - 50.6)	(17.2 - 23.9)	(6.6 - 17.6)
Proportion	0.14	0.14 ± 0.09	0.13 ± 0.04	0.05 ± 0.04	0.12 ± 0.04	0.13 ± 0.04	0.15 ± 0.04
spent flying	-	(0.06 - 0.28)	(0.07 - 0.17)	(0.01 - 0.12)	(0.07 - 0.17)	(0.08 - 0.17)	(0.1 - 0.18)
Spatial Distribution							
N tracks	-	7	7	5	5	-	5
Home range (km^2)	-	1761.1	3055.8	627.4	1445.4	-	2686.0
Core range (km^2)	-	433.6	800.0	167.4	384.0	-	692.3

* denotes the number of complete, one-day foraging trips used in analysis of foraging bout characteristics

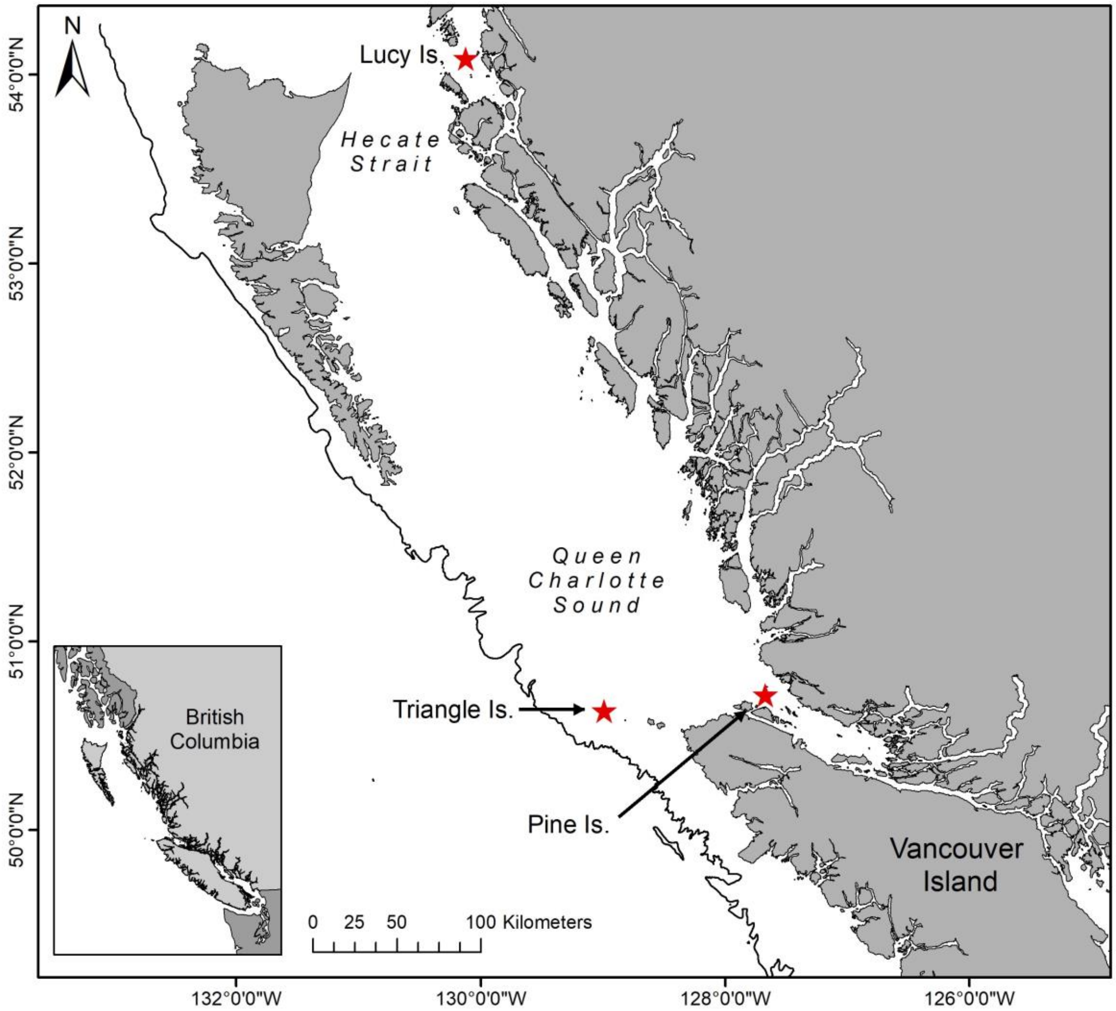

Figure 3.1 Locations of the rhinoceros auklet breeding colonies at Lucy Islands, Pine Island, and Triangle Island, B.C. Location of the 1000 m isobath is also shown.

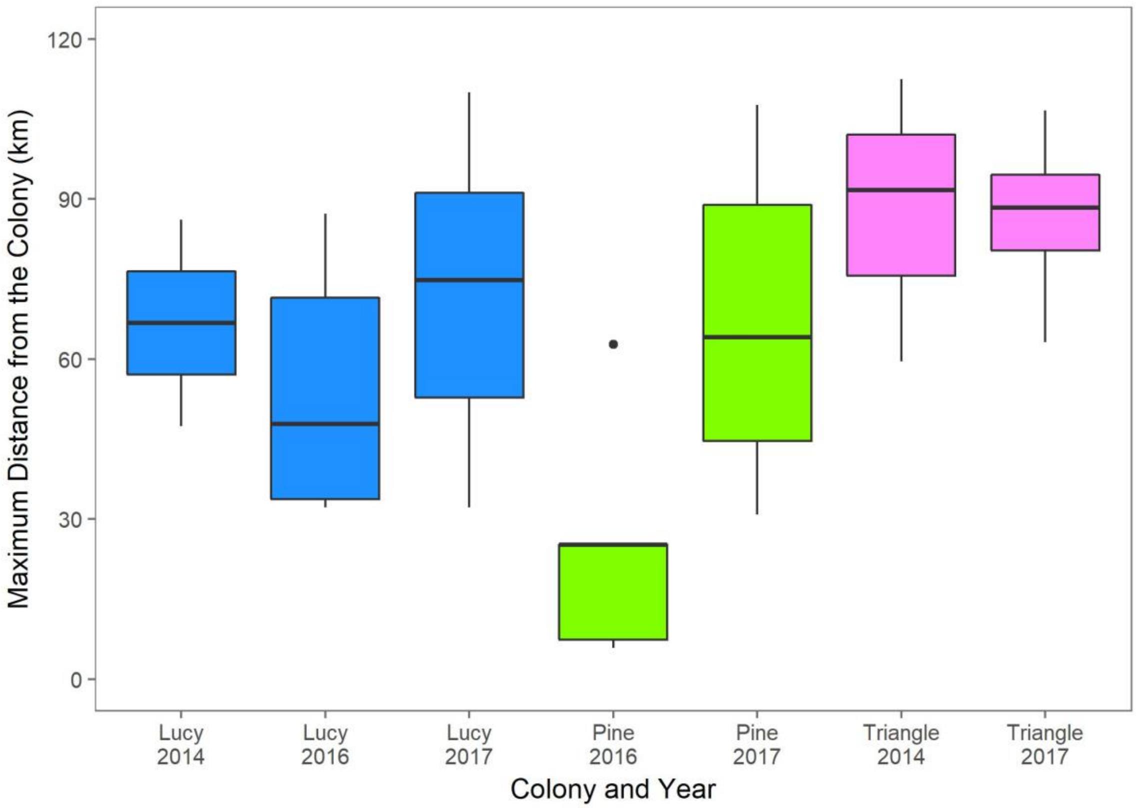

Figure 3.2 Maximum distance travelled for each colony-year of the study (N=39).

