POPULATION GENETICS OF RHINOCEROS AUKLETS THROUGHOUT THE NORTH PACIFIC OCEAN

MARIE MAY PRILL
BSc Environmental and Conservation Sciences,
University of Alberta, 2009

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

MASTER OF SCIENCE

Department of Biological Sciences
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

POPULATION GENETICS OF RHINOCEROS AUKLETS THROUGHOUT THE NORTH PACIFIC OCEAN

MARIE MAY PRILL

Date of Defense: Aug 3, 2018

Dr. T. Burg Thesis Supervisor	Associate Professor	Ph.D.
Dr H. Jiskoot Thesis Examination Committee Member	Associate Professor	Ph.D.
Dr. E. Schultz Thesis Examination Committee Member	Associate Professor	Ph.D.
Dr. Igor Kovalchuk Chair, Thesis Examination Committee	Professor	Ph.D.

DEDICATION

For my mom – without you I wouldn't be who I am today.
Your strength and teachings are my everything.

ABSTRACT

Levels of gene flow among populations have a critical role in evolution and are affected by geographic, ecological, and behavioural barriers. Reductions in gene flow lead to population genetic structure. Seabirds have high potential for gene flow but, can show spatial genetic structure. Using molecular techniques, I examined levels of population genetic structure in rhinoceros auklets. I examined 424 individuals from 18 breeding colonies from Japan to California. Results from ten microsatellite markers showed significant genetic differentiation among and between North Pacific Ocean metapopulations. Isolation by distance, foraging segregation, site fidelity, oceanic conditions, and divergent breeding times are suggested to promote genetic differentiation for rhinoceros auklets. Using a population genetic approach, I tested if assignment tests could identify the genetic origin of rhinoceros auklets found at sea. From 124 birds of the eastern North Pacific Ocean, our research indicates assignment tests are limited with the current set of microsatellites.

ACKNOWLEDGEMENTS

It was always my goal pursue a Master's degree as those who know me understand I always loved higher education. However, many thought my Master's would consist of field work and lots of it. What a surprised when they learnt I would be working in a lab. Now, over two years later I wish to thank all those who have made this possible.

I would love to share my appreciation for my supervisor Theresa Burg for providing me the opportunity to work on this project. Her lab skills are spectacular and I'm grateful to have learnt how to complete lab work under her supervision. Her mentorship, guidance, and skill in the lab was a great blessing.

I will also like to thank all those who have helped me along the way. This includes my committee member Dr. Hester Jiskoot and Elizabeth Schultz who have provided me guidance throughout my project. I want to thank all those in the biology department, particularly Joanne Golden and Jenny Burke. Joanne Golden made it possible for me to teach the wonders of science to the university students, which is an opportunity I will always cherish. I will always be appreciative to Jenny Burke who not only dealt with me out in the field, but also as a teaching assistant for her classroom assignments. I'm truly grateful to be able to work with such a great botanist.

Big thanks goes out to all who collected or processed rhinoceros auklet samples including: Mark Hipfner, Katie Studholme, Ken Morgan, Laurie Wilson, Scott Pearson, Ryan Carle, Claudia Alonso, Motohiro Ito, and Yutaka Watanuki. Without your help this project wouldn't be possible.

I especially want to thank all the friends I made here, particularly the amazing lab mates I had throughout my journey. Cat, Libby, Zach, & Ashley – we had the best wine

and cheese parties! For Ian, Brendan, & Amanda – thank-you for all your support. Ian, thank you for the coffee – it saved me! I also want to thank Leanne and John for providing a wonderful home throughout this degree. The animals in the home also kept me busy when everyone was away, especially the kitten, now a cat – your Siamese dad really gave you a voice and you know how to use it! Even in the middle of the night…but, I still love you anyway.

Finally, I like to thank my mom for all the love and support she has given me over the years. Without you this journey wouldn't have been possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

AICc	corrected Akaike's Information Criterion
AK	Alaska
A_R	allelic richness
AUC	area under curve
BC	British Columbia
BIC	Bayesian information criterion
CA	California
DNA	deoxyribonucleic acid
dNTP	deoxynucleoside triphosphate
E	east
ESRI	Environmental Systems Research Institute
FDR	false discovery rate
F_{ST}	Wright's fixation index
F'_{ST}	standardized measure of genetic differentiation
$F_{ST}/(1-F_{ST})$	linearised F_{ST}
GBIF	Global Biodiversity Information Facility
GIS	Geographical Information System
H_E	expected heterozygosity
H_O	observed heterozygosity
HWE	Hardy-Weinberg equilibrium
IBD	isolation by distance
K	number of clusters
km	kilometers
lnPr(X|K)	estimated log probability of the data
m	metre
$m \bullet s^{-1}$	metre per second
max	maximum
Maxent	maximum entropy
McMC	Markov chain Monte Carlo
$MgCl_2$	magnesium chloride
$mg.m^{-3}$	one milligram per cubic meter
min	minimum
mM	millimolar
mtDNA	mitochondrial deoxyribonucleic acid
$mol.m^{-3}$	mol per cubed meter
OR	Oregon
n	sample size
N	north
Na	number of alleles
nDNA	nuclear deoxyribonucleic acid
p	significance value (p-value)
P_A	private allele
PCA	principal component analysis
PCoA	principal coordinate analysis

PCR	polymerase chain reaction
PSS	Practical Salinity Scale
Q	ancestry coefficient
r	correlation coefficient
r^2	coefficient of determination
sd	standard deviation
SDM	species distribution model
SSR	simple sequence repeat
SST	sea surface temperature
T_{a1}	annealing temperature one
T_{a2}	annealing temperature two
U	units
U.S.	United States
v	version
W	west
WA	Washington
µl	microliter
µM	micromolar
$\mu mol.m^{-3}$	micromole per cubed meter
ΔK	delta K
°	degrees
°C	degrees Celsius

Populations

AN	Año Nuevo
CH	Chowiet
CL	Cleland
DAI	Daikoku
DE	Destruction
LU	Lucy
MAT	Matsumae-Kojima
MID	Middleton
MO	Moore
PI	Pine
PR	Protection
SGG	SGaang Gwaii
SEF	Southeast Farallon
STL	St. Lazaria
TAI	Tai
TEU	Teuri
TOD	Todo
TRI	Triangle

CHAPTER 1:

General Introduction

1.1 Evolution of populations

Determining levels of genetic variation and gene flow are integral for understanding evolution. Genetic variation is fundamental to evolution as it allows species to adapt to changing conditions (Holderegger et al., 2006). Evolutionary processes such as gene flow (the exchange of genetic material between populations) contribute to genetic variation (Slatkin, 1985) as movement of individuals or propagules has the potential to introduce new alleles. Thus, high levels of gene flow homogenize allele frequencies (Holderegger et al., 2006) and reduce the effects of genetic drift (Wright, 1931). In contrast, limited gene flow promotes genetic divergence between populations (Palumbi, 1994). Since the evolutionary trajectories of populations are strongly influenced by gene flow, quantifying genetic factors contributes to our understanding of evolution.

Gene flow is often associated with dispersal (Slatkin, 1985; Slatkin, 1987; Anderson et al., 2010). Although, for dispersal to affect genetic diversity migrants must reproduce. Often ecological or demographic factors can impede breeding success (Tinnert et al., 2016). Migrants may not survive, find a mate or have suitable habitat to raise young (Freeland et al., 2011). For example among endangered puma (*Puma concolor*) populations of California, separated by an interstate highway, seven migrations are known to have occurred over 15 years. However, genetic analysis shows only a single migrant successfully produced offspring in a new population (Gustafson et al., 2017). Thus, dispersal ability

does not always correlate with gene flow and other factors can limit dispersal among populations.

For organisms that live in the open ocean populations are not always separated by visible barriers. The leopard shark (*Triakis semifasciata*) is found in the open ocean and has high dispersal ability. Barker et al. (2015) found that two genetically distinct populations of leopard shark occur along the California coastline, with geographical distance and a biogeographic barrier suggested to be limiting gene flow among groups.

1.2 Factors influencing dispersal and gene flow

Any barrier can limit or reduce gene flow including physical features (e.g. bodies of water), environment (e.g. climate gradients), ecology (e.g. competition), and behaviour (e.g. mate choice; Slatkin 1987; Ross, 2001; Pilot et al., 2006; Giordano et al., 2007; Jha, 2015). Barriers can depend on species dispersal ability, life history, and/or environment. (Palumbi, 1994; Storfer et al., 2010). For example, linear features such as rivers or seismic lines reduce dispersal in woodland caribou (*Rangifer tarandus caribou*; Oberg, 2001) and promote dispersal in wolves (*Canis lupus*; Latham et al., 2011). For two species of European forest bats, roads are a species-specific barrier to Bechstein's bats (*Myotis bechsteinii*), but not to barbastelle bats (*Barbastella barbastellus*; Kerth & Melber, 2009). Burney & Brumfield (2009) showed that populations of Neotropical canopy rainforest birds separated by the Andes and Amazon rivers had greater potential to disperse among these features compared to populations of understory birds. Thus, each barrier is dependent on how organisms interact or perceive their environment and inferences about dispersal is difficult if barriers to gene flow have not been identified for a species.

Physical barriers can promote genetic separation among breeding groups. Mountains are a common barrier for populations of Canada lynx (*Lynx canadensis*; Rueness et al., 2003) and Asian elephants (*Elephas maximus*; Vidya et al., 2005). Intrinsic physical aspects of habitat can be a barrier to movement. Altitude and topography of mountain habitat promote genetic variation among groups of long-toed salamander (*Ambystoma macrodactulym*; Giordano et al., 2007). Physical features can also influence movement for organisms with high dispersal capability such as flight. Several species of forest-dwelling birds show decreased movement between areas with limited canopy cover (Desrochers & Hannon, 1997; Awade & Metzger, 2008; Tremblay & St. Clair, 2009) and for insects, such as the yellow-faced bumblebee (*Bombus vosnesenskii*), dispersal is limited over oceanic and anthropogenic features (Jha, 2015).

Environmental and ecological factors can also promote genetic divergence. Thomassen et al. (2013) found regional differences in the timing of precipitation and availability of vegetation promote genetic divergence among giraffe species; with these regional differences segregating species from each other during the breeding season. For wolves of eastern Europe, genetic differences for populations are correlated to climate, habitat type, and diet (Pilot et al., 2006). In marine environments variability of sea surface temperature (SST) has been suggested to promote fine scale genetic differences for sea urchins (*Centrostephanus rodgersii*) near southeast Australia (Banks et al., 2007).

Similarly, behaviours that influence mate selection, breeding location, or habitat preference also influence gene flow. For instance, vocalisations used during the breeding season can be used to threaten rivals, establish territory, and increase chances of mating (Bartholomew & Collias, 1962; Krebs et al., 1978). Social behaviour, including differences between foraging, dialect, and dispersal between pods of killer whales (*Orcinus orca*) limit

gene flow between resident and transient populations (Hoelzel et al., 1998). Site fidelity to breeding or foraging sites is another behaviour contributing to genetic divergence for various species of birds and fish (Greenwood, 1980; Greenwood & Harvey, 1982; Storfer et al., 2010; Lowther et al., 2012; Shitikov et al., 2012; Wilson et al., 2016; Knope et al., 2017).

1.3 Population genetics

Population genetics has a long history that includes understanding genetic variation and differences among breeding groups. Molecular tools are used to quantify the number and frequency of alleles (e.g. average number of alleles per locus, average expected heterozygosity) to understand inter- and intra-population diversity. The degree of genetic similarity between populations indicates how genetically similar populations are to one another (Grünwald et al., 2017). For nearly all species, some degree of genetic variation exists among populations (Ehrlich & Raven, 1969) because microevolutionary processes (i.e. selection, mutation, genetic drift, gene flow) drive differentiation between breeding groups (Freeland et al., 2011; Hedrick, 2011). Likewise, population genetic structure develops if species depart from panmixia forming genetically distinct subpopulations (Parker et al., 1998; Waples & Gaggiotti, 2006; Colonna et al., 2009). Consequently, understanding the spatial genetic structure of a species provides insights into what barriers are limiting gene flow among populations and how populations are evolving (Smouse & Peakall, 1999; Manel et al., 2005; Pometti et al., 2014).

1.4 Molecular markers

Molecular markers are nucleotide sequences of DNA or RNA from specific locations within a genome (Barrandeguy & García, 2014). They are often used to determine the evolutionary history and measure genetic diversity among organisms (Bhargava & Fuentes, 2010; Freeland et al., 2010; Pepper et al., 2011). Historically, morphological or behavioural data were used to infer the amount of gene flow among populations (Freeland et al., 2011). These methods, although valuable, can be time consuming and provide a limited amount of information as to population connectivity and genetic structure (Whitlock & McCauley, 1999). Current technology, including the polymerase chain reaction (PCR), now allows indirect measures of population connectivity to be completed using genetic material and molecular markers. Thus, gene flow can be inferred by comparing genetic similarity among populations (Sunnucks, 2000).

Molecular markers need to be selected to answer specific research questions. To study population connectivity, non-adaptive (neutral) molecular markers provide an unbiased measurement of divergence. Non-adaptive loci are not under selection, and have limited to no effect on an organism's fitness (Ouborg et al., 1999; Holderegger et al., 2006). As a result, patterns at non-adaptive loci are primarily affected by gene flow or genetic drift (Parker et al., 1998). In comparison, adaptive loci show inconsistent levels of divergence as allele frequencies are also determined by selection (Kirk & Freeland, 2011). To answer questions related to fitness or adaptive variation (Holderegger et al., 2006), non-neutral loci can be used to understand factors of natural selection (Ouborg et al., 1999) or phenotypic variation (Naish & Hard, 2008). Thus, markers need to be selected with the appropriate

properties to answer research questions and understand either historical or recent evolutionary processes (Grünwald & Goss, 2011).