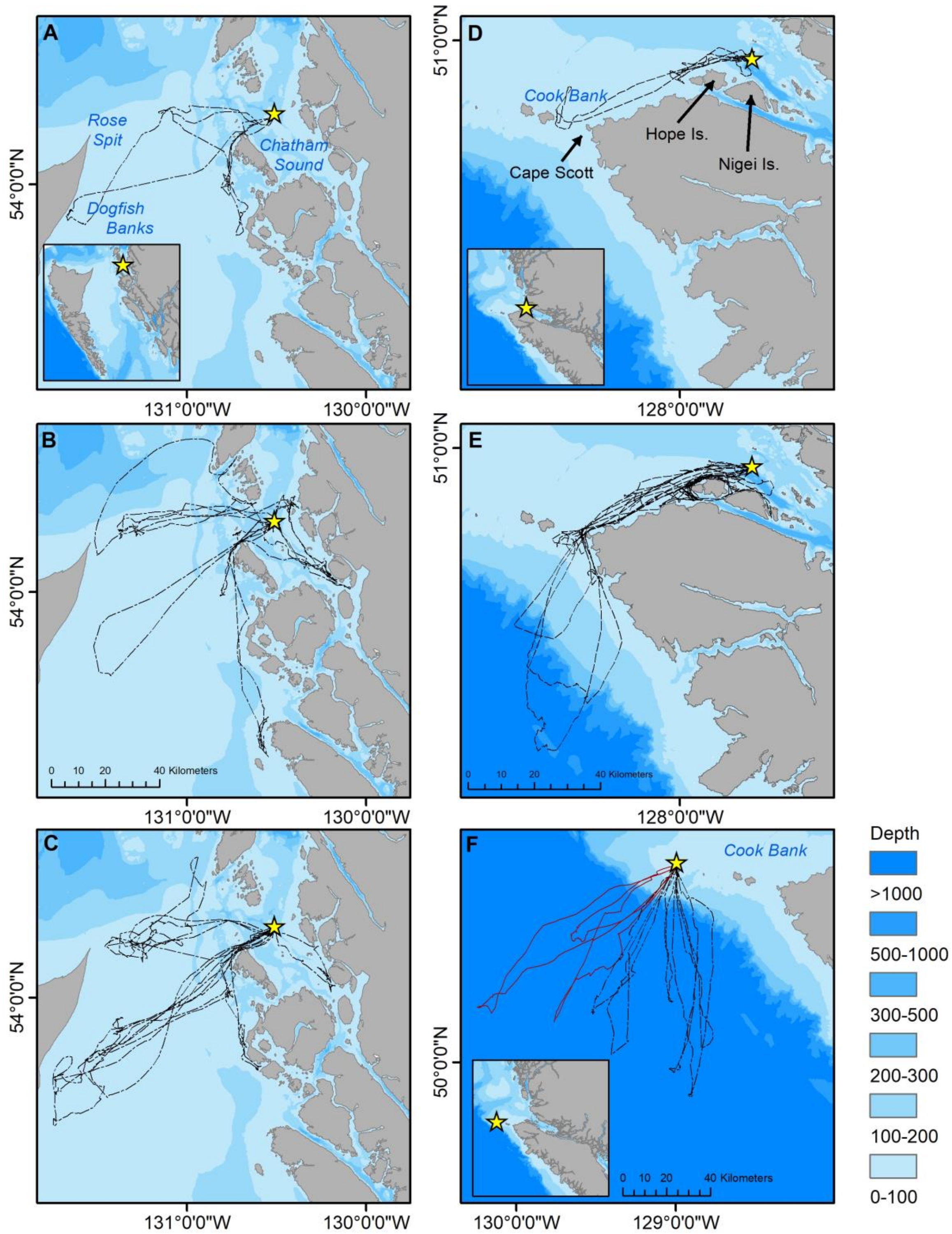

Figure 3.3 Complete and incomplete foraging tracks of chick-rearing rhinoceros auklets recorded via GPS logger. A) Lucy Islands in 2014 (n=2), B) Lucy Islands in 2016 (n=9), C) Lucy Islands in 2017 (n=8), D) Triangle Island in 2014 (*red*, n=3) and 2017 (*black*, n=6), E) Pine Island in 2016 (n=5), and F) Pine Island in 2017 (n=7). Depth contours (m) are shown in *blue*.

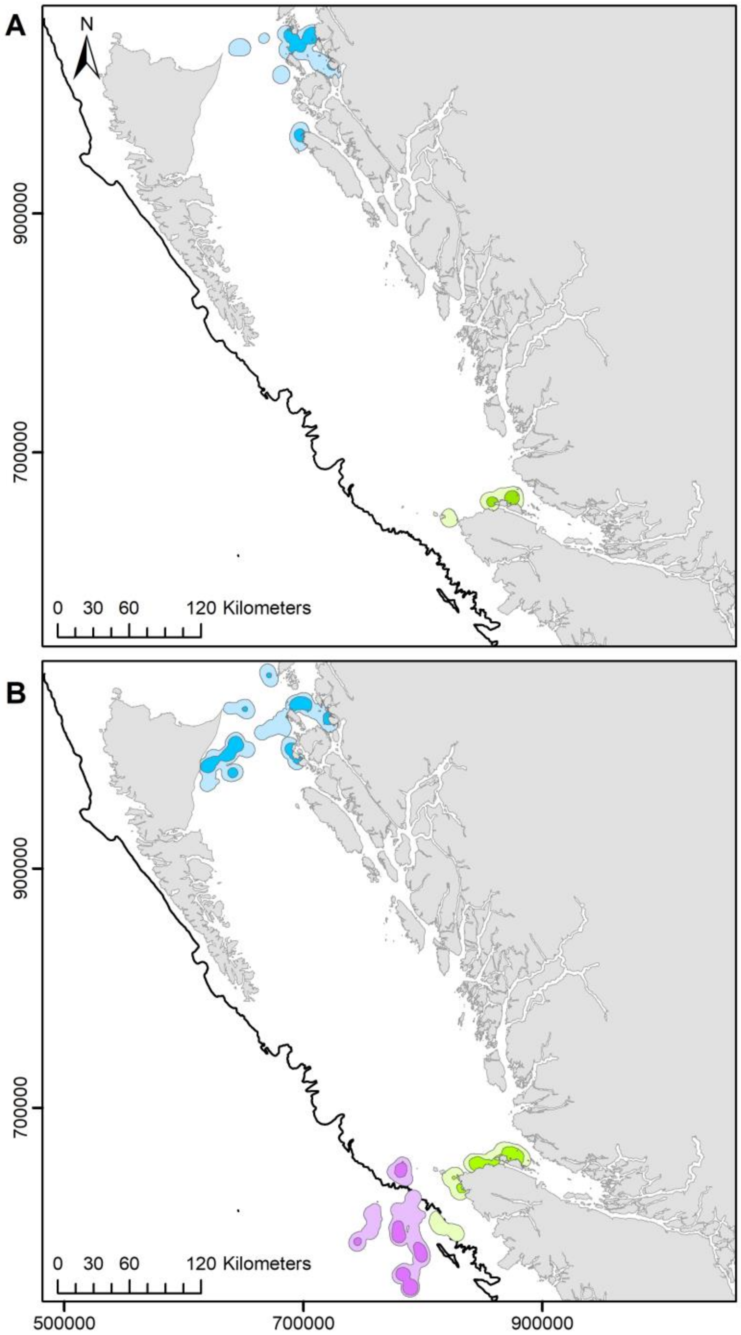

Figure 3.4 Rhinoceros auklet foraging distributions for the Lucy Islands (*blue*), Pine Island (*green*), Triangle Island (*purple*) during A) 2016 and B) 2017. Light contours indicate the home range (95% volume contours), and dark contours indicate the core foraging range (50% volume contours). Also shown is the 1000 meter isobath.

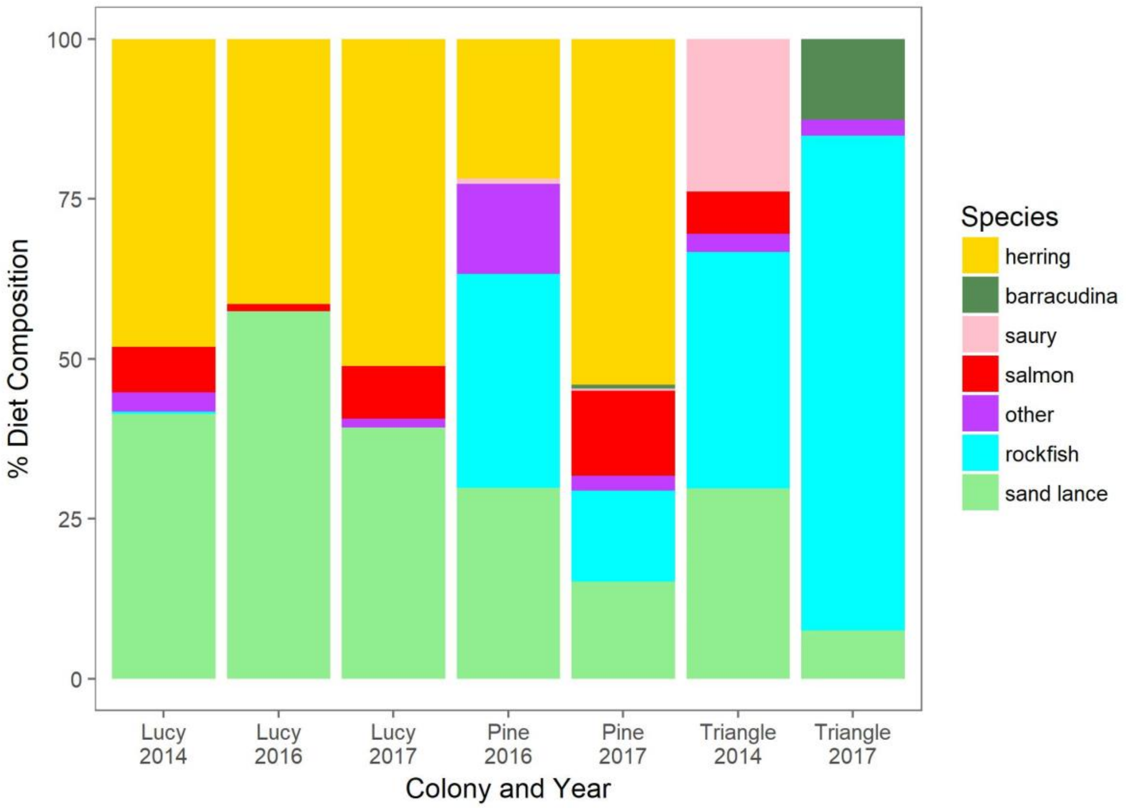

Figure 3.5 Average percent composition (by number) of fish species delivered in bill loads by breeding rhinoceros auklets for each colony-year (n=418).

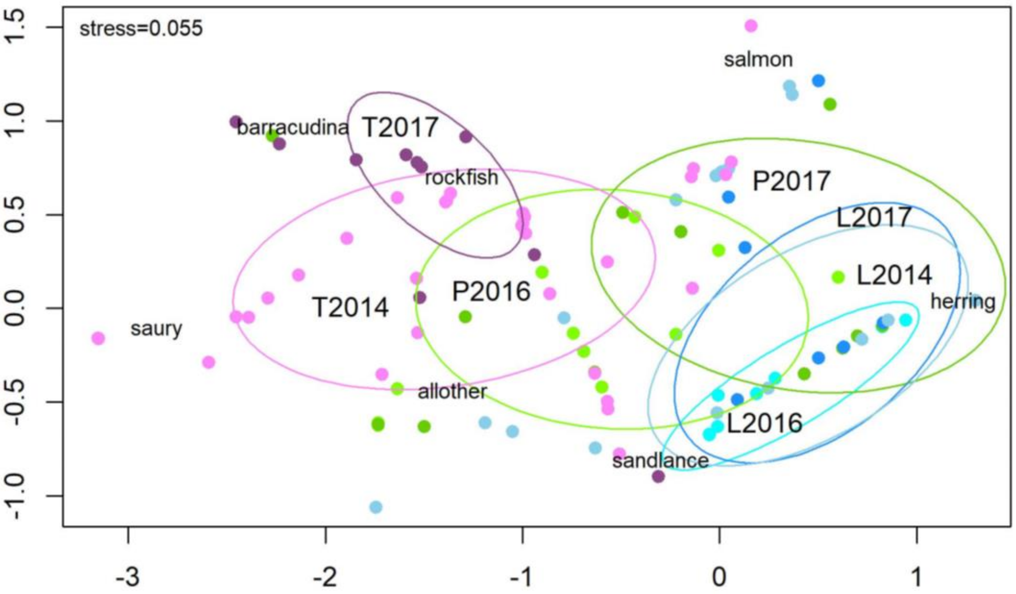

Figure 3.6 Nonmetric multidimensional scaling of diet composition from 418 rhinoceros auklet bill loads collected over the study period. Points and ellipses are colored by the seven colony-years of sample collection: Lucy 2014 (*turquoise*), Lucy 2016 (*blue*), Lucy 2017 (*dark blue*), Pine 2016 (*light green*), Pine 2017 (*dark green*), Triangle 2014 (*light purple*), and Triangle 2017 (*dark purple*). Ellipses show the standard deviations of the colony-year centroids.

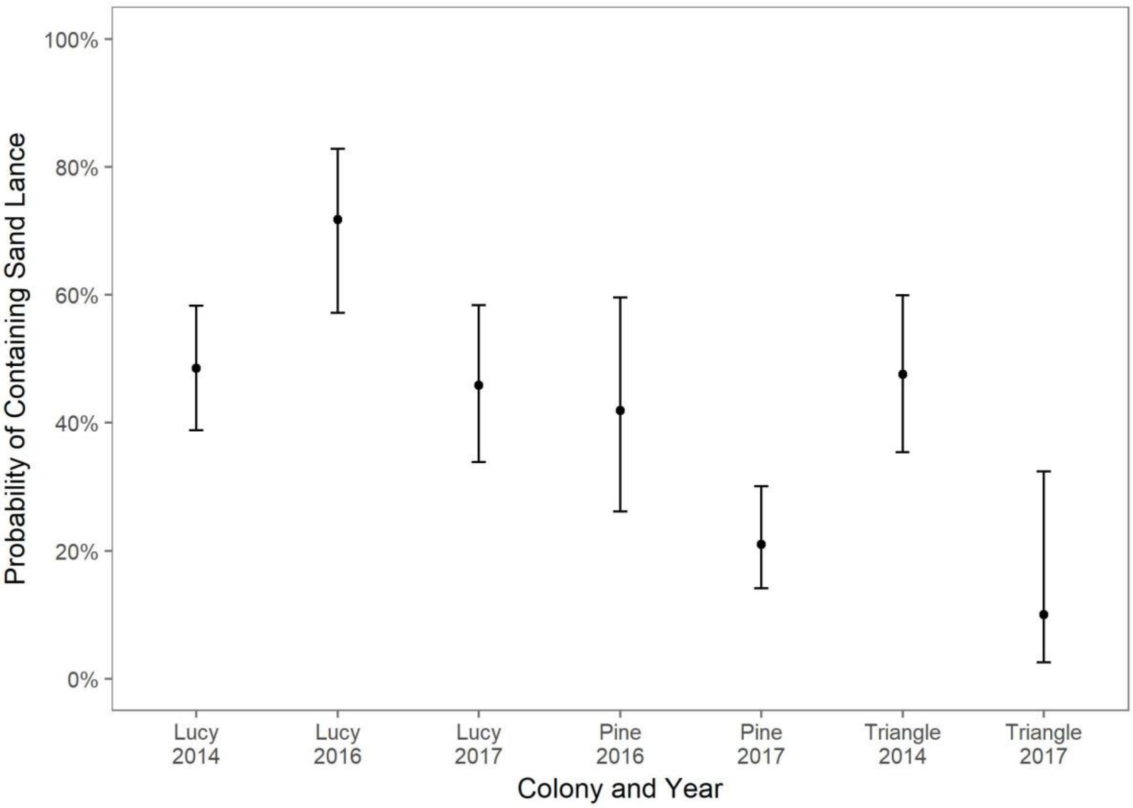

Figure 3.7 Probability of a bill load containing at least one sand lance for each colony-year, predicted by logistic regression (n=418). Error bars show the 95% confidence intervals.