Eukaryotic cells contain both nuclear [nDNA] and organelle DNA: mitochondrial DNA [mtDNA] in animal and plants and chloroplast DNA in plants (Sunnucks, 2000). Each type of DNA differs in its mode of inheritance. For nDNA, biparental inheritance means genetic history can be inferred from both sexes (FitzSimmons et al., 1997). In comparison, mtDNA typically has maternal inheritance, thus, infers female dispersal and gene flow (Choupina & Martins, 2014).

Molecular markers have different rates of mutation. Different rates of evolution influence a marker's spatial-temporal resolution. Thus, distant evolutionary events are best studied using markers with slower mutation rates as genetic history remains preserved in the genetic material (Selkoe & Toonen, 2006). On the other hand, markers with high mutation rates (i.e. microsatellites) are highly polymorphic, accumulating genetic differences quickly. The allelic diversity within these markers provides resolution to measure recent genetic change (e.g. ~100 generations) among closely related populations (Selkoe & Toonen, 2006). Thus, markers that evolve quickly are used to measure contemporary genetic differences occurring between populations (Parker et al., 1998; Kalinowski, 2002).

1.4.1 Microsatellites

Microsatellites are one of the most commonly used molecular markers in population genetics. Often called simple sequence repeats (SSR), they are short tandem nucleotide repeats usually between 1-6 base pairs long (Bhargava & Fuentes, 2010). They are present

at a high frequency throughout nuclear genomes and have biparental mode of inheritance. Most microsatellites are selectively neutral with co-dominant Mendelian inheritance (Selkoe & Toonen, 2006). Individuals are genotyped as heterozygous (two different alleles at a locus) or homozygous (two copies of the same allele) at each locus (Wan, 2004). The high mutation rate (10^{-6} to 10^{-2} mutations/per generation; Schlötterer, 2000) for microsatellites allows for analyses to occur using only a few highly polymorphic loci (Kalinowski, 2002; Wan, et al., 2004). Microsatellite mutations occur by polymerase strand slippage, when nucleotide repeats are added or removed from a motif during DNA replication (Putman & Carbone, 2014). The statistical power improves as the number of loci increases (Landguth et al., 2012).

Microsatellites do have limitations. One is the high cost of finding and developing microsatellite loci. When target species loci are not available, primers from closely related taxa (same family) are used (Selkoe & Toonen, 2006). However, allelic diversity can decrease with primers from non-focal species (Primmer et al., 1996). Cross-species amplification also increases the frequency of allelic dropout, which can occur if mutations are present on primer binding sites. Null alleles are a good example of allelic dropout and occur when some alleles fail to amplify. Individuals then appear as a homozygote although they are heterozygous (Chapuis & Estoup, 2007; Carlsson, 2008). Low quality DNA can also increase allelic dropout (Wandeler et al., 2003) as short alleles are preferentially amplified over long alleles (Wattier et al., 1998; van Oosterhout et al., 2004). Large allele dropout results in genotyping error, particularly, if significant size differences exist between alleles.

Methods are available to mediate these limitations. To reduce scoring errors, genotypes can be confirmed by a second person and scored alongside positive and negative

controls. A subset of samples can be run on calibration gels to confirm scoring is consistent between gels. As well, loci with inconsistent amplification can be discarded and software is available to check for genotype errors from allele dropout, null alleles, and excess stutter (van Oosterhout et al., 2004).

1.5 Statistical methods

Statistical techniques are used to quantify genetic diversity and population differentiation. There are a number of methods to choose from depending on the organism, molecular marker, and research objectives (Grünwald et al., 2017). Because results can vary between methods, using a variety of techniques can help verify results.

1.5.1 Genetic diversity and population genetic structure

Genetic diversity represents the total amount of genetic variation in individuals within populations (Barrandeguy & García, 2014). Descriptive statistics are used to characterise each population with observed and expected heterozygosities, and allelic diversity (e.g. number of alleles, private alleles, allelic richness; Freeland et al., 2011). Populations are also checked for deviations from Hardy-Weinberg Equilibrium. Allele frequencies in populations in Hardy-Weinberg equilibrium remain constant over time unless evolutionary mechanisms (e.g. non-random mating, genetic drift) are acting upon populations (Hardy, 1908; Weinberg, 1908; Waples, 2015).

Genetic structure measures levels of genetic differentiation (Caballero & García-Dorado, 2013). Summary statistics, such as Wright's (1951) F-statistics are one of the most

common methods to quantify population differentiation and describe how genetic variation is divided among subpopulations. In essence, it uses *a priori* groupings to calculate genetic distance for three different measures: F_{IS} measures the degree of inbreeding within individuals relative to their subpopulation, F_{ST} measures genetic differentiation between subpopulations, and F_{IT} provides an overall inbreeding coefficient of an individual relative to the total population (Wright, 1965; Freeland et al., 2011). F_{ST} (the fixation index) is the universal measurement for differentiation among subpopulations (Caballero & García-Dorado, 2013) and F_{ST} values range from 0-1.

1.5.2 Bayesian clustering

Clustering analyses are a valuable method for understanding spatial genetic structure. Compared to traditional analyses (e.g. F-statistics) that use *a priori* groupings, clustering methods characterise samples *a posterior* (François et al., 2006; Grünwald et al., 2017). This can reduce potential errors incurred from *a priori* sampling (Latch et al., 2006). Many clustering methods use a Bayesian framework to quantify the percentage an individual's genome belongs and then groups individuals by genotype similarity. Most software programs allow users to specify the number of clusters (K). For each K value, the proportion of each individual genome originating from each cluster is estimated using Markov chain Monte Carlo (McMC) simulations. The best value of K is then inferred post hoc from posterior probabilities of the data (François & Durand, 2010; Gilbert, 2016). Selection of K depends on many factors including pre-defined parameters, biological vs. statistical significance, and properties of the dataset (Latch et al., 2006; Guillot, 2008; Porras-Hurtado et al., 2013; Gilbert, 2016; Wang, 2017). Thus, multiple runs are performed

(François et al., 2006) and software programs are available to help collate results (Jakobsson & Rosenberg, 2007; Earl & vonHoldt, 2012; Kopelman et al., 2015).

Quality of the results can be influenced by a number of factors one being the starting point in the McMC chain. Dependent on the clustering algorithm, the McMC simulation starts after a burn-in period or a length of chain where no data are collected. Before the simulation each run should be in equilibrium, thus, the burn-in reduces noise or error in the posterior probabilities (Excoffier & Heckel, 2006; Porras-Hurtado et al., 2013). As well, the stochastic nature of the McMC algorithm increases the chances of inconsistency between runs. Hence, each value of K should have a number of independent runs to check for consistency (Gilbert et al., 2012). Clustering depends on properties of the data. Programs can overlook weak population structure and perform best when F_{ST} values are ≥ 0.05 (Latch et al., 2006). Properties of the dataset, such as unbalanced sampling, can influence results leading to incorrect K value estimates (Wang, 2017). Thus, results from Bayesian clustering should be compared with other statistical measures.

1.5.3 Multivariate and distance analyses

Multivariate methods are a powerful statistical tool to visualize and evaluate complex genetic data (Paliy & Shankar, 2016). These methods reduce data into a few informative variables that are used to explain the main patterns of a dataset (Reich et al., 2008) and have several advantages over other population genetics analyses. Multivariate methods can be used to explain genetic variability in large datasets and those with a large number of variables. Compared to clustering methods (i.e. STRUCTURE), multivariate methods compute large datasets quickly and do not depend on the data meeting specific assumptions

(e.g. Hardy-Weinberg equilibrium; Patterson et al., 2006). One disadvantage of multivariate methods is the limited number of options that can add strength and resilience to data, when compared to the clustering program STRUCTURE (Patterson et al., 2006; Reich et al. 2008).

To detect population genetic structure, two popular multivariate methods are: principal component analysis (PCA) and principal coordinates analysis (PCoA; Patterson et al., 2006). Each method compresses a number of measures (i.e. dimensions) into a few principal components (PC; Reich et al. 2008). This multi-dimensional genetic data can then be viewed in two or three dimensions (e.g. scatterplot). The amount of genetic differentiation is shown by the degree of spatial separation among the variables (e.g. points on a scatterplot). The maximum amount of genetic variation between variables is preserved on the first few axes (PCA_1, PCA_2 or PCA_3), with the greatest amount of genetic variation shown in on the first axis (PCA_1). Of the two methods, PCoA is often used to display genetic distance (F_{ST}) as it can be used on any Euclidean distance while PCA is better at preserving canonical Euclidean distance (Jombart et al., 2009; Paliy & Shankar, 2016). Thus, multivariate methods can be a useful tool to visualize and compare statistical results.

The Mantel test is an approach used to measure genetic distance effects on gene flow. First applied in population genetics by Sokal (1979), the Mantel test can be used to examine the traditional model of isolation by distance (IBD; Wright, 1943). IBD assumes gene flow among populations decreases with the increase of spatial-distance. The Mantel test is used to evaluate if IBD is a barrier to gene flow by comparing pairwise genetic measures with geographic distance.

1.5.4 Seascape genetics

Seascape genetics studies how environmental features influence genetic structure of marine organisms. Conceptually, seascape genetics is similar to landscape genetics as it uses similar theoretical and analytical approaches (Riginos & Liggins, 2013). Landscape genetics uses environmental data to examine how spatial genetic patterns correlate with features in the environment (Manel et al., 2003; Holderegger & Wagner, 2008). Landscape features can promote or reduce dispersal among populations (Manel, et al., 2003), and in oceanic environments, varying physical and ecological factors can influence dispersal of organisms. Variables including sea-surface temperature, salinity, and current velocity can influence reproduction and survival of marine species (Kolding, 1985; Bernardi et al., 1993; Andersson et al., 2008; Seidel et al., 2010).

Techniques used in landscape genetics, such as resistant surfaces can be used to understand how environmental factors influence genetic structure among ocean populations (Galindo et al., 2006; White et al., 2010; Amaral et al., 2012; Lal et al., 2017). Resistant surfaces are spatial data layers that provide a quantitative estimation of how environmental factors influence the ability of organism to move throughout the landscape. These spatial layers are developed by parameterizing environmental variables to 'levels of resistance' or 'cost' of movement for an organism. When a variable facilitates dispersal it has low resistance and if the variable impedes dispersal, it is given a high resistance value (reviewed in Zeller et al., 2012). Using these techniques, one can determine the ecological factors contributing to dispersal and gene flow in marine populations.

1.5.5 Assignment tests

Genetic assignment tests use genetic data to place individuals of unknown origin (population) into populations. These tests use allele frequencies or genotypes to classify individuals back to a population based on the likelihood that genotypes arose from specific breeding groups (Cornuet et al., 1999; Paetkau et al., 2004). These tests have been used for numerous applications such as stock assessment (e.g. fisheries), forensics (e.g. poaching), species dispersal (e.g. sex-based, invasive species, pathogens) and conservation (e.g. oil spills; Berry et al., 2004; Grapputo et al., 2005; Manel et al., 2005; Riffaut et al., 2005; Gómez-Díaz & González-Solís, 2007; Green et al., 2014; Christie et al., 2017). A number of algorithms are available for assignment applications and include frequency-based, partial Bayesian, and fully Bayesian assignment tests (Rannala & Mountain, 1997; Pritchard et al., 2000).

The frequency-based assignment method was the original assignment test used by Paetkau et al. (1995) on polar bears (*Ursus maritimus*). Individual bears were assigned to their population with the highest probability based on allele frequencies. From this various Bayesian-assignment methods have been developed (Rannala & Mountain, 1997; Pritchard et al. 2000). Bayesian methods can determine the genetic origin of an individual, but their usefulness depends on whether or not populations are in HWE, if all source populations have been sampled, and if populations are genetically different (Manel et al., 2005). Assignment accuracy with Bayesian methods has shown to be 100% accurate when F_{ST} values are above 0.1, ten microsatellites are used, and 30-50 individuals per populations are sampled. When differentiation is weak ($F_{ST} < 0.1$), the accuracy of assignments often

decreases. Studies can improve assignment accuracy when the number of source individuals and number of loci are added to the analyses (Cornuet et al., 1999).

1.6 Study species

1.6.1 Rhinoceros auklet

The rhinoceros auklet (*Cerorhinca monocerata*) is a pursuit diving seabird. This puffin is a member of the Alcidae family referred to as an "auk" and most members of this family are colonial nesters that breed throughout the northern hemisphere. Rhinoceros auklets breed in unevenly distributed island colonies throughout the North Pacific from California to Japan (Figure 1; BirdLife International, 2017). Breeding begins in early spring with pairs incubating a single egg in an enclosed burrow. After hatching, adults provision their young by carrying a bill load of forage fish, collected during the last third of daylight, to their chick (Gaston & Dechesne, 1996; Davoren & Burger, 1999). When chicks are being provisioned, adult rhinoceros auklets are often found in waters close to breeding islands (Wahl & Speich, 1994). However, post-breeding dispersal of auklets can vary. In the eastern Pacific some birds remain near breeding colonies year round while a large portion of the population moves south towards the California Coast (Gaston & Dechesne, 1996). Birds of the western Pacific have been found to have a 3-step migration pattern (northward, southward, northward) during the non-breeding season. These movements follow spatial and seasonal changes in prey availability. Birds feed on higher trophic-level prey during the autumn and winter months, but switch to lower trophic-level prey in the early spring when foraging is confined closer to the breeding colony (Takahashi et al., 2015). Thus, dispersal of rhinoceros auklets can be tied to foraging and prey availability.