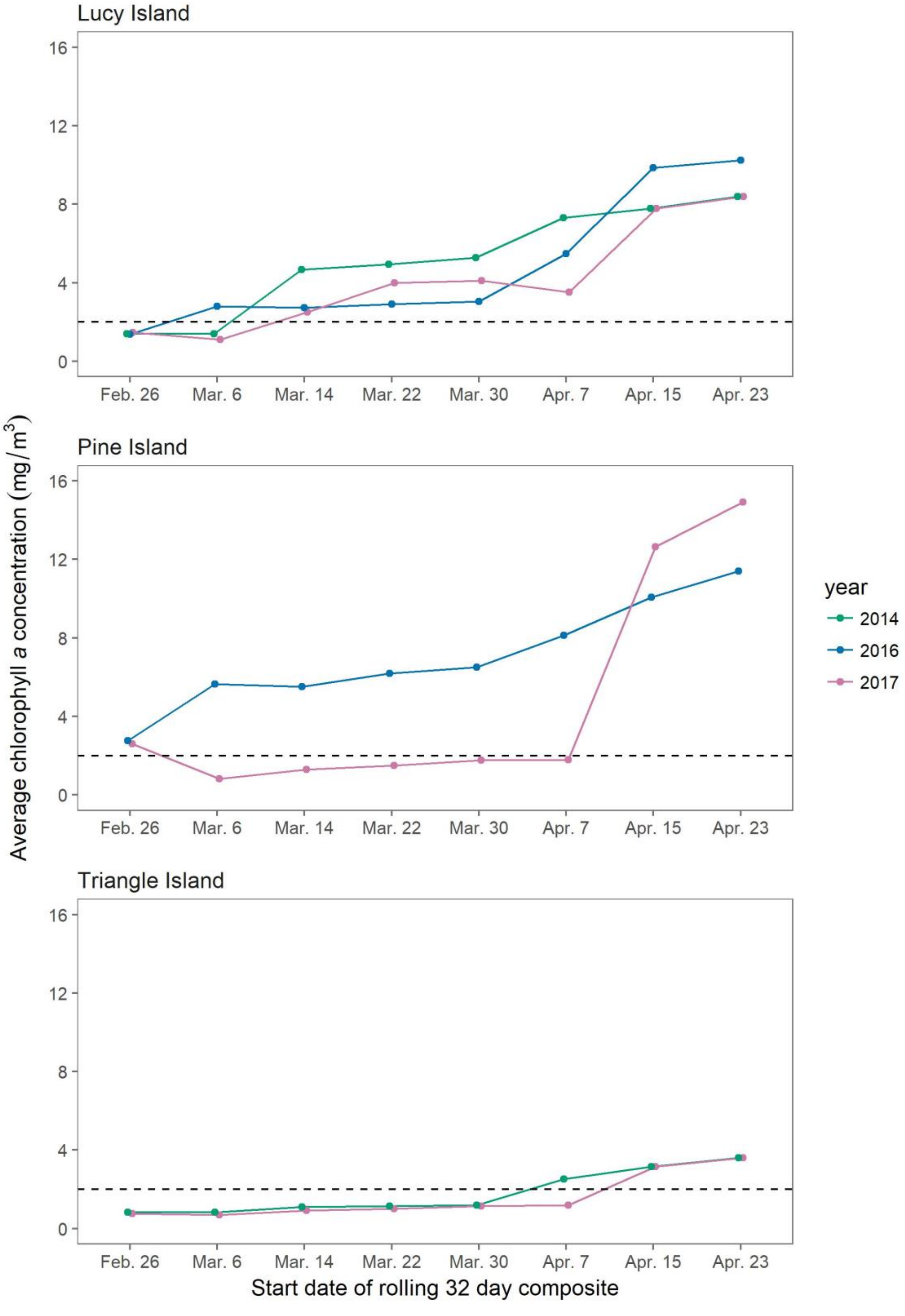

Figure 3.8 Rolling average, at 8-day intervals, of chlorophyll *a* concentrations over a 45 km radius of each colony. Values above 2 mg/m^3 (*dashed line*) are considered significantly elevated from winter concentrations, indicating the onset of the spring phytoplankton bloom.

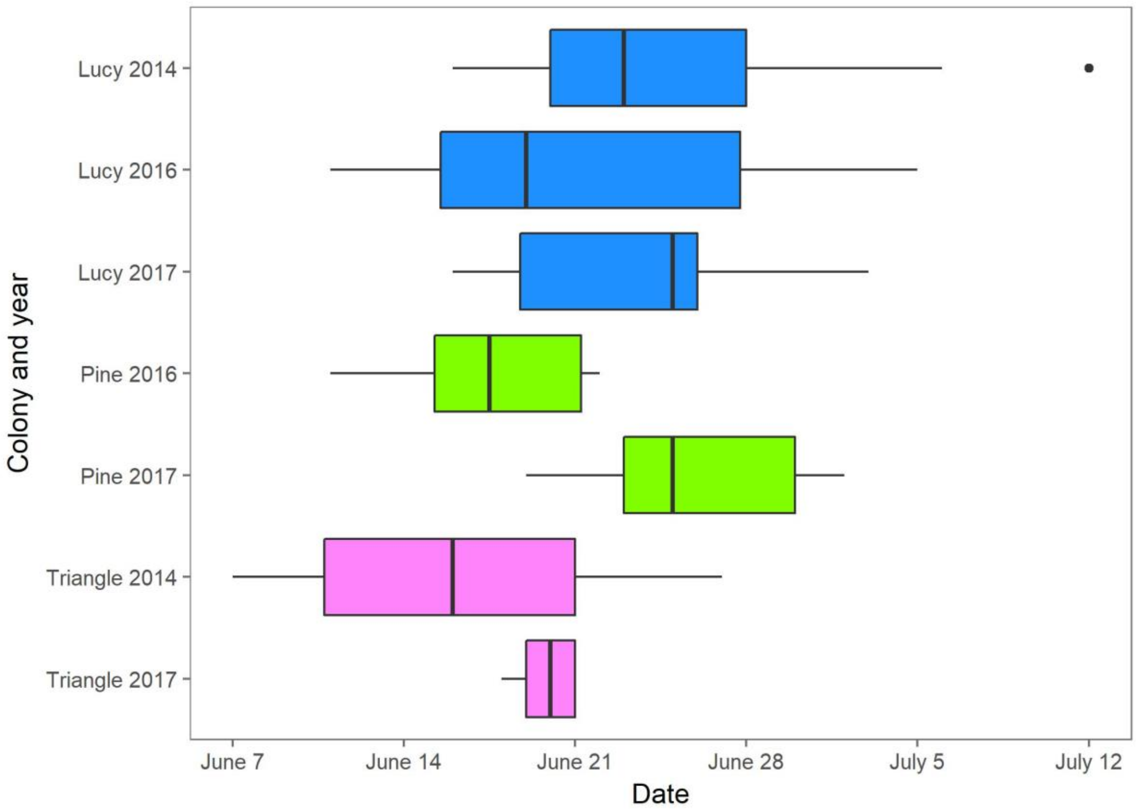

Figure 3.9 Estimated hatch date for each colony-year.

Chapter 4. General Conclusions

Understanding the fine-scale movements and habitat-use patterns of seabirds is crucial to support Marine Spatial Planning activities along the coastline of B.C. In this thesis, I used GPS tracking technology to study the at-sea movements of Cassin's auklets and rhinoceros auklets, both of which have over half of their global populations breeding in B.C. waters. In Chapter 2, I assessed inter-annual variation in movement patterns of Cassin's auklets breeding on Triangle Island, B.C., and tested for relationships between environmental variables and habitat use. In Chapter 3, I compared spatiotemporal variation in movement patterns of rhinoceros auklets by comparing movements at three breeding colonies differing in their local oceanographic processes.

Using three years of GPS tracking data, Chapter 2 provides insights into the fine-scale movements and habitat use of Cassin's auklets breeding at Triangle Island, the world's largest colony of this species. Notably, I found changes in the at-sea distribution of Cassin's auklets between years; birds used areas west of the colony towards the shelf-break in 2015 and 2017, and areas northwest of the colony over the continental shelf in 2014. I also found that Cassin's auklets foraged at considerably greater distances from Triangle Island than previously reported, travelling a mean maximum distance of 75 km, and spending two-thirds of their time in the most distal third of their foraging trajectory. These foraging trips routinely took Cassin's auklets outside the boundary of the Scott Islands Marine National Wildlife Area, which is intended to protect the foraging habitat of seabirds nesting on the Scott Islands archipelago. Finally, I found that SST was the best predictor of Cassin's auklet habitat use. In an individual-based analysis, I found that Cassin's auklets spent more time foraging in cells with cooler SSTs, relative to other areas visited over the course of a foraging trip. Similarly, in a population-based approach, I found that the probability of foraging in a grid cell increased with cooler SSTs, suggesting that SST might be related to the inter-annual changes in their at-sea distribution.

In Chapter 3, I compared the foraging behaviour of rhinoceros auklets breeding at three different colonies in B.C. I found that rhinoceros auklets breeding on the Lucy Islands showed little variation in their movement patterns across years (2014, 2016, and 2017), and that they consistently provisioned chicks with bill loads containing a high proportion of sand lance. Unsurprisingly, I found that the timing and magnitude of the spring phytoplankton bloom in this region was consistent across years, confirming the greater oceanographic stability of the region. Furthermore, I found that birds from the Lucy Islands targeted areas comprising shallow, sandy habitat, including coastal waters of Chatham Sound, Dogfish Banks and Rose Spit, which are known to support abundant sand lance. In contrast, I found that movement patterns of birds from Pine and Triangle Islands were more variable, apparently in response to oceanographic variability surrounding these islands. For example, rhinoceros auklets breeding on Pine Island in 2016 foraged in shallow nearshore areas, and sand lance were common in nestling diets. In contrast, rhinoceros auklets breeding on Pine Island in 2017 altered their foraging behaviour to exploit both nearshore and offshore habitats, which coincided with a delayed spring bloom and a higher prevalence of secondary prey species. Similarly, birds breeding on Triangle Island used offshore habitats in both years, which coincided with delayed spring blooms and the use of secondary prey species.

4.1. Management Implications

This thesis provides data relevant to three Marine Spatial Planning activities in B.C., the Pacific North Coast Integrated Management Area (PNCIMA) Plan, the Marine Plan Partnership for the North Pacific Coast (MaPP), and the Oceans Protection Plan. The PNCIMA Plan, produced by federal, provincial, and First Nations governments, provides a framework for conservation and the management of anthropogenic activities in central and northern B.C. waters. Similarly, MaPP is a partnership between the province of B.C. and First Nations to develop marine use plans for B.C.'s north coast. Of interest to both the PNCIMA Plan and MaPP, I found that Cassin's auklets routinely left the boundary of the Scott Islands Marine National Wildlife Area, particularly when birds travelled northwest of the colony. Consequently, the suitable habitat falling outside the MPA will need to be considered when managing anthropogenic activities. Furthermore, my results support previous research that have found Dogfish Banks and Rose Spit to be important foraging areas for rhinoceros auklets (Fox et al. 2016), and adding to the evidence that these two regions are key habitat for a diversity of seabird species (Clarke and Jamieson 2006, Morgan 1997, Palm 2012, Fox et al. 2016). While anthropogenic activities in this region are relatively minimal, identifying this region as biologically important will hopefully guide sustainable development under the PNCIMA Plan and

MaPP. Finally, the Oceans Protection Plan in part aims to improve emergency response readiness, and requires baseline information on the marine distribution of seabirds to support decision-making during a marine pollution incident. Notably, I found that foraging areas of rhinoceros auklets breeding on Pine and Lucy Islands included areas of high anthropogenic activity, such as Chatham Sound, Queen Charlotte Strait, and the northern coast of Vancouver Island. These three areas experience significant ship traffic have high predicted probabilities of chronic oil pollution (Williams and O'Hara 2010, Fox et al. 2016). Taken together, these three regions may be deserving of emergency response stations to facilitate an efficient response in the case of an environmental emergency. More broadly, my results highlight that effective conservation of seabirds requires multiple years of tracking data, particularly for marine ecosystems that experience higher oceanographic variability.