Many studies have been conducted to understand aspects related to rhinoceros auklet biology (e.g. feeding ecology, diving behaviour, breeding; Kuroki et al., 2003; Sorensen et al., 2010), but not a lot of research has focused on understanding population genetic structure. A recent study found three genetically distinct populations among rhinoceros auklet breeding colonies throughout the North Pacific (Abbott et al., 2014). Limitations of this study include the fact that only one western Pacific island was examined and large rhinoceros auklet breeding colonies from Washington-California were not included.

As many rhinoceros auklet breeding colonies have not been examined, further population genetic structure may be present among the species. For seabirds, population structure can result because of physical barriers, site fidelity, IBD, and non-breeding distribution. The marbled murrelet (*Brachyramphus marmoratus*; Friesen et al., 2005; Hall et al., 2009) and Cassin's auklet (*Ptychoramphus aleuticus*; Wallace et al., 2015) have been found to have genetic structure south of BC, as a result of IBD or a biogeographical barrier between populations.

Movements among rhinoceros auklet breeding colonies are not well known (Takahashi et al., 2015) and knowledge that genetic structure exists among colonies can help understand dispersal patterns. In particular, genetic structure among colonies has potential to determine the population of origin for birds killed at sea from oil spills or fisheries bycatch (Riffaut et al. 2005; Gomez-Diaz & Gonzalez-Solis, 2007). Thus, understanding genetic divergence among rhinoceros auklet colonies provides a baseline to be used for long-term management and conservation of a species.

1.7 Thesis objectives

The overall objective of this thesis is to utilize data from molecular markers to understand contemporary patterns of population genetic structure for rhinoceros auklets. I used ten microsatellite markers to detect genetic differences among 18 rhinoceros auklet breeding colonies throughout the North Pacific Ocean. Populations include five western and 13 eastern North Pacific Ocean breeding islands (Figure 1). This research improves our understanding of the population connectivity and gene flow for seabirds of the western North Pacific Ocean, as I compare genetic data among five rhinoceros auklet breeding colonies surrounding Japan. To further investigate patterns of population genetic structure among rhinoceros auklet colonies breeding in the eastern North Pacific Ocean, I compare genetic data from breeding colonies extending from Alaska to California. I use seascape resistance surfaces to detect environmental barriers among colonies. My two hypotheses are:

i. Genetic structure will be present between the western and eastern North Pacific Ocean colonies as gene flow is limited due to isolation by distance,

ii. Genetic structure will be present within western and eastern island colonies due to site fidelity to nesting sites.

Rhinoceros auklets are often observed on water on the continental shelf (Gaston & Dechesne, 1996; BirdLife International, 2017; Figure 1). I hypothesis genetic divergence occurs between the western and eastern North Pacific Ocean rhinoceros auklet breeding colonies because rhinoceros auklets limit dispersal over open expanses of water, showing a pattern of IBD between the western and eastern North Pacific Ocean breeding groups. I

test the hypothesis that gene flow among colonies is limited because of site fidelity to nesting location, as adult rhinoceros auklets have been observed returning to the same nesting burrow over sequential breeding seasons (Richardson, 1961). To examine barriers to movement, I develop a spatial resistance surface to measure if oceanic environmental factors influence dispersal among colonies.

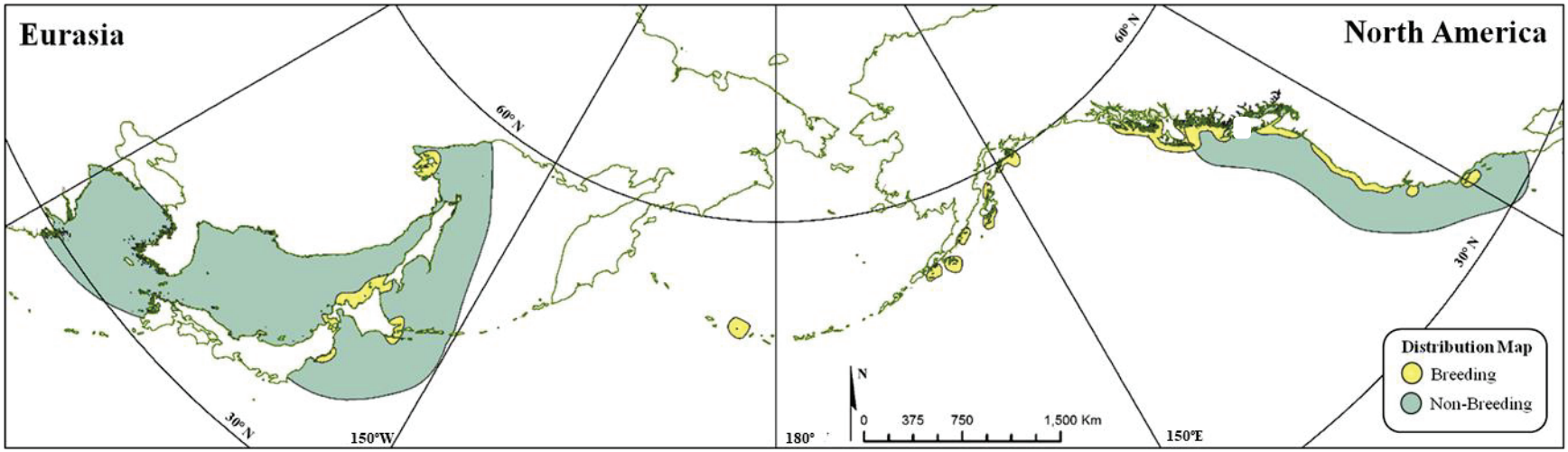


Figure 1: Map of the breeding and non-breeding distribution for rhinoceros auklet (*Cerorhinca monocerata*) throughout the North Pacific Ocean. Distribution map created with reference to BirdLife International (2017) with modification. Breeding areas are denoted in yellow. Non-breeding distribution displayed in turquoise-green. Map was visualised in ArcMap 10.2 (ESRI®) in the North Pole Lambert Azimuthal Equal Area (180° meridian). Continent shapefiles and graticules courtesy of Natural Earth (2017).

CHAPTER 2:

Contemporary genetic structure of rhinoceros auklets throughout the North Pacific Ocean

2.1 Introduction

From an evolutionary perspective, understanding how population structure arises in widespread mobile species can be an intriguing issue, particularly when there is no obvious barrier to dispersal between populations. With unimpeded gene flow, populations should form a panmictic breeding unit with no genetic structure. However, numerous highly mobile organisms show population genetic structure in the absence of physical barriers. Spatial genetic structure can be explained by an increase in genetic differentiation with geographical distance (Wright, 1943), habitat specificity (e.g. Gottelli et al., 2004; Rayner et al., 2011), behavioural traits (e.g. Hoelzel et al., 1998; Lowther et al., 2012) and ecological conditions (e.g. Pilot et al., 2006; Banks et al., 2007; Thomassen et al., 2013). Likewise, variation in the environment can influence movement, resource use, and reproduction leading to genetic structure among groups (Gauffre et al., 2008; Keller et al., 2009; Liu et al., 2013).

Marine populations display extreme patterns of heterogeneity as the unique physical properties of the ocean influence the abundance, dispersal, and spatial distribution (Roughgraden et al., 1988; Sagarin et al., 2006; Navarrete et al., 2008; Robinson et al., 2011). Heterogeneity within marine systems can be accredited to environmental factors such as bathymetry, ocean currents, primary productivity, salinity, and sea surface temperature (Gratwicke & Speight, 2005; Sagarin et al., 2006). These variables often are

factors in the development of spatial genetic structure as varying oceanographic conditions help drive dispersal (Crow, 1987; Fullard et al., 2000; Sunday et al., 2014; Benestan et al., 2016). Other barriers to marine dispersal include land masses (Knowlton et al., 1993; Goetze, 2005; Johnson & Black, 2006), oceanic current systems (Sunday et al., 2014; Møller Nielsen et al., 2016), and ocean basins (Valsecchi et al., 1997; Lal et al., 2017) all of which can promote population structure in a marine habitat (Hedgecock, 1994; Palumbi, 1994). Similarly, oceanic environments can be characterised by localised or 'chaotic' genetic patchiness, with small but significant genetic differences over small areas and no obvious spatial pattern (Johnson & Black, 1982; Roughgraden et al., 1988; Hedgecock, 1994; Selkoe et al., 2010; Selwyn et al., 2016). 'Chaotic' genetic patchiness results from oceanographic drivers such as currents (Selkoe et al., 2006). These drivers can promote areas of high heterogeneity where, under varying physical and chemical conditions, high productivity provides areas rich in foraging resources (e.g. fronts). Highly mobile species disperse to these areas to feed (Russell et al., 1992; Pérez-Ortega & İsfendiyaroğlu, 2017) and genetic structure can develop as a result of prey abundance (Hoelzel et al., 1998; Ward et al., 2009; Amaral et al., 2012) and foraging specialization (Hoelzel, 2009; Lowther et al., 2012).

Highly mobile seabirds can have spatial genetic structure (Burg & Croxall, 2001; Burg & Croxall, 2004; Faria et al., 2010; Wiley et al., 2012). Numerous mechanisms are proposed to help explain why seabirds have restrictions in gene flow including natal philopatry (returning to the natal site to breed), site fidelity, or mate selection (reviewed in Friesen et al., 2007; Friesen, 2015; Munro & Burg, 2017). Geographical distance corresponds to genetic divergence among the masked (*Sula dactylatra*), red-footed (*S. sula*), and brown (*S. leucogaster*) boobies (Steeves et al., 2003; Morris-Pocock et al., 2011).

Factors, including ocean regimes (e.g. front, currents, climate), can exert varying dispersal and selective pressures on populations (Francis et al., 1998; Shanks & Eckert, 2005). Marine fronts (e.g. Cory shearwater, *Calonectris diomedea*; Gómez-Díaz et al., 2009) and foraging locations during the breeding season (e.g. black-browed albatrosses, *Thalassarche melanophris* and *T. impavida*; Burg & Croxall, 2001) can be effective barriers to gene flow. Oceanic regimes also influence the breeding phenology of seabirds. Specifically, for Arctic/Antarctic nesting seabirds, timing of breeding and its success can be highly dependent on sea ice (Barbraud & Weimerskirch, 2006; Ramírez et al., 2017). These asynchronies between breeding times provide a temporal barrier to gene flow shown by the Cook's petrel (*Pterodroma cookii*). However, genetic divergence for the Cook's petrel is not a result of this mechanism alone, but the interaction of several: breeding time asynchronies, non-breeding distribution, and philopatric behaviour (Rayner et al., 2011). Hence, genetic structure among seabirds can arise as a result of different mechanisms acting upon populations at varying spatial-temporal scales.

This study aims to improve our understanding of population genetic structure among breeding colonies of the rhinoceros auklet (*Cerorhinca monocerata*), in the North Pacific Ocean. This seabird breeds on islands from California to Japan (Figure 2.1a; BirdLife International, 2017) and recently genetic analysis using eight microsatellites found at least three genetically distinct populations among eight rhinoceros auklet breeding colonies throughout the North Pacific (Abbott et al., 2014). Specifically, genetic structure was split between the western and eastern Pacific Ocean and among eastern Pacific islands where at least two genetically different groups exist (Triangle Island, BC vs. other BC islands; Abbott et al., 2014). The aims of this study are to assess gene flow and determine if additional genetic differentiation exists among rhinoceros

auklet breeding colonies. In this study we included the eight populations from Abbott et al. (2014) along with ten newly sampled breeding colonies, throughout the western and eastern North Pacific Ocean and screened samples at ten loci for contemporary population genetic structure. We hypothesised population genetic structure would exist among the North Pacific breeding colonies resulting from isolation by distance (IBD). In addition, we hypothesised population genetic structure would occur among breeding colonies because of site fidelity to nesting sites. Adult rhinoceros auklets have been observed returning to the same nesting burrow over sequential breeding seasons (Richardson, 1961) potentially limiting dispersal and gene flow among colonies.

2.2 Methods

2.2.1 Sampling and DNA extraction

Blood samples were collected from rhinoceros auklets at 18 breeding colonies throughout the North Pacific (Figure 2.1). Seven to eighty birds were sampled per population for a total of 704 individuals (Appendix 2.1). Samples were stored in ethanol and at -20°C upon return to the lab. DNA was extracted from four populations (DAI, TAI, MAT, TOD) using the DNeasy® Blood and Tissue Kit (Qiagen) and forty birds from AN using Macherey-Nagel DNA extraction kit. For the remaining samples from TEU, CH, MID, STL, LU, MO, SGG, TRI, PI, CL, PR, DE, & SEF, DNA was extracted using a modified Chelex protocol (Walsh et al., 1991; Burg & Croxall, 2001).

2.2.2 Microsatellite genotyping

A small set of samples (three to six) were genotyped to check for amplification and polymorphism with microsatellite loci from the rhinoceros, crested, and whiskered auklet genomes (Table 2.4). From a total of 31 microsatellite loci, 12 were polymorphic (CMms2, CMms3, CMms4, CMms9, CMms14, CMms22, CMms23, CMms26, Hasegawa et al., 2005; Pal11, Pal26, Wallace et al., 2015; Apy06, Apy09, Dawson et al., 2005). Due to inconsistent amplification, Pal26 and Apy09 were removed from the study and individuals were genotyped at the remaining ten microsatellite loci.

DNA was amplified in a 10 µL polymerase chain reaction (PCR) containing: Colorless GoTaq® Flexi (Promega) or Truin buffer, 0.2 mM dNTP, 2.5 mM $MgCl_2$, 0.5 µM forward and 1 µM reverse primers, 0.05 µM M13 fluorescently labelled primer and 0.5 U GoTaq® Flexi or 1 U Truin Taq polymerase with the exception of CMms4 where 3 mM $MgCl_2$ was used (See Table 2.4 for buffer type and $MgCl_2$ concentrations) and one percent formamide was added to CMms4, CMms9, and CMms14 reactions. A M13 sequence was incorporated onto the 5' end of the forward primer sequence to allow binding of a fluorescently labelled M13 primer for visualization of the PCR product. The Apy09 reverse primer was pigtailed (gtttctt) at the 5' end to improve scoring (Brownstein et al., 1996). Nine loci were amplified using the thermal cycling profile of 120 s at 94°C, 45 s at 55°C, and 60 s at 72°C; seven cycles of 60 s at 94°C, 30 s at 55°C, and 45 s at 72°C; 31 cycles of 30 s at 94°C, 30 s at 57°C and 45 s at 72°C; and a final cycle at 72°C for 300 s. The tenth locus (Pal11) was amplified using same program as above except annealing T_{a1} and T_{a2} were increased to 60°C and 62°C respectively (Table 2.4).

PCR products were run on a 6% polyacrylamide gel using a LI-COR 4300 DNA Analyzer (LI-COR Inc.). Alleles were scored via visual inspection with all genotypes confirmed by a second person. To maintain consistent scoring, three positive controls of known allele sizes were present on each load.

2.2.3 Genetic diversity analyses

Seven to fifty-three individuals remained in each population after excluding individuals missing three or more loci for a total of 424 individuals from 18 breeding colonies genotyped with ten microsatellites loci (Figure 2.1b). For the seven individuals from the SEF population, CMms3 failed to amplify. CMms26 had a high percent of missing data (> 35%). Thus, analyses sensitive to missing data, described in the results, excluded the SEF population and CMms26 locus.

GENEPOP v4.2 (Raymond & Rousset, 1995; Rousset, 2008) was used to check populations and loci for linkage disequilibrium and deviations from Hardy-Weinberg equilibrium (HWE) using Markov chain, parameters of: 1000 iterations, 300 batches, and 2,000 dememorization steps. MICRO-CHECKER v2.2.3 (van Oosterhout et al., 2004) was used detect scoring error due to stutter, null alleles, and drop out of large alleles.

To determine levels of population genetic diversity, GenAlEx v6.5 (Peakall & Smouse, 2006, 2012) was used to calculate observed and expected heterozygosities, private alleles, and number of alleles per locus. Allelic richness measurements are dependent on sample size with smaller sample sizes expected to have a fewer number of alleles (Kalinowski, 2004). Thus, allelic richness was calculated using statistical rarefaction in HP-

Rare v1.1 (Kalinowski, 2005) which standardizes the allelic richness measurement to account for differences in sample size.

2.2.4 Population structure analyses

2.2.4.1 F-statistics

GenAlEx v6.5 (Peakall & Smouse, 2006, 2012) was used to calculate both global and pairwise F_{ST} and F'_{ST} values to characterise population genetic structure and 999 permutations to test significance. Theoretically, the maximum F_{ST} value of one occurs for markers with two alleles. To address the multi-allelic nature of microsatellites, F'_{ST} provides a standardized value by dividing each F_{ST} with the maximum possible F'_{ST} for the data (Meirmans & Hedrick, 2011). For all tests with multiple comparisons, statistical levels of significance were adjusted using the modified False Discovery Rate (FDR) correction (Benjamini & Yekutieli, 2001).

2.2.4.2 Bayesian clustering analyses

STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003) is a non-spatial Bayesian method used to determine the number of clusters present among populations. The software uses genotypes to assign individuals to groups using a likelihood analysis. The software maximizes HWE by creating clusters of individuals with distinctive allele frequencies (Kalinowski, 2011). When individuals are correctly assigned, likelihood values of the data (i.e. $\ln Pr(X|K)$) increase (François & Durand, 2010). From a user defined range of K (i.e. number of genetic clusters), individuals are assigned ancestry coefficients (Q-

matrix coefficients, admixture proportions) for each genetic cluster. As noted by Kalinowski (2011) applying a realistic or small value of K can maximize global likelihood of the data and improve clustering among populations. This approach captures the underlying population structure of the data without overestimating it. However, the program struggles to cluster individuals when genetic differentiation is low ($F_{ST} \leq 0.03$; Latch et al., 2006) and substructure might be present among populations. Therefore, applying a hierarchical STRUCTURE approach (i.e. separate multistep runs with admixed individuals) may detect genetic structure that is not apparent when all populations are run together (Evanno et al., 2005).

Within STRUCTURE, two ancestry models can be applied to the data: the *no-admixture* or *admixture* models. The *no-admixture* model is applied when there is no prior knowledge of origin or when limited gene flow occurs between groups. The *admixture* model is applicable for populations which have shared recent ancestry or have a high potential for gene flow among groups (Pritchard et al., 2000; Porras-Hurtado et al., 2013). Likewise, two allele frequency models, *correlated* and *independent*, can be used. The *independent* model is applied when populations have essentially zero gene flow. In comparison, the *correlated* model assumes populations arose from a single ancestral population in the recent past and allele frequencies have diverged due to drift (Falush et al., 2003; Martien et al., 2007). The *correlated* allele frequencies model provides greater power when populations are closely related (Porras-Hurtado et al., 2013) and the use of the *no-admixture* model can incorrectly assign individuals to populations if samples are admixed (François and Durand, 2010).

STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003) was run using the recommended *admixture* ancestry model and *correlated* allele frequencies with sampling locations as *locpriors*. The *locpriors* option allows geographical location to be included in the model and can be informative when population structure is weak (Porras-Hurtado et al., 2013). However, using *locpriors* this information will not create clusters when none are present (Hubisz et al., 2009). For the 18 breeding populations, ten independent runs were completed over a range of K (1-6) with a burn-in of 100,000 and 120,000 Markov chain Monte Carlo (McMC) repetitions. The most appropriate number of clusters (K) was determined using several methods including visual inspection of STRUCTURE plots and comparison among highest lnPr(X|K) values. STRUCTURE HARVESTER v0.6.94 (Earl & vonHoldt, 2012) was used to obtain a graphical visualization for the highest mean likelihood examining the plateau of the lnPr(X|K) (Pritchard et al., 2000) and for delta K (ΔK; Evanno et al., 2005). Using multiple assessment methods can be helpful in the selection of K as ΔK, which is based on the second order rate of change in the log probability of the data, cannot detect K=1 and evaluation then requires the lnPr(X|K) value (Evanno et al., 2005). To further measure if substructure is present within the populations, a hierarchical analysis for both the western (n=5) and eastern (n=13) breeding groups were completed using a burn-in of 60,000 and 70,000 McMC repetitions. The user defined K ranged from K=1-4 for the western group and K=1-5 for the eastern group. Once K was determined, five additional runs were completed at the optimal K to ensure the algorithm had reached convergence.

2.2.4.3 Multivariate and distance analyses

GenAlEx v6.5 (Peakall & Smouse, 2006, 2012) was used to perform a principal coordinates analysis (PCoA) using standardized covariance from the F'_{ST} pairwise matrix. Three analyses were performed: the combined western and eastern, the western, and the eastern breeding colonies.

A Mantel test was used to test IBD with linearised pairwise F_{ST} in GenAlEx v6.5. Significance was measured using 999 permutations. Geographic distances were calculated as straight-line Euclidean distance from latitude and longitude for each breeding colony (Table 2.1) in GenAlEx v6.5. Three assessments were completed: all sites using log transformed Euclidean distance, only western, and only eastern breeding colonies using Euclidean distance.

2.2.5 Resistance surfaces

Habitat-based resistance surfaces are increasingly being utilized to help understand patterns of gene flow and dispersal. Resistance surfaces are spatial environmental layers that measure how landscape features influence species dispersal (Oberg, 2001; Wang et al., 2008). Often created as Geographical Information System (GIS) rasters, they are developed using environmental variables (e.g. temperature, habitat type); each variable is assigned "friction" values based on how a variable hinders or facilitates species' movement (Spear et al., 2010). These resistance layers are then used to measure population connectivity through downstream applications including least-cost path and corridor modelling (Adriaensen et al., 2003).

Although the use of resistance surfaces can be a valuable tool to understand animal movement, analytical methods to quantify resistance values for environmental layers are limited. This can be a disadvantage in the development of friction layers as incorrect assessment of resistance values can lead to incorrect conclusions about the role of resistance to dispersal in an environment (Spear et al., 2010; Zeller et al., 2012). Friction layers developed from inverted species distribution model maps (SDM) can provide a resistance surface where areas of low habitat suitability have high dispersal cost and vice versa. Thus, inverting an SDM, to use as a friction layer, can reduce resistance bias and improve parameterisation among environmental variables (Zeller et al., 2012; Brown, 2014).

SDM combines environmental and occurrence data to identify areas of suitable habitat for a species and maps the current distribution. Occurrence data for rhinoceros auklet for the breeding season were downloaded from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org, accessed 6 Jan. 2018). Records that were not reviewed or moderated were removed and the downloaded dataset included: records of human observations with coordinates for May-July from 1980-2017. Environmental data were obtained from the Bio-ORACLE v2.0 dataset (Tyberghein et al., 2012; Assis et al., 2017) which consists of five arcmin resolution for surface and benthic marine rasters for ocean climate, biotic and geophysical variables. Bio-ORACLE layers of current marine climate are derived from monthly averages for the period of 2000–2014 (Assis et al., 2017). In total, 11 environmental layers applicable to current marine conditions were downloaded each with a maximum, mean, minimum, and range (total of 44 layers). Variables important to seabird distribution models (i.e. sea surface temperature [SST], chlorophyll concentration, and salinity; Engler et al., 2017) were included along with variables important to marine foraging resources (Appendix 2.2). Seabirds are often associated with ocean fronts (Louzao

et al., 2009) as these features provide important foraging habitat (Thaxter et al., 2012). The standard deviation of SST range was used to calculate ocean fronts (sd of SST range over 3x3 grid; Quillfeldt et al., 2013; Engler et al., 2017). Shelf break is a physical feature that influences seabird distributions (Skov & Durinck, 1998; Lieske et al., 2014), thus, depth to seafloor (bathymetry) was obtained from MARSPEC (Sbrocco & Barber, 2013) at a resolution of five arcminutes.

Data were prepared for the SDM model using the SDMtoolbox v2.2b (Brown, 2014; Brown et al., 2017). A total of 17,589 rhinoceros auklet occurrences were downloaded from GBIF and edited to remove duplicate records. To reduce spatial bias, which will improve the predictability of a SDM model (Beck et al., 2014; Boria et al., 2014), occurrence points were further rarified using the SDM toolbox to a distance of 50 km. This measurement corresponds to the approximate distance birds are seen foraging from their colony during chick rearing (mid July; Wahl & Speich, 1994). After editing, 301 rhinoceros auklet occurrence points were retained for the model.

Environmental layers were projected using North Pole Lambert Azimuthal Equal Area (180° meridian) in ArcMap 10.2 (ESRI®). All 12 environmental layers were clipped to encompass the species range. As it is advised not to use Bio-ORACLE layers over 70°N latitude (Tyberghein et al., 2012), spatial layers were masked to a rectangular area between ~65°N to ~30°N latitude and ~120°E to ~110°W longitude. To remove highly correlated variables, a Pearson's correlation was completed in the SDM toolbox. As variables with a correlation $r > 0.7$ leads to unstable predictions (Dormann et al., 2013), environmental layers with this value were removed from further analyses (Appendix 2.3). Variables retained for the model included: bathymetry, SST (range), SST (front), nitrate (min), dissolved molecular oxygen (min), phosphate (min, range), chlorophyll (min), current

velocity (max, range), and salinity (range; Appendices 2.2 and 2.3). To limit the effect of geographical sampling bias within northern regions, a bias grid was developed using the Gaussian kernel density tool in the SDM toolbox. This grid applies weights to areas with few neighbouring values thereby improving model performance when sampling intensity differs between regions (Phillips et al., 2009).

Various algorithms are available for the development of SDMs. Maximum entropy (Maxent) which has repeatedly been demonstrated to have high predictability and performance when analyzing presence-only data for species with widespread distributions (Elith et al., 2010; Cao et al., 2013). Maxent v3.4.1 (Phillips et al., 2006; Phillips & Dudík, 2008) was used to develop the SDM. A total of 11 environmental layers, 301 rarefied occurrence points, and Gaussian kernel bias file were used to develop the model. To determine the optimal regularization parameter (to reduce model complexity and reduce overfitting; Radosavljevic & Anderson, 2014), the corrected Akaike's information criterion (AIC_C) and Bayesian information criterion (BIC) were measured using ENMTools v1.3 (Warren et al., 2010). The final model was run using: default feature types of hinge, product, linear, quadratic (with regularization values of linear/quadratic/product 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500), regularization multiplier of 1, replicate of 10 cross-validations, 30,000 background points, 500 iterations, and 25% of occurrence points were used for training. The resulting SDM was visualized and displayed using ArcMap 10.2 (ESRI®).