4.2. Limitations and Future Directions

An obvious limitation of my study is that I have relatively small sample sizes within each year, and data only from two to three years per colony. In each colony year, small sample sizes may have led to underestimates of the foraging area of rhinoceros auklets, particularly if there is high individual variation in movement patterns. Furthermore, I documented pronounced inter-annual variation, but two years of data is not adequate to capture the range of oceanographic conditions experienced in the northeastern Pacific, particularly in the Transition Zone Domain. To address this limitation, GPS tracking of rhinoceros auklets should be replicated at all three colonies to test my hypothesis that foraging movements are more variable at colonies where primary productivity is mainly driven by upwelling (e.g. Pine and Triangle Islands).

Even when conducted over sufficiently long periods, documenting the presence of strong inter-annual variation is only the first step in Marine Spatial Planning for seabirds. Managers need to balance the protection of important at-sea habitat with needs of other stakeholders (e.g. transportation, offshore energy development, fishing industries), which often limits the size of protected areas and therefore makes it difficult to adequately incorporate inter-annual variation in the distribution of suitable habitat (Lascelles et al. 2012). To address these limitations, conservation biologists are increasingly proposing the adoption of dynamic Marine Spatial Planning. For example, using information on the environmental drivers of seabird habitat use, managers could implement dynamic MPAs that have their boundaries shift to the track the distribution of suitable habitat. While dynamic MPAs have yet to be implemented, other forms of dynamic management provide evidence that they are feasible (Lascelles et al. 2012). For example, the TurtleWatch program in Hawaii uses satellite-based SST data to predict the at-sea distribution of loggerhead turtles (Howell et al. 2008). Weekly maps are then distributed to longline fisherman, who are asked to avoid certain areas to reduce the likelihood of turtle bycatch (Howell et al. 2008). In a similar manner, my results could be extended to develop predictive models that use oceanographic conditions to predict the at-sea distribution of Cassin's and rhinoceros auklets. In Chapter 2, my population-based analysis suggesting that SST might be responsible for the inter-annual changes in the at-sea distribution of Cassin's auklets. Following improvements to model performance, this model could be extended to predict whether Cassin's auklets are using areas to the northwest or west of Triangle Island in a given year. Such information could be used in a dynamic management strategy that protects suitable habitat lying outside of the boundary of the MPA. Similarly, my results suggest that the broad-scale distribution of rhinoceros auklets could be predicted based on ocean productivity. For example, future research could combine sand lance habitat models in B.C. (currently in development, C. Robertson, pers. comm.) with environmental data on early spring conditions to infer where rhinoceros auklets are likely to be distributed in a given year.

Finally, MSP for seabirds not only involves the identification of important at-sea habitat, but also requires knowledge of the distribution of anthropogenic activities and the level of threat posed by each. While both Cassin's auklets and rhinoceros auklets are known to be susceptible to oiling and bycatch in gillnets (Page et al. 1990, Oka and Okuyama 2000, Smith and Morgan 2005, Fox et al. 2016), we currently have poor information regarding spatial overlap between breeding auklets and these threats. Therefore, future research should quantify how the at-sea distribution of rhinoceros auklets and Cassin's auklets overlaps with fisheries and transportation. Furthermore, we know very little about how auklets might respond to the development of offshore wind energy, which likely to occur within the foraging habitat of rhinoceros auklets from the Lucy Islands (LGL et al. 2009). Other species of alcids have shown strong avoidance of wind farms, which could exclude them high quality habitat and lead to declines in population productivity (Vanermen et al. 2015; Busch and Garthe 2016). I therefore recommend that the behavioural responses of rhinoceros auklets to other forms of disturbance (e.g. ship or helicopter) to be further explored, which may be used to infer how they would respond to wind farms (Furness et al. 2013).

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Appendix A.

Supplementary Material for Chapter 2

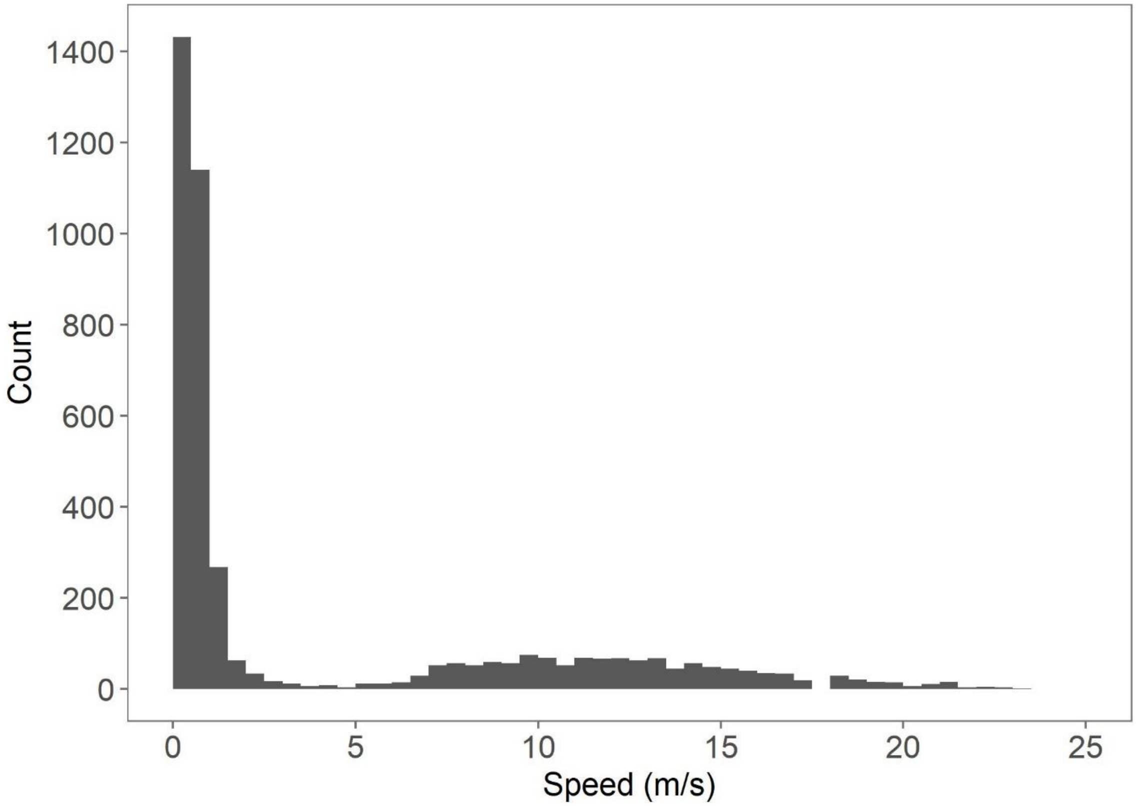

Figure A1: Frequency distribution of instantaneous flight speeds for chick-rearing Cassin's auklets during foraging trips.

Table A1: Summary data for complete GPS tracks obtained from 24 individual Cassin's auklets (n=7 for 2014, n=8 for 2015, and n=9 for 2017).