Evaluation of the model's predictive performance was done by examining the area under the curve (AUC) value for the receiver operating characteristic (ROC) score calculated by Maxent. AUC values range between 0.5 and 1 and values closer to 1 indicate a model with higher performance. Environmental predictors were then evaluated and

compared for training gain from the jackknifed test along with each variable's contribution and permutation importance.

A resistance layer was developed using the friction layer function in the SDM toolbox. This inverts the SDM model such that areas of high habitat suitability are areas of high dispersal and vice versa. Friction values for areas with no data were set at 10. The friction layer was then analysed using the least-cost corridors and paths function with the default parameters options in the SDM toolbox for the 18 rhinoceros auklet populations. The output is a map that depicts areas of high and low dispersal resistance. This provides a visual representation of where movement can be limited.

2.3 Results

2.3.1 Genetic diversity analyses

Over all populations and loci, the number of alleles ranged from 2-16 alleles with seven populations having one private allele. Excluding the SEF population due to its small sample size and missing data from locus CMms3, overall mean expected heterozygosity across all loci and samples was 0.62. Expected heterozygosity ranged from 0.59 (CH) to 0.66 (CL, DE, & AN) with observed heterozygosity 0.59 (CH) to 0.77 (TAI). Allelic richness (corrected to a sample size of 10) was similar between populations ranging between 3.44-3.97 (Table 2.1).

After FDR correction, two loci (CMms2, CMms22 for STL) showed deviations from HWE (Table 2.2) and there was no evidence for linkage disequilibrium between any of the loci. MICRO-CHECKER found no evidence of null alleles, large allele dropout or scoring error due to stutter.

2.3.2 Population structure analyses

2.3.2.1 F-statistics

F_{ST} statistics excluded the SEF population and CMms26 locus because of small sample sizes and the amount of missing data respectively. Using 17 colonies and nine microsatellite loci, global F_{ST} was 0.039 ($p < 0.001$) with pairwise values ranged from -0.003 (PI & CH) to 0.112 (LU & TEU) and F'_{ST} values ranged from -0.009 to 0.307 (Table 2.3). After FDR correction, 106 out of 136 tests were significant indicating a high level of genetic differentiation among populations.

The western populations were significantly differentiated at $p < 0.01$ from the eastern populations based on F_{ST} values with the exception of the TAI western populations being significantly different from the eastern populations of DE and AN at $p < 0.05$. This could be the result of limited sample size of TAI (n=10).

Among the western North Pacific populations, F_{ST} significance varied between populations. Out of the five western populations, TEU is significantly different from three populations (DAI, TAI, and MAT) at $p < 0.01$. TAI is significantly different from three populations (TOD, TEU, MAT; Table 2.3).

Among the eastern breeding colonies, 41 of the 66 were significant (Table 2.3). Each population was significantly different from at least one other population. CH was only significantly different from two other populations. The remaining eleven populations were significantly different from six-nine populations (Table 2.3).

2.3.2.2 Bayesian clustering analyses

Visual inspection of the STRUCTURE and delta K (ΔK) plots show two distinct clusters: western (DAI, TAI, MAT, TEU, TOD) and eastern (CH, MID, STL, LU, SGG, MO, TRI, PI, CL, DE, PR, SEF, AN). Most individuals had ancestry coefficient Q > 80% for one cluster (Figure 2.5a). Comparison between the average lnPr(X|K) values at K=2 (-10381) and K=3 (-10352) indicate three genetically distinct populations. At K=3, most individuals from the five western populations have Q > 70% for the same cluster; the eastern populations split into two clusters: Q > 60% for one cluster of CH, MID, STL, LU, SGG, TRI, PI, DE, PR, SEF and the second cluster of MO, CL, with 60% of the AN populations showing Q > 50% for one cluster (Figure 2.5b). Results from the hierarchical STRUCTURE analysis for the western breeding populations is K=1 (highest ln(P(X|K) value -2157). For the eastern breeding groups, the highest lnPr(X|K) value occurs at K=2 (-8176.5). The eastern populations split into two clusters of CH, MID, STL, LU, SGG, TRI, PI, DE, PR, SEF for cluster one (Q > 60%), with 67% and 64% of the individuals in the SEF and MID having Q > 60% for cluster one. The populations of MO, CL, PR, & AN have Q > 60% for cluster two (Figure 2.6). No further substructure was found through sequential hierarchical analyses.

2.3.2.3 Multivariate and distance analyses

The PCoA with ten loci and 17 breeding populations showed clear separation between the western (DAI, TAI, MAT, TEU, TOD) and eastern breeding populations (CH, MID, STL, LU, SGG, MO, TRI, PI, CL, DE, PR, AN). The first two axes explained 55.68%

and 17.53% of the variation (third axis 8.38%; Figure 2.7a) and the clustering is concordant with the STRUCTURE results.

When the western breeding colonies were examined alone, the first two axes explained 77.46% and 15.42% of the variation (third axis 6.80%). Three clusters include TEU with TOD; MAT with DAI, and TAI (Figure 2.7b). When the eastern breeding colonies were examined alone, the first two axes explained 47.31% and 16.48% (third axes 13.15%) of the variation. The majority of AK and BC colonies clustered together (CH, MID, LU, SGG, PI) with TRI forming a separate cluster and WA colonies (DE, PR) forming a third cluster. The remaining colonies of STL, MO, CL, and AN showed some degree of separation from the other colonies.

The Mantel test with linearised pairwise F_{ST} resulted in a moderate but significant pattern of IBD when all samples were compared (r^2=0.5179; $p < 0.01$ Figure 2.8a). No significant pattern of IBD was found among islands within the five western or 12 eastern North Pacific populations (Figures 2.8b & c).

2.3.3 Resistance surfaces analyses

The resulting SDM for the rhinoceros auklet closely matches the species' known distribution and performed well with the omission rate close to the predicted omission rate and a high AUC value of 0.959 (Appendix 2.5).

The environmental layer that contributed the highest percent to the model was bathymetry (64.3%) followed by SST range (10.4%) and nitrate (min; 8.4%). Environmental variables that explained permutation importance (modelled distribution)

were explained by bathymetry (59.8%) and followed by min dissolved molecular oxygen (11.4%) and SST range (8.9%; Appendix 2.3).

Jackknifed tests of regularized training gain indicate bathymetry was the variable that has the most information by itself (highest training gain). Bathymetry was also the variable that contributed to the highest loss of model performance when it was excluded (Appendix 2.4).

2.4 Discussion

2.4.1 Genetic structure of rhinoceros auklet

Results support the prediction that contemporary population genetic structure exists for rhinoceros auklets. Significant genetic differentiation occurs between and among the western and eastern North Pacific breeding groups based on multiple analyses (Table 2.3, Figures 2.5 & 2.7).

Among the western (Japanese) breeding populations, the F_{ST} results show Teuri Island (TEU) is significantly different from three of the western Pacific breeding populations (DAI, MAT, and TAI; Table 2.3), but no significant genetic structure occurs between Teuri Island and the neighbouring Todo (TOD) population. Gene flow could possibly be occurring between these northeast islands of Hokkaido as birds from Teuri Island travel northward with the Tsushima current throughout the spring and summer to forage (Deguchi et al., 2010). Likewise, F_{ST} values show Tai (TAI) is significantly different from all western Pacific colonies, except for Daikoku Island (Table 2.3). Both Tai and Daikoku are situated near or on the Pacific Coast of Japan near the Kuroshio and Oyashio

current convergent zone (Figure 2.2). Physical features in this region affect the primary productivity, survival of fish larva, and fish migration routes (Ito et al., 2004). A number of rhinoceros auklet prey species can change their spawning or migration patterns depending on oceanic conditions along the Pacific Coast of Hokkaido and Honshu (e.g. Japanese sardine, *Sardinops melanostictus*; Noto & Yasuda, 1999; Pacific herring, *Clupea pallasi;* Nagasawa, 2001; Pacific saury, *Cololabis saira*; Ito et al., 2004). Thus, gene flow among geographical proximate colonies could be occurring because of rhinoceros auklets' foraging movements following the changes in fish migration along the Japanese Coast.

For the eastern (North America) North Pacific populations, significant genetic structure occurs among islands as shown by pairwise F_{ST} and STRUCTURE results (Table 2.3; Figure 2.6). Our results indicate that breeding populations north (MO) and south (CL, DE, PR, AN) of Triangle Island are also significantly distinct from other eastern North Pacific breeding colonies. Our research also shows, contrary to Abbott et al. (2014), that Triangle Island (TRI) is not significantly differentiated from Chowiet (CH) or St. Lazaria (STL) based on the F_{ST} comparisons (Table 2.3). When the populations are examined using only the eight CMms loci in the original study with the additional individuals Triangle Island is not genetically different from St. Lazaria, but is significantly different from Chowiet Island (data not shown). Thus, increasing sampling size for populations (CH from 9 to 18; STL from 14 to 22) and adding two loci alters some of the original results. However, our results still indicate Triangle Island is significantly different from the other four islands used in the original study (MID, LU, SGG, PI; Table 2.3 Figure 2.7c). With an increase in sample size, our results confirm that Chowiet is not genetically different from the other AK and BC populations (Table 2.3) and clusters with MID, STL, LU, SGG, and PI (Figure 2.7c). However, our results do indicate that Chowiet is significantly different

from the newly sampled southern colonies of Destruction (DE) and Año Nuevo (AN) Islands (Table 2.3).

2.4.2 Oceanic barriers

Rhinoceros auklet populations between Japan and North America show high levels of genetic differentiation (Figure 2.1). Genetic differentiation between ocean basins has been shown for other highly mobile marine species including humpback whales (*Megaptera novaeangliae*; Baker et al., 1998), Pacific herring (*Clupea pallasi*; Grant & Utter, 1984) and harbor seals (*Phoca vitulina*; Stanley et al., 1996). As predicted, IBD occurs between the western and eastern North Pacific breeding islands (r^2=0.5179, $p < 0.001$; Figure 2.8a). Thus, physical distance between each metapopulation limits gene flow. The resistance surface map indicates that deep ocean water and area along the northern continental shelf (from the Kamchatka Peninsula, Russia to the Aleutian Islands, Alaska) could limit dispersal of rhinoceros auklet through these regions (Figure 2.4).

Rhinoceros auklets are known to forage throughout the shallow waters of the continental shelf (Gaston & Dechesne, 1996) with both the resistance map and SDM showing ocean depth contributes to species distribution throughout the North Pacific Ocean (Figures 2.3 & 2.4). Thus, the edge of the continental shelf can be a barrier to movement, limiting gene flow between the western and eastern North Pacific Ocean. As neither the Japanese nor American coastal colonies shows resistance to dispersal among islands (Figure 2.3 & 2.4), intrinsic factors (behavioural, ecological) may be promoting genetic divergence among rhinoceros auklet breeding islands.

2.4.3 Intrinsic barriers to gene flow

As there is no clear spatial pattern to the genetic structure among rhinoceros auklets, ecological or behavioural factors may be influencing genetic divergence among breeding colonies. For seabirds, oceanic environmental conditions can impact seabird reproduction and their dispersal (Lewis et al., 2002; Becker et al., 2007; Renner et al., 2008; Adams & Flora, 2010; Watanuki & Ito, 2012). Restrictions in gene flow can arise with foraging segregation (Burg & Croxall, 2001; Wiley et al., 2012), site fidelity (Dearborn et al., 2003), and divergent breeding time among populations (Burg & Croxall, 2004; Overeem et al., 2008).

Adult rhinoceros auklets can adjust chick provisions to different types of prey depending on the oceanic conditions (Ito, et al., 2009; Deguchi et al., 2010). This behavioural plasticity allows rhinoceros auklets to forage on different species of epipelagic fish throughout the breeding season (Davoren, 2000). Adult birds are recorded to forage close to their breeding islands in the spring (Takahashi et al., 2015) and during the breeding season (Wahl & Speich, 1994). Foraging close to their nesting colony would save energetic costs related to reproduction as many pursuit diving seabirds have high wing-loading that leads to high energy expenditure during flight (Elliott et al., 2013). Due to species' preference of diving versus flight, foraging segregation could reduce movement among rhinoceros auklet colonies. Genetic structure among islands may be occurring as adults are limiting dispersal among islands while breeding, and exhibiting site fidelity to nesting and foraging locations.

For birds on Triangle Island, fine-scale environmental conditions may be promoting genetic structure for the colony (Figure 2.7c). Annual breeding success can vary between

years on Triangle Island, with oceanic conditions surrounding the island being one factor contributing to breeding success (Borstad et al., 2011). Bertram et al. (2002) investigated nestling growth, performance, and diet among three rhinoceros auklet colonies of the eastern North Pacific (SG̱aang Gwaii, Triangle, and Seabird Rocks [~85 km south of Cleland Island along the Vancouver Island Shelf], BC) over four years (1995-1998) and concluded that large-scale ocean climate conditions had similar influence on colony breeding performance throughout the colonies, however, inter-colony differences in chick performance was influenced by local fish prey populations. Chicks on Triangle Island had reduced growth compared to chicks on SG̱aang Gwaii or Seabird Rocks because of the type of fish and mass of fish load provisioned to chicks on Triangle Island. Hedd et al. (2006) demonstrated that over 15 breeding seasons, chicks on Triangle Island had enhanced growth when Pacific sandlance (*Ammodytes hexpterus*) constituted most of the chick's diet. This research indicates among colonies, local environmental conditions can promote differences in breeding success and reproduction can vary between breeding seasons.

Different environmental pressures at breeding colonies can lead to birds breeding at different times, thus limiting gene flow among islands (Hendry & Day, 2005). This may be occurring for colonies in the southern portion of the rhinoceros auklet range. Thayer & Sydeman (2007) measured the reproduction of rhinoceros auklets over a ten year period for the California Islands of Southeast Farallon and Año Nuevo CA, located 90 km from each other. They concluded that the inshore environment of Año Nuevo may be less variable than the offshore environment of Southeast Farallon Island as birds on Año Nuevo Island were found to breed five days earlier and had higher offspring survival compared to Southeast Farallon Island. Wilson (1986) compared breeding among three Washington islands (Destruction, Protection, and Smith Islands located ~240 km to 16.5 km apart) from

1974 to 1983. Results showed that female laying dates were similar between Destruction and Protection Islands, however, egg laying occurred later on Smith Island. In comparison, breeding success was higher on the inland island of Protection Island, WA; chicks were heavier at fledgling compared to chicks from the offshore Destruction Island. This research indicates that rhinoceros auklet colonies in close proximity (~16.5 km) can have temporal differences in the time of egg-laying and that local environment can impact breeding success among closely situated colonies. For our study, we were not able to compare the genetic structure between Southeast Farallon and other islands such as Año Nuevo due to small sample size. For the populations of Protection and Destruction Islands, the F_{ST} values show the islands to be genetically similar (Table 2.3). However, Destruction and Protection Islands show some genetic differentiation in the STRUCTURE plot (Figure 2.5 & 2.6). Thus, additional investigation is needed to help understand if local ecological conditions and differences between egg laying dates are promoting genetic differences.

Other marine organisms surrounding the islands of BC and Japan have been shown to have genetic structure as a result oceanic conditions (Perez-Enriquez & Taniguchi, 1999; Withler et al., 2001; Yoshida et al., 2001; Siegle et al., 2013). These marine factors have been found to influence breeding success and foraging by rhinoceros auklets. Thayer et al. (2008) showed a significant relationship between primary type of forage fish and SST for rhinoceros auklets. This was correlated with larval fish survival and fish food availability in the eastern North Pacific. In contrast, breeding success for rhinoceros auklets in the western North Pacific has not been found to be as highly linked to factors such as SST or ocean conditions (Thayer et al., 2008; Watanuki et al., 2009). However, much of the research into understanding rhinoceros auklet reproduction has been focused on birds from Teuri Island (Figure 2.1b) with limited understanding of breeding success at other Japanese

colonies. The SDM model indicated that SST temperature range was the third highest variable for permutation importance (8.9%) with bathymetry being the variable with the highest importance (59.2%), followed by min. dissolved oxygen (11.4%). Genetic structure among the two metapopulations could be a result of different mechanisms operating on each breeding group as the western North Pacific may not be as influenced by oceanic climatic conditions as greatly as eastern North Pacific birds. Thus, future investigation could include examining the western and eastern metapopulations as separate biological entities for SDM analyses, as biologically relevant spatial information can get masked when populations of a widespread organism are grouped as a single entity (Gonzalez et al., 2011). As oceanic conditions and current movements have been found to promote genetic structure among marine organisms within the western and eastern North Pacific, further study is needed to understand foraging movements of rhinoceros auklets throughout their breeding range. This can be used to help understand if local climatic conditions are promoting genetic structure among colonies as a result of local prey resources and their availability.

2.5 Conclusions

Our research indicates significant population genetic structure exists among rhinoceros auklet breeding colonies. Both physical and oceanic variables are a semipermeable barrier to gene flow between the western and eastern North Pacific Ocean breeding groups. Reasons for genetic differentiation among island colonies include foraging segregation, site fidelity to breeding or feeding site, oceanic conditions, and divergence between time of egg laying among populations. Overall, it is highly probable

that interactions of a number of variables over different spatial and temporal scales are limiting gene flow among rhinoceros auklet breeding populations.

Further studies are required to understand breeding and non-breeding dispersal of rhinoceros auklets. Specifically, non-breeding distribution is a contributing mechanism to the pattern of genetic structure among some seabirds (Rayner et al., 2011) and further investigation into these patterns for the rhinoceros auklet will be able to improve our understanding of population foraging patterns and juvenile dispersal for North Pacific Ocean rhinoceros auklets. This information will help clarify rhinoceros auklet movement among islands, providing a method to examine what ecological factors and behaviours are promoting genetic structure among rhinoceros auklet colonies.

Table 2.1: Rhinoceros auklet breeding colonies (populations) used in analyses, colony abbreviation (ID), sample size (*n*), number of alleles (Na), expected heterozygosity (H_E), observed heterozygosity (H_O), private alleles (P_A), allelic richness (A_R), latitude (°N), longitude (°W), and location. Measures included populations with samples sizes ≥ 10 individuals.

Breeding Colony	ID	*N*	N_a	H_E	H_O	P_A	A_R	Latitude (°N)	Longitude (°W)	Location
Daikoku	DAI	20	5.3	0.65	0.68	1	3.89	42.954744	144.866057	Japan
Tai	TAI	10	4.8	0.65	0.77	0	3.97	41.263284	140.345585	Japan
Matsumae-Kojima	MAT	25	5.3	0.64	0.71	0	3.76	41.360155	139.818113	Japan
Teuri	TEU	21	5.4	0.63	0.66	1	3.61	44.417646	141.312281	Japan
Todo	TOD	12	4.6	0.64	0.67	0	3.75	45.366808	141.035141	Japan
Chowiet	CH	18	4.9	0.59	0.59	0	3.58	56.015513	-156.740272	Alaska, U.S.
Middleton	MID	50	6.3	0.64	0.60	1	3.71	59.415254	-146.345472	Alaska, U.S.
St. Lazaria	STL	22	5.9	0.65	0.65	1	3.87	56.986502	-135.710838	Alaska, U.S.
Lucy	LU	26	5.3	0.60	0.63	0	3.53	54.294418	-130.621907	British Columbia, Canada
SG̲aang Gwaii	SGG	53	5.5	0.62	0.61	1	3.56	52.092634	-131.225633	British Columbia, Canada
Moore	MO	18	4.8	0.62	0.62	0	3.55	52.678344	-129.418847	British Columbia, Canada
Triangle	TRI	26	4.7	0.61	0.62	0	3.44	50.851023	-129.066292	British Columbia, Canada
Pine	PI	27	5.6	0.63	0.60	0	3.64	50.976062	-127.729909	British Columbia, Canada
Cleland	CL	30	5.8	0.66	0.64	1	3.85	49.171516	-126.091075	British Columbia, Canada
Destruction	DE	18	4.9	0.66	0.71	0	3.94	47.674599	-124.484817	Washington, U.S.
Protection	PR	19	5.2	0.61	0.63	0	3.71	48.126341	-122.930289	Washington, U.S.
Southeast Farallon	SEF	7	3.3	-	-	-	-	37.695357	-123.000752	California, U.S.
Año Nuevo	AN	22	5.5	0.66	0.68	1	3.83	37.107584	-122.337026	California, U.S.

Table 2.2: Microsatellite diversity measures for ten microsatellite loci and 18 rhinoceros auklet breeding populations. Table includes the population, sample size (*n*), number of alleles (Na), expected heterozygosity (H_E), observed heterozygosity (H_O) for each of the ten loci. Locus-population comparisons with significant deviations from HWE after FDR correction are denoted by asterisk*. See Table 2.1 for population abbreviations.

Breeding Colony	*Locus*	Pal11	Apy06	CMms02	CMms03	CMms04	CMms09	CMms14	CMms22	CMMs23	CMms26
DAI	N_a	6	4	3	9	6	4	6	3	7	5
(*n*=20)	H_E	0.833	0.750	0.700	0.833	1.000	0.474	0.462	0.700	0.700	0.375
	H_O	0.756	0.705	0.636	0.846	0.809	0.382	0.651	0.524	0.715	0.500
TAI	N_a	5	7	3	7	5	3	4	3	6	5
(*n*=10)	H_E	0.778	1.000	0.800	0.889	0.900	0.200	0.714	0.800	0.778	0.857
	H_O	0.728	0.786	0.535	0.790	0.740	0.335	0.602	0.545	0.741	0.673
MAT	N_a	5	7	3	12	6	4	4	2	6	4
(*n*=25)	H_E	0.783	0.783	0.636	0.950	0.917	0.360	0.632	0.625	0.737	0.667
	H_O	0.742	0.765	0.582	0.878	0.740	0.316	0.525	0.499	0.722	0.653
TEU	N_a	5	7	3	10	6	4	3	2	8	6
(*n*=21)	H_E	0.769	0.789	0.550	0.762	0.833	0.524	0.429	0.571	0.737	0.600
	H_O	0.707	0.687	0.639	0.780	0.668	0.508	0.418	0.499	0.744	0.608
TOD	N_a	4	5	3	7	6	3	5	3	5	5
(*n*=12)	H_E	0.500	0.727	0.667	1.000	0.917	0.417	0.667	0.583	0.636	0.600
	H_O	0.656	0.744	0.622	0.759	0.774	0.351	0.642	0.531	0.711	0.635
CH	N_a	7	5	3	12	4	2	3	3	5	5
(*n*=18)	H_E	0.688	0.733	0.294	0.786	0.833	0.167	0.667	0.611	0.667	0.500
	H_O	0.813	0.609	0.388	0.855	0.656	0.239	0.563	0.569	0.682	0.527
MID	N_a	7	7	3	16	5	3	3	4	9	6
(*n*=50)	H_E	0.745	0.698	0.420	0.766	0.653	0.380	0.500	0.520	0.620	0.739
	H_O	0.789	0.769	0.516	0.834	0.668	0.320	0.557	0.563	0.662	0.754

STL	N_a	8	7	3*	12	4	4	3	6*	6	6
(***n*=22**)	H_E	0.864	0.810	0.333	0.778	0.700	0.318	0.524	0.688	0.773	0.714
	H_O	0.817	0.732	0.475	0.815	0.678	0.418	0.550	0.658	0.711	0.686
LU	N_a	7	6	4	13	4	2	3	3	5	6
(***n*=26**)	H_E	0.680	0.857	0.308	0.731	0.692	0.308	0.577	0.692	0.538	0.923
	H_O	0.774	0.729	0.384	0.838	0.661	0.260	0.517	0.582	0.500	0.762
SGG	N_a	6	8	3	12	5	4	3	3	5	6
(***n*=53**)	H_E	0.867	0.660	0.245	0.774	0.698	0.365	0.660	0.538	0.558	0.769
	H_O	0.792	0.740	0.320	0.853	0.657	0.335	0.567	0.563	0.626	0.723
MO	N_a	6	6	3	9	4	2	3	2	7	6
(***n*=18**)	H_E	0.722	0.706	0.556	0.692	0.722	0.444	0.529	0.588	0.600	0.600
	H_O	0.733	0.699	0.415	0.802	0.681	0.346	0.552	0.484	0.649	0.800
TRI	N_a	5	6	3	11	5	2	3	3	4	5
(***n*=26**)	H_E	0.750	0.680	0.417	0.792	0.654	0.154	0.654	0.680	0.611	0.850
	H_O	0.776	0.666	0.556	0.806	0.696	0.204	0.532	0.598	0.620	0.676
PI	N_a	7	6	4	13	4	3	3	3	7	6
(***n*=27**)	H_E	0.773	0.636	0.370	0.778	0.600	0.333	0.370	0.593	0.815	0.704
	H_O	0.813	0.595	0.438	0.885	0.706	0.359	0.514	0.522	0.658	0.762
CL	N_a	7	6	4	14	6	3	3	3	5	7
(***n*=30**)	H_E	0.714	0.667	0.520	0.778	0.750	0.500	0.667	0.704	0.519	0.591
	H_O	0.811	0.754	0.474	0.894	0.709	0.418	0.565	0.590	0.583	0.754
DE	N_a	7	5	3	9	4	2	4	3	7	5
(***n*=18**)	H_E	0.941	0.813	0.500	0.769	0.833	0.294	0.727	0.875	0.778	0.600
	H_O	0.813	0.703	0.586	0.858	0.708	0.251	0.711	0.633	0.693	0.600
PR	N_a	7	6	2	12	5	3	2	4	6	5
(***n*=19**)	H_E	0.714	0.833	0.222	0.786	0.947	0.389	0.583	0.556	0.611	0.647
	H_O	0.821	0.755	0.198	0.875	0.711	0.323	0.497	0.559	0.699	0.699

SEF	**N_a**	7	4	2	-	4	2	3	3	3	5
(*n*=7)	**H_E**	0.667	0.500	0.143	-	0.857	0.143	0.200	0.667	0.500	0.833
	H_O	0.819	0.514	0.133	-	0.643	0.133	0.460	0.569	0.594	0.722
AN	**N_a**	5	5	4	11	5	3	3	5	8	6
(*n*=22)	**H_E**	0.684	0.773	0.364	0.733	0.947	0.409	0.722	0.667	0.714	0.750
	H_O	0.756	0.681	0.536	0.864	0.719	0.385	0.573	0.583	0.729	0.775
Average	**N_a**	**6**	**6**	**3**	**11**	**5**	**3**	**3**	**3**	**6**	**6**
for each	**H_E**	**0.773**	**0.702**	**0.468**	**0.791**	**0.701**	**0.327**	**0.555**	**0.560**	**0.669**	**0.684**
locus	**H_O**	**0.748**	**0.745**	**0.447**	**0.755**	**0.803**	**0.343**	**0.571**	**0.648**	**0.661**	**0.684**