Year	Sex	Date of tracking	Track status	Colony departure time	Colony return time	Duration (hr)	Max. distance from the colony (km)	Total distance travelled (km)	Time to reach 2/3 maximum distance (min)	# of foraging/ resting bouts	Mean duration of flying bouts (min)	Mean duration of foraging/ resting bouts (min)	Prop. of trip beyond 2/3 max distance
2014	F	May 20	complete	4:21	22:48	1110	104.5	285.3	70	18	19.6	43.9	0.81
	F	May 20	complete	4:54	22:54	1080	43.6	120.6	91	14	6.9	65.5	0.67
	U	May 20	complete	4:59	22:42	1062	101.3	167.6	157	18	9.0	47.4	0.69
	M	May 20	complete	4:28	22:41	1092	47.4	145.9	145	13	14.3	70.8	0.77
	M	May 21	complete	4:39	00:53	1212	111.1	242.4	69	10	35.2	83.4	0.72
	M	May 21	complete	4:57	00:52	1194	106.3	234.9	98	12	27.5	76.5	0.67
	U	May 20	incomplete	4:23	-	-	113.5	-	-	-	-	-	-
2015	M	May 15	complete	4:32	22:56	1104	41.3	102.8	158	11	7.8	85.7	0.63
	U	May 15	complete	3:45	23:00	1158	92.3	272.9	284	25	12.8	29.9	0.53
	M	May 15	complete	3:39	23:02	1164	70.2	173.2	210	16	9.5	57.7	0.63
	U	May 15	complete	4:19	23:00	1122	82.3	199.7	301	24	9.4	34.5	0.33
	M	May 15	complete	3:55	22:50	1134	41.3	93.6	161	9	5.6	111.3	0.67
	F	May 15	complete	4:08	22:43	1116	73.7	181.2	280	16	12.1	53.4	0.60
	F	May 15	incomplete	4:20	-	-	57.5	-	-	-	-	-	-
	F	May 15	incomplete	4:08	-	-	96.0	-	-	-	-	-	-
2017	F	May 15	complete	4:34	23:04	1110	57.9	135.1	194	10	12.9	89.0	0.70
	F	May 15	complete	3:40	23:05	1164	100.2	226.4	241	11	20.5	80.4	0.66
	F	May 18	complete	3:54	22:58	1188	108.3	259.1	279	14	23.8	59.6	0.60
	F	May 19	complete	4:16	23:15	1140	76.3	179.7	116	12	15.6	76.0	0.73
	F	May 20	complete	3:44	23:07	1164	82.4	207.8	202	11	19.5	79.1	0.66
	U	May 11	incomplete	4:41	-	-	38.5	-	-	-	-	-	-
	M	May 11	incomplete	5:21	-	-	53.5	-	-	-	-	-	-
	U	May 15	incomplete	5:00	-	-	55.7	-	-	-	-	-	-
	M	May 15	incomplete	4:46	-	-	44.0	-	-	-	-	-	-

Table A2: Individual-based analysis of time spent in a cell, with individual as a random effect (n=1165). We report: K = number of parameters estimated, AICc, ΔAICc, wt, % deviance explained = % deviance explained relative to an intercept only model, marginal R^2 = variance explained by the fixed effects, and conditional R^2 = variance explained by fixed and random effects (Nakagawa & Schielzeth 2013).

Parameters	AIC	ΔAICc	K	wt	% Dev.	Marginal R^2	Conditional R^2
SST*DIST$_{colony}$	3476.5	0.0	8	0.21	4.61	0.07	0.19
slope*DIST$_{colony}$	3476.9	0.4	8	0.17	4.60	0.04	0.13
DIST$_{1000}$*DIST$_{colony}$	3478.3	1.7	8	0.09	4.56	0.04	0.09
(DIST$_{1000}$ + slope)*DIST$_{colony}$	3478.3	1.9	10	0.08	4.67	0.04	0.10
slope + DIST$_{1000}$	3479.1	2.5	7	0.06	4.48	0.02	0.02
(SST + chlorophyll)*DIST$_{colony}$	3479.1	2.7	10	0.05	4.65	0.07	0.19
DIST$_{colony}$	3479.3	2.7	6	0.05	4.42	0.03	0.13
slope	3479.6	3.0	6	0.04	4.41	0.01	0.01
(depth + slope)*DIST$_{colony}$	3480.1	3.6	10	0.03	4.62	0.04	0.14
depth + slope + DIST$_{1000}$	3480.2	3.6	8	0.03	4.51	0.02	0.02
depth + slope	3480.5	4.0	7	0.03	4.44	0.01	0.01
(SST + chlorophyll + depth + DIST$_{1000}$ + slope)*DIST$_{colony}$	3480.3	4.2	16	0.03	4.94	0.09	0.21
(slope + DIST$_{1000}$ + depth)*DIST$_{colony}$	3480.6	4.2	12	0.03	4.72	0.05	0.12
(depth + DIST$_{1000}$)*DIST$_{colony}$	3480.8	4.4	10	0.02	4.60	0.05	0.11
chlorophyll*DIST$_{colony}$	3481.6	5.0	8	0.02	4.47	0.04	0.12
DIST$_{1000}$	3481.6	5.0	6	0.02	4.36	0.02	0.02
SST + chlorophyll + depth + DIST$_{1000}$ + slope	3482.1	5.6	10	0.01	4.56	0.03	0.03
depth + DIST$_{1000}$	3482.3	5.7	7	0.01	4.40	0.02	0.02
depth*DIST$_{colony}$	3483.0	6.5	8	0.01	4.43	0.04	0.13
depth	3484.9	8.3	6	0.00	4.27	0.01	0.01
SST	3485.1	8.5	6	0.00	4.26	0.01	0.01
chlorophyll	3485.8	9.2	6	0.00	4.24	0.00	0.00
SST + chlorophyll	3486.3	9.7	7	0.00	4.28	0.01	0.01

Table A3: Population-based analysis of the probability of foraging with in a cell, with year as a random effect. We report: K = number of parameters estimated, AICc, ΔAICc, wt, % deviance = % deviance explained relative to an intercept only model, marginal R^2 = variance explained by the fixed effects, and conditional R^2 = variance explained by fixed and random effects (Nakagawa & Schielzeth 2013).

Parameters	AICc	ΔAIC	K	wt	% Deviance	Marginal R^2	Conditional R^2
SST*DIST$_{colony}$	1338.2	0.0	6	0.65	44.7	0.234	0.234
(SST + chlorophyll)*DIST$_{colony}$	1342.0	3.9	8	0.09	44.7	0.351	0.351
SST	1342.9	4.7	4	0.06	44.3	0.183	0.185
DIST$_{colony}$	1343.3	5.2	4	0.05	44.5	0.177	0.177
depth*DIST$_{colony}$	1344.0	5.8	6	0.04	44.6	0.255	0.259
SST + chlorophyll	1344.1	5.9	5	0.03	44.4	0.202	0.257
slope*DIST$_{colony}$	1344.9	6.7	6	0.02	44.6	0.302	0.302
DIST$_{1000}$*DIST$_{colony}$	1345.3	7.2	6	0.02	44.6	0.146	0.146
(depth + slope)*DIST$_{colony}$	1346.8	8.7	8	0.01	44.7	0.175	0.175
(depth + DIST$_{1000}$)*DIST$_{colony}$	1347.3	9.1	8	0.01	44.7	0.193	0.193
chlorophyll*DIST$_{colony}$	1347.3	9.1	6	0.01	44.5	0.163	0.164
SST + chlorophyll + depth + DIST$_{1000}$ + slope	1347.8	9.6	8	0.01	44.5	0.195	0.195
(SST + chlorophyll + depth + DIST$_{1000}$ + slope)*DIST$_{colony}$	1348.0	10.0	14	0.00	45.0	0.203	0.203
(DIST$_{1000}$ + slope)*DIST$_{colony}$	1348.3	10.1	8	0.00	44.6	0.223	0.223
(slope + DIST$_{1000}$ + depth)*DIST$_{colony}$	1350.6	12.5	10	0.00	44.7	0.189	0.190
slope	1351.4	13.2	4	0.00	44.2	0.177	0.177
DIST$_{1000}$	1351.6	13.4	4	0.00	44.1	0.176	0.176
chlorophyll	1351.8	13.7	4	0.00	44.1	0.174	0.174
depth	1352.1	13.9	4	0.00	44.2	0.214	0.220
depth + slope	1352.8	14.6	5	0.00	44.2	0.177	0.178
depth + DIST$_{1000}$	1353.0	14.8	5	0.00	44.2	0.175	0.175
slope + DIST$_{1000}$	1353.1	14.9	5	0.00	44.2	0.176	0.176
depth + slope + DIST$_{1000}$	1354.4	16.2	6	0.00	44.2	0.193	0.193

Table A4: Population-based analysis of the intensity of use of a cell, with year as a random effect. We report: K = number of parameters estimated, AIC, ΔAICc, wt, % deviance = % deviance explained relative to an intercept only model, marginal R^2 = variance explained by the fixed effects, and conditional R^2 = variance explained by fixed and random effects (Nakagawa & Schielzeth 2013).