Table 2.3: Pairwise F_{ST} values (below diagonal) and F'_{ST} values (above diagonal) for 17 rhinoceros auklet breeding colonies based on nine microsatellite loci. One population and one locus were removed because of small sample size and missing data (SEF and CMms26). Bold underlined values indicate statistical significant at $p < 0.05$; with asterisk* at $p < 0.001$ following corrections for multiple tests. See Table 2.1 for population abbreviations

		WESTERN					EASTERN											
		DAI	**TAI**	**MAT**	**TEU**	**TOD**	**CH**	**MID**	**STL**	**LU**	**SGG**	**MO**	**TRI**	**PI**	**CL**	**DE**	**PR**	**AN**
WESTERN	**DAI**		0.044	0.026	**0.117***	0.046	**0.264**	**0.254**	**0.252**	**0.301**	**0.288**	**0.214**	**0.254**	**0.258**	**0.196**	**0.166**	**0.213**	**0.174**
	TAI	0.013		**0.075**	**0.228***	**0.107**	**0.202***	**0.215***	**0.254***	**0.254***	**0.284***	**0.1878***	**0.251***	**0.221***	**0.138***	**0.152**	**0.192***	**0.166**
	MAT	0.008	**0.022**		**0.122***	0.034	**0.205***	**0.196***	**0.212***	**0.246***	**0.245***	**0.175***	**0.166***	**0.237***	**0.168***	**0.158***	**0.188***	**0.174***
	TEU	**0.036***	**0.071***	**0.038***		0.034	**0.302***	**0.272***	**0.284***	**0.307***	**0.275***	**0.269***	**0.223***	**0.248***	**0.293***	**0.305***	**0.283***	**0.244***
	TOD	0.014	**0.032**	0.010	0.011		**0.234***	**0.196***	**0.218***	**0.274***	**0.250***	**0.191***	**0.175***	**0.217***	**0.191***	**0.166***	**0.203***	**0.200***
EASTERN	**CH**	**0.086***	**0.067***	**0.067***	**0.105***	**0.078***		0.009	0.010	0.008	0.013	0.045	0.037	-0.009	0.034	**0.070**	0.019	**0.051**
	MID	**0.083***	**0.071***	**0.064***	**0.093***	**0.065***	0.003		**0.037**	0.005	0.009	**0.062**	**0.037**	0.019	**0.053**	**0.080**	**0.076**	**0.093**
	STL	**0.07***	**0.075***	**0.064**	**0.090***	**0.066***	0.003	**0.012**		**0.045**	**0.041**	**0.052**	0.029	0.027	0.031	**0.054**	**0.062**	0.039
	LU	**0.104***	**0.090***	**0.086***	**0.112***	**0.098***	0.003	0.002	**0.016**		-0.001	**0.098**	**0.064**	0.012	**0.066**	**0.124**	**0.097**	**0.136**
	SGG	**0.098***	**0.098***	**0.084***	**0.098***	**0.087***	0.005	0.003	**0.014**	0.000		**0.077**	**0.036**	0.005	**0.075**	**0.104**	**0.061**	**0.094**
	MO	**0.070***	**0.062***	**0.057***	**0.093***	**0.064***	0.016	**0.022**	**0.017**	**0.037**	**0.028**		**0.064**	**0.062**	0.026	**0.103**	**0.061**	**0.052**
	TRI	**0.081***	**0.081***	**0.055***	**0.076***	**0.058***	0.013	**0.013**	0.010	**0.024**	**0.013**	**0.023**		**0.033**	**0.081**	**0.098**	**0.099**	**0.103**
	PI	**0.084***	**0.073***	**0.078***	**0.085***	**0.072***	-0.003	0.007	0.009	0.004	0.002	**0.022**	**0.012**		**0.043**	**0.103**	**0.069**	**0.074**
	CL	**0.056***	**0.039***	**0.048***	**0.089***	**0.055***	0.011	**0.017**	0.009	**0.022**	**0.025**	0.008	**0.025**	**0.014**		0.030	0.033	**0.061**
	DE	**0.048***	**0.044**	**0.047***	**0.095***	**0.049***	**0.023**	**0.026**	**0.016**	**0.043**	**0.035**	**0.034**	**0.032**	**0.034**	0.009		0.032	0.024
	PR	**0.066***	**0.060***	**0.059***	**0.094***	**0.064***	0.007	**0.026**	**0.020**	**0.035**	**0.022**	**0.021**	**0.034**	**0.024**	0.010	0.010		0.037
	AN	**0.052***	**0.049**	**0.052***	**0.077***	**0.060***	**0.017**	**0.031**	0.012	**0.048**	**0.032**	**0.017**	**0.033**	**0.024**	**0.018**	0.007	0.012	

Table 2.4: Information for microsatellite primers used in this study including locus, repeat type and sequences. A M13 tag sequence (5'- cacgacgttgtaaaacgac - 3') was added to the 5' end of each forward primer. PCR conditions include annealing temperatures (T_{a1}, T_{a2}), buffer type, and magnesium chloride ($MgCl_2$) concentration used to amplify each primer pair.

Locus	Repeat Type	Sequence (5'-3') F and R	Size (bp)	T_{a1} °C	T_{a2} °C	Buffer	$MgCl_2$ (mM)	Reference
Pal11F-M13	$(ATGG)_{13}$	M13 - AAACTGAAGAACTACACTCTGAAGGG	232-260	60	62	Truin	2.5	Wallace et al. 2015
Pal11R		CAACCGCTTCACTTAGCTTGG						
Apy06F-M13	$[(GATA)_2(GAGA)]_2$	M13 - CCAAAGTCTAAGGACAGGC	185-237	55	57	Truin	2.5	Dawson et al. 2005
Apy06R		gtttcttATCTATTTTAACGTACATAGAGTTTATC						
CMms2F-M13	$(TG)_{11}$	M13 - TCTCCCCTCAAAATGGCTCTC '	146-154	55	57	Truin	2.5	Hasegawa et al. 2005
CMms2R		GCAGGCTTCTCCCACTTTCA						
CMms3F-M13	$(AG)_{29}$	M13 - GTTCCCTCAGGCAAAAGCAA	214-258	55	57	Flex	2.5	Hasegawa et al. 2005
CMms3R		CGTAGCCACCTGTTACACCCTT						
CMms4F-M13	$(TC)_7$, $(AC)_9$	M13 - GCAGTGTCTTAACTACCCGTACAC	136-150	55	57	Truin	3	Hasegawa et al. 2005
CMms4R		GCTGCCACGTCAAGGAAATAG						
CMms9F-M13	$(AC)_{10}$	M13 - TCAAGGCCCTGGACTCTGAC	200-214	55	57	Truin/Flex	2.5	Hasegawa et al. 2005
CMms9R		CAGTGTGGGCTGGACTATTTCA						
CMms14F-M13	$(TG)_{11}$	M13 - TCATTGTGCGCTGCTCAAAG	184-192	55	57	Flex	2.5	Hasegawa et al. 2005
CMms14R		ATGCACAGGTGTCACGGCT						
CMms22F-M13	$(AC_{)11}$	M13 - CCATCGTGCAGCTCAATAAT	115-127	55	57	Truin/Flex	2.5	Hasegawa et al. 2005
CMms22R		TGGTCGCCATATTCTCATTC						
CMms23F-M13	$(AC)_{24}$	M13 - GCTTAATTCATCCTCACTCCCC	129-161	55	57	Flex	2.5	Hasegawa et al. 2005
CMms23R		GGCTCTCAAACGTCAACACG						
CMms26F-M13	$(AC)_{12}$	M13 - CTATGTTCACACCCCCTCCG	207-221	55	57	Flex	2.5	Hasegawa et al. 2005
CMms26R		ATCGATTGCATTTGCCCG						

a)

b)

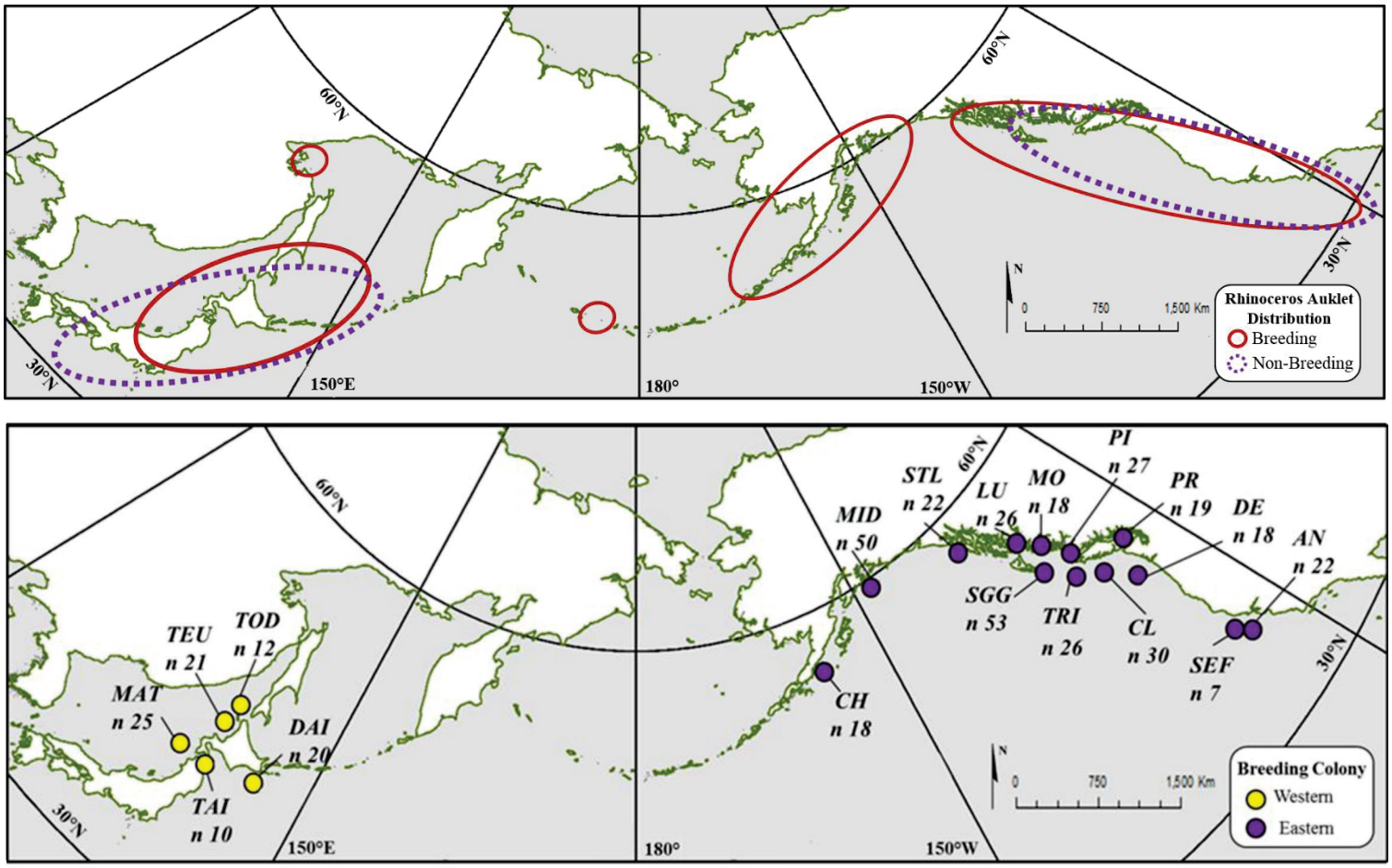


Figure 2.1: Rhinoceros auklet (*Cerorhinca monocerata*) a) breeding and non-breeding distributions (BirdLife International, 2017) and b) colonies used for this study. Number of samples used for final analyses denoted by *n*. See Table 2.1 for population abbreviations. Map was visualised in ArcMap 10.2 (ESRI®) in the North Pole Lambert Azimuthal Equal Area (180° meridian). Graticules and ocean shapefiles courtesy of Natural Earth (2017).

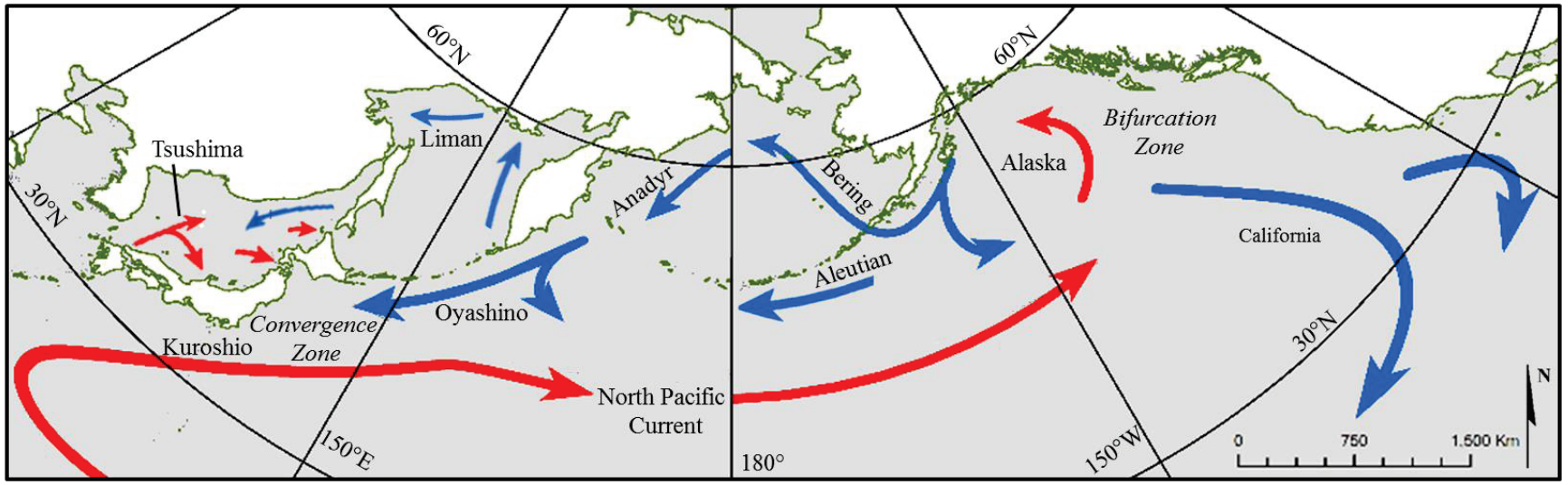


Figure 2.2: Ocean currents occurring throughout the North Pacific Ocean. Zones where ocean currents meet or diverge denoted in italics. Blue arrows indicate cool currents and red arrows show warm currents. Map was visualised in ArcMap 10.2 (ESRI®) in the North Pole Lambert Azimuthal Equal Area (180° meridian). Ocean current polygons modified from ESRI®.

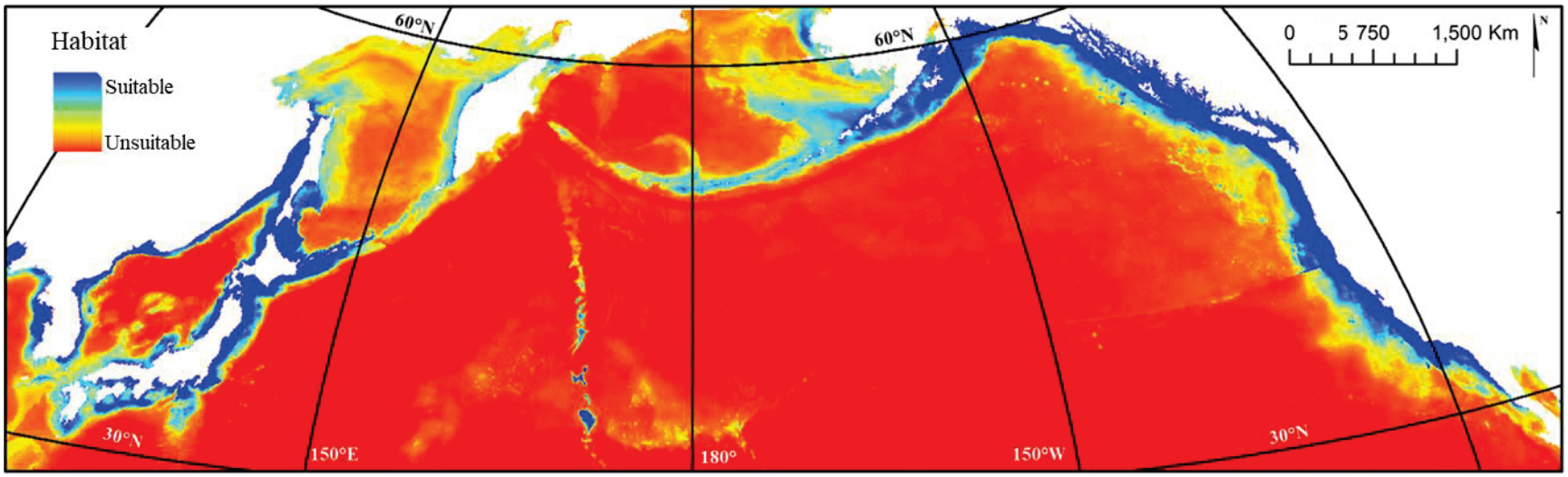


Figure 2.3: Species distribution model (SDM) for rhinoceros auklet created from GBIF breeding season occurrences (May-July). Environmental layers used to develop the SDM are listed in Appendix 2.3. Map was produced using the SDM toolbox (Brown, 2014; Brown et al., 2017), Maxent (Phillips et al., 2006; Phillips & Dudík, 2008), and ArcMap. The final map was visualised using ArcMap 10.2 (ESRI®) in the Azimuthal Equidistant (180° meridian) projection. Most suitable habitat for rhinoceros auklet is shown in cool colours (blue) with unsuitable habitat shown in warm colours (orange to red).

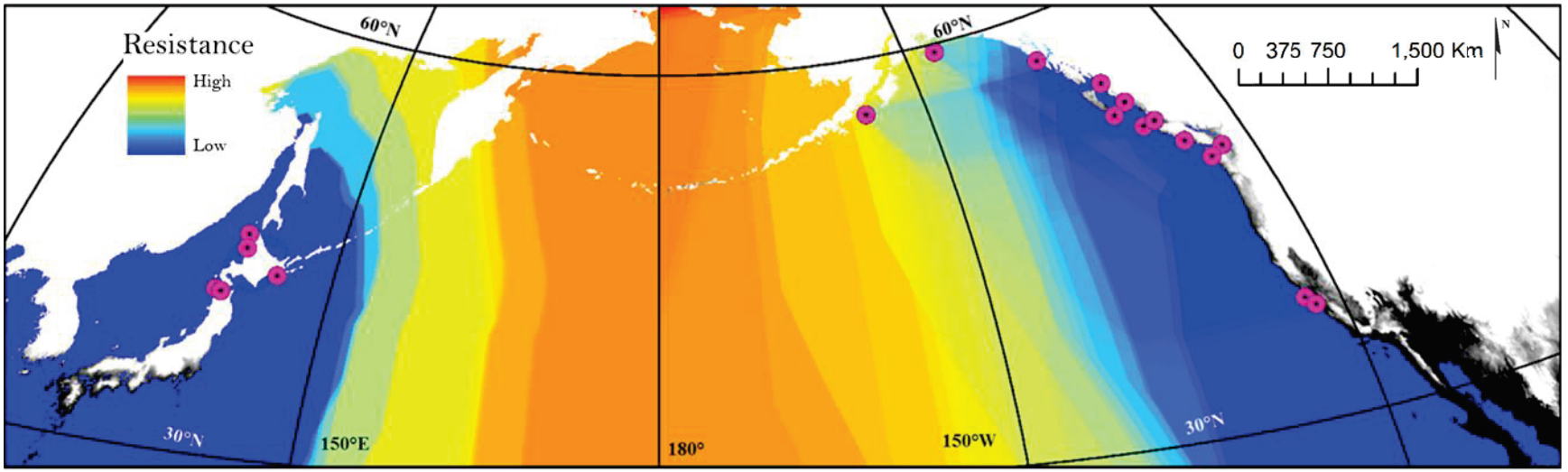
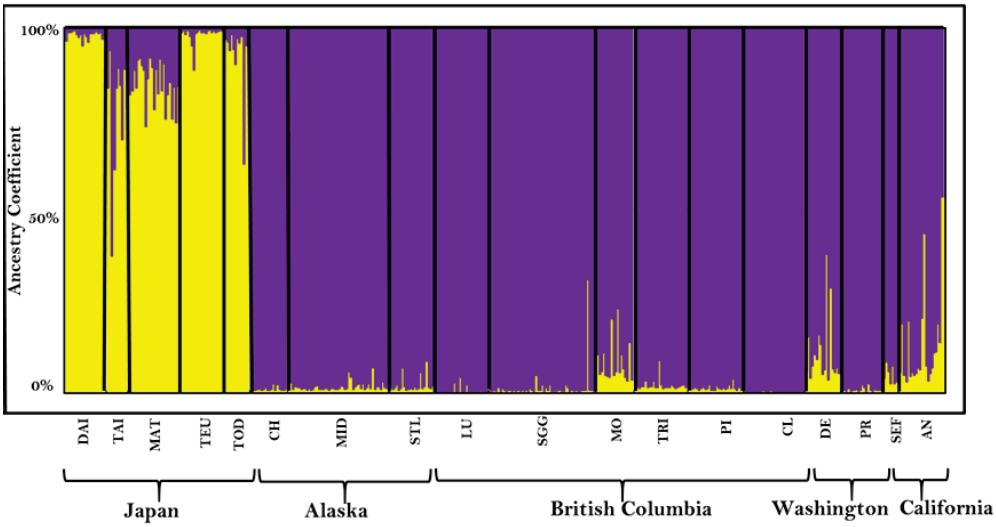


Figure 2.4: Resistance surfaces for 18 rhinoceros auklet breeding colonies located throughout the North Pacific Ocean. Areas of low resistance are in blue with gradients of orange to red indicating area of higher resistance. Breeding colonies denoted by the pink-circled-star. See Figure 2.1 for island names and sample sizes. Resistance surfaces were developed using friction surfaces from an inverted SDM for rhinoceros auklet (Figure 2.3) and least-cost corridors function within the SDM toolbox (Brown, 2014; Brown et al., 2017). The final map was visualised using ArcMap 10.2 (ESRI®) in the Azimuthal Equidistant (180° meridian) projection.

a)



b)

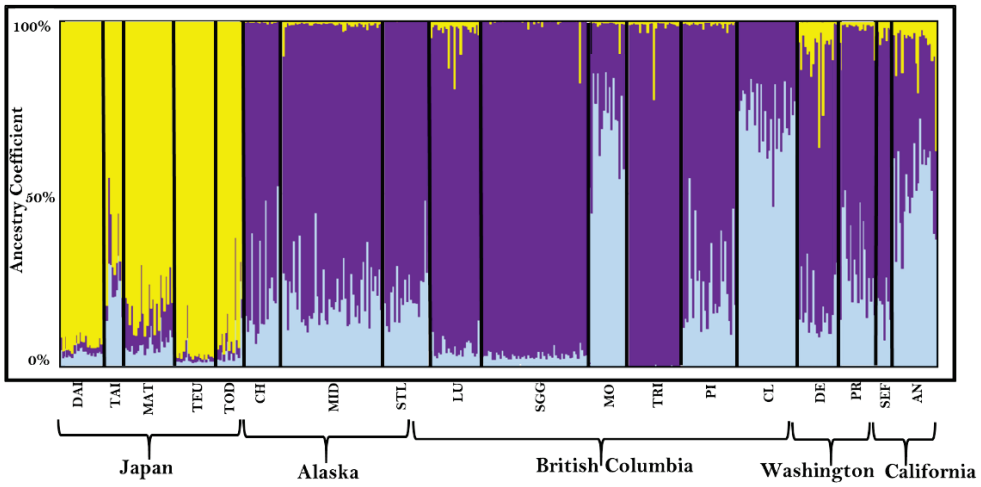


Figure 2.5: Genetic groups for 18 rhinoceros auklet North Pacific Ocean breeding colonies for ten microsatellite loci as inferred by STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003). Histogram plots show ancestry coefficient (Q) for each individual. Breeding populations are listed from the western North Pacific (left) to eastern North Pacific (right; see Table 2.1 for population abbreviations). a) At K=2 two genetic clusters occur between the western Pacific (Q > 70% yellow; DAI, TAI, MAT, TEU, TOD) from the eastern Pacific (Q > 80% purple; CH, MID, STL, LU, SGG, MO, TRI, PI, CL, DE, PR, SEF, AN). b) At K=3 one cluster occurs for the western Pacific (Q > 70 % yellow) and two for the eastern Pacific; purple Q > 70% CH, MID, STL, LU, SGG, TRI, PI, DE, PR, SEF and light blue Q > 60% MO, CL; 60% of the birds from AN having Q > 50 % for light blue.

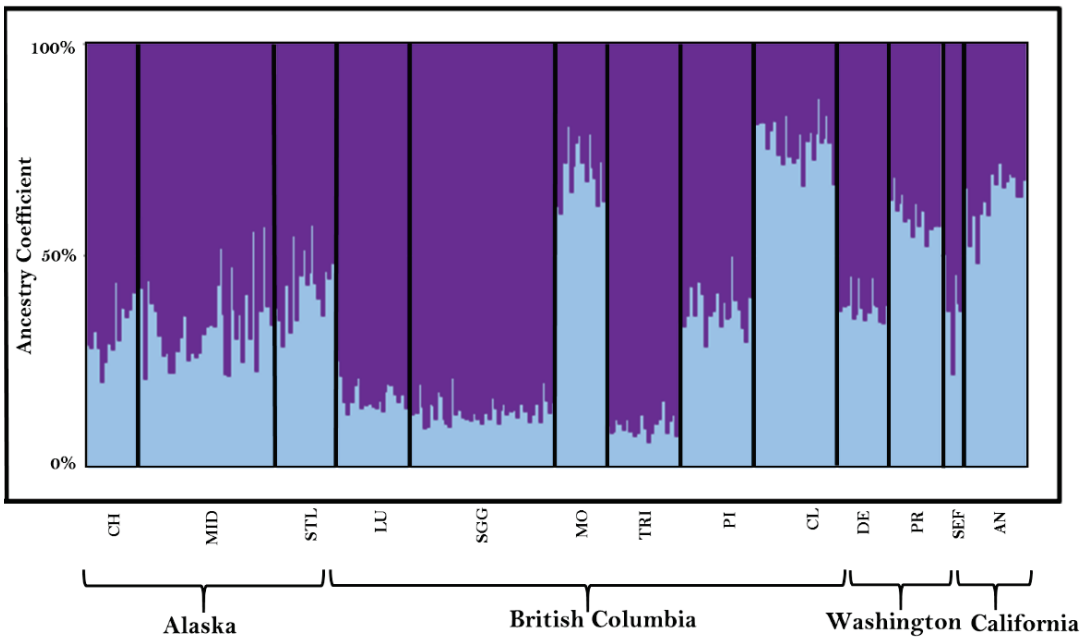