Parameters	AIC	ΔAIC	K	wt	% Deviance	Marginal R^2	Conditional R^2
SST	1415.2	0.0	6	0.18	3.28	0.005	0.005
(SST + chlorophyll)*$\text{DIST}_{\text{colony}}$	1415.4	0.5	10	0.14	3.82	0.027	0.027
SST + chlorophyll	1416.3	1.1	7	0.10	3.35	0.003	0.003
SST*$\text{DIST}_{\text{colony}}$	1416.2	1.1	8	0.10	3.49	0.004	0.004
DIST_{1000}*$\text{DIST}_{\text{colony}}$	1416.7	1.6	8	0.08	3.46	0.016	0.016
DIST_{1000}	1417.5	2.2	6	0.06	3.13	0.006	0.006
SST + chlorophyll + depth + DIST_{1000} + slope	1417.7	2.8	10	0.04	3.66	0.037	0.037
(depth + DIST_{1000})*$\text{DIST}_{\text{colony}}$	1418.0	3.1	10	0.04	3.64	0.027	0.027
slope + DIST_{1000}	1418.6	3.4	7	0.03	3.19	0.018	0.018
chlorophyll*$\text{DIST}_{\text{colony}}$	1418.7	3.6	8	0.03	3.32	0.037	0.037
slope	1418.9	3.7	6	0.03	3.03	0.013	0.013
depth + DIST_{1000}	1419.2	4.0	7	0.02	3.15	0.030	0.030
(SST + chlorophyll + depth + DIST_{1000} + slope)*$\text{DIST}_{\text{colony}}$	1418.8	4.7	16	0.02	4.41	0.056	0.056
$\text{DIST}_{\text{colony}}$	1420.1	4.8	6	0.02	2.95	0.007	0.007
(DIST_{1000} + slope)*$\text{DIST}_{\text{colony}}$	1419.8	4.9	10	0.02	3.52	0.017	0.017
depth + slope + DIST_{1000}	1420.2	5.1	8	0.01	3.22	0.019	0.019
chlorophyll	1420.3	5.1	6	0.01	2.93	0.020	0.020
depth + slope	1420.6	5.5	7	0.01	3.05	0.025	0.025
depth*$\text{DIST}_{\text{colony}}$	1420.9	5.8	8	0.01	3.17	0.048	0.048
slope*$\text{DIST}_{\text{colony}}$	1421.1	6.0	8	0.01	3.15	0.040	0.040
(slope + DIST_{1000} + depth)*$\text{DIST}_{\text{colony}}$	1421.3	6.6	12	0.01	3.69	0.051	0.051
(depth + slope)*$\text{DIST}_{\text{colony}}$	1422.6	7.6	10	0.00	3.33	0.049	0.049
depth	1429.3	14.0	6	0.00	2.31	0.088	0.088

Appendix B.

Supplementary Material for Chapter 3

Table B1: Sample sizes and sample dates for each colony year. Loggers deployed = number of loggers deployed on chick-rearing rhinoceros auklets, N tracks = number of deployed loggers that yielded at least one foraging trip, N chicks = number of chicks measured for estimates of hatch date, and N bill loads = number of bill loads collected for estimates of nestling diet composition.

Colony	**Year**	**Deployment dates**	**Loggers deployed**	**N tracks**	**N chicks**	**Diet sampling dates**	**N bill loads**
Pine	2016	July 9 – 11	11	5	10	July 6 – 8, 10	31
	2017	July 3 – 5	12	7	11	July 1 – 6	100
Triangle	2014	July 1	4	3	44	June 30 – July 5	61
	2017	June 21 – 23	10	6	8	June 25 – 27	20
Lucy	2014	July 16	4	2	53	July 12 – 17, 19	99
	2016	July 7 – 11	14	8	24	July 7	46
	2017	July 13 – 16	14	8	10	July 11 – 13, 15 – 16	61
Total			**69**	**39**	**160**		**418**

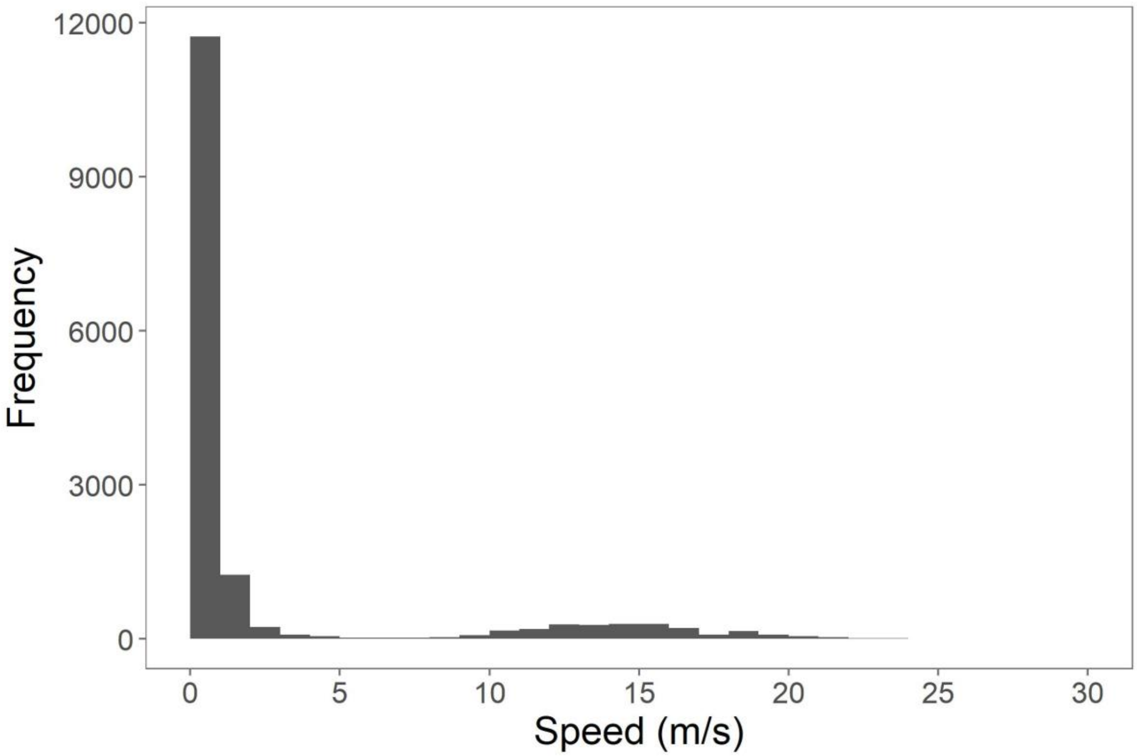

Figure B1: Frequency distribution of instantaneous flight speeds for chick-rearing Rhinoceros auklets during foraging trips.

Table B2: Summary data for GPS tracks obtained from 39 individual rhinoceros auklets (n=5 for 2014, n=13 for 2015, and n=21 for 2017).

Year	Colony	Sex	Date	Start time	Days at sea	Max. dist. (km)	Total dist. (km)	Bearing (0 - 360)	Avg. dur. of flying bouts (s)	Avg. dur. of foraging bouts (s)	Avg. dist. of flying bouts (km)	Num. of flying bouts	Prop. trip flying	GPS samp. freq.
2014	Lucy	M	July 16	4:12	2	47.4	280.8	267	581	6034	6.8	25	0.09	2
	Lucy	F	July 16	3:08	1	86.1	220.8	240	849	4882	11.5	14	0.14	2
	Triangle	F	July 1	4:39	1	59.6	137.4	232	1410	21710	23.9	4	0.08	2
	Triangle	NA	July 1	3:16	1	91.7	205.9	216	1133	7367	17.2	9	0.13	2
	Triangle	F	July 1	3:40	1	112.5	250.4	232	1360	6807	23.1	9	0.17	2
2016	Lucy	F	July 7	4:00	2	87.2	253.8	178	-	-	-	-	-	2
	Lucy	M	July 7	4:28	1	32.7	144.2	130	437	3302	5.1	20	0.12	2
	Lucy	M	July 8	3:48	1	34.1	94.8	212	669	11340	8.1	7	0.06	2
	Lucy	F	July 8	4:16	1	57.6	149.1	260	777	6438	9.7	11	0.12	2
	Lucy	M	July 10	23:36	1	85.6	184.9	226	-	-	-	-	-	60
	Lucy	M	July 11	4:18	1	32.2	108.3	129	-	-	-	-	-	2
	Lucy	U	July 11	4:33	1	38	111.8	128	471	3878	4.5	17	0.11	2
	Lucy	M	July 11	3:10	1	66.8	378.2	260	965	2455	12.8	25	0.28	2
	Pine	U	July 10	2:09	1	7.4	34.6	274	-	-	-	-	-	2
	Pine	M	July 10	4:09	1	25.2	63.8	259	348	6281	3.3	10	0.05	2
	Pine	U	July 10	2:57	1	25.3	68.9	258	485	11925	5.5	6	0.04	2
	Pine	M	July 11	1:55	1	62.8	174.6	250	1419	9435	17.7	7	0.12	2
	Pine	M	July 11	4:46	1	5.8	25.8	256	186	13550	1	5	0.01	2

Year	Colony	Sex	Date	Start time	Days at sea	Max. dist. (km)	Total dist. (km)	Bearing (0 - 360)	Avg. dur. of flying bouts (s)	Avg. dur. of foraging bouts (s)	Avg. dist. of flying bouts (km)	Num. of flying bouts	Prop. trip flying	GPS samp. freq.
2017	Lucy	F	July 13	4:04	1	88.4	213.2	228	1894	9591	24.1	7	0.16	5
	Lucy	M	July 13	4:18	2	86.2	227.8	231	1161	15849	15.3	10	0.07	5
	Lucy	F	July 13	3:51	1	53.4	186.4	183	829	5184	9.1	14	0.14	5
	Lucy	F	July 13	4:22	2	110	298.8	224	1196	10224	14.3	15	0.1	5
	Lucy	M	July 13	4:25	1	50.8	156.3	253	920	6887	11.2	9	0.12	5
	Lucy	M	July 15	4:14	2	63.3	348.7	260	-	-	-	-	-	5
	Lucy	M	July 16	2:55	1	99.4	228.9	232	1372	5995	15.9	11	0.17	5
	Lucy	M	July 16	3:28	1	32.2	109.8	130	643	8214	6.3	9	0.07	5
	Pine	M	July 4	3:35	2	49.3	298.1	248	1054	8486	12	16	0.1	5
	Pine	M	July 4	3:38	1	30.8	146.3	246	745	6840	7.7	11	0.09	5
	Pine	F	July 4	3:52	1	64.1	172	247	704	4967	8.4	13	0.12	5
	Pine	F	July 4	2:48	1	91.2	252.8	227	3690	14814	50.6	4	0.17	5
	Pine	M	July 4	3:17	2	107.6	287	216	-	-	-	-	-	5
	Pine	F	July 5	1:44	1	86.6	273.4	235	1001	5638	14.2	14	0.15	5
	Pine	M	July 5	4:39	1	40	113	256	780	10834	9.9	7	0.07	5
	Triangle	M	June 22	4:40	1	78.9	179.2	207	607	3870	6.6	18	0.13	5
	Triangle	F	June 22	4:03	1	106.6	233	175	1440	6548	17.6	10	0.17	5
	Triangle	M	June 23	4:21	1	95.3	221.7	179	1193	4971	13.5	13	0.18	5
	Triangle	F	June 24	2:53	1	63.2	137.3	180	753	6496	8.4	11	0.1	5
	Triangle	F	June 24	3:27	1	84.5	178.3	169	-	-	-	-	-	5
	Triangle	F	June 24	3:52	1	92.3	199.7	197	-	-	-	-	-	5

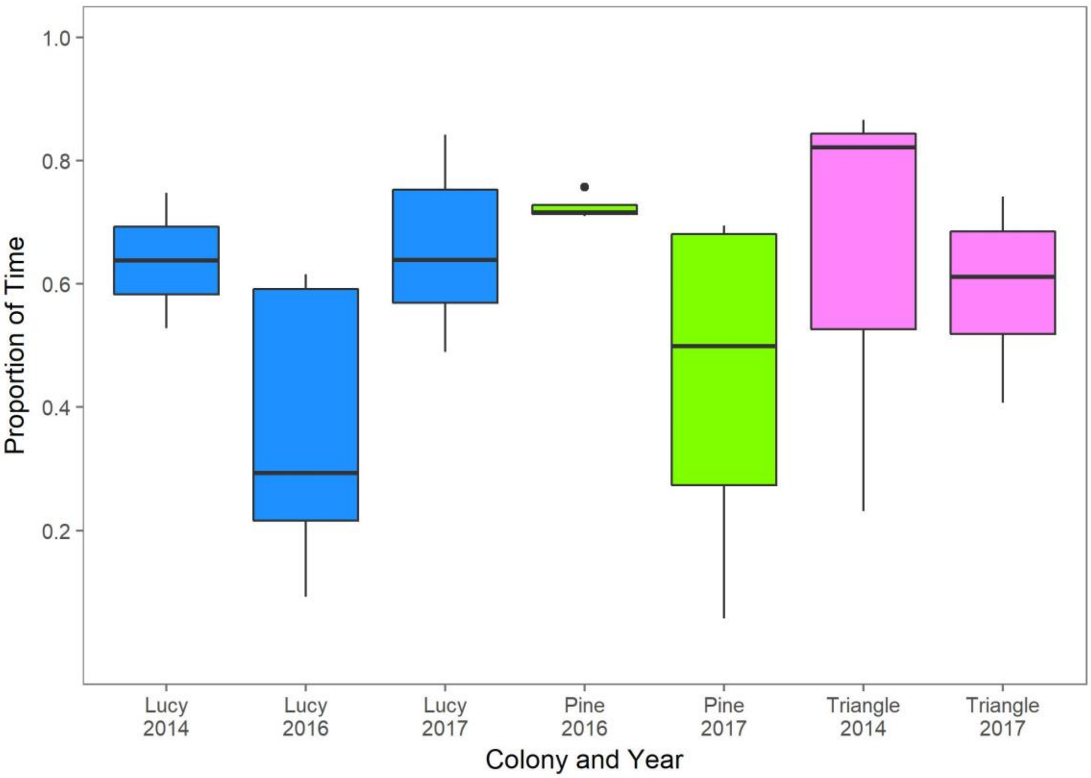

Figure B2: Proportion of time spent in the distal third of the foraging route in each colony-year of the study (N = 31).

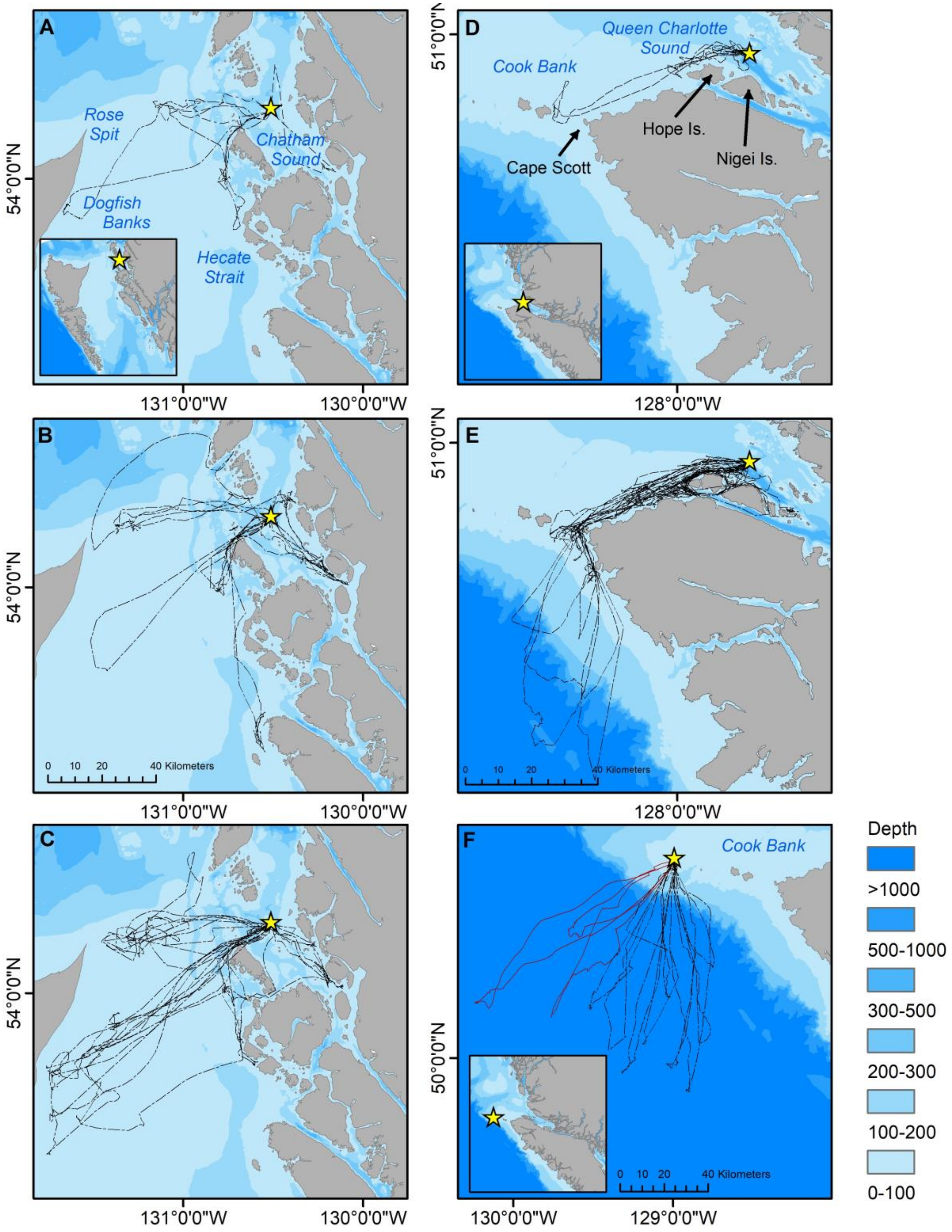

Figure B3: All foraging tracks (including 2nd and 3rd trips) of chick-rearing rhinoceros auklets recorded via GPS logger. A) Lucy Islands in 2014 (n=2), B) Lucy Islands in 2016 (n=9), C) Lucy Island in 2017 (n=8), D) Triangle Island in 2014 (*red*, n=3) and 2017 (*black*, n=6), E) Pine Island in 2016 (n=5), and F) Pine Island in 2017 (n=7). Depth contours (m) are shown in *blue*.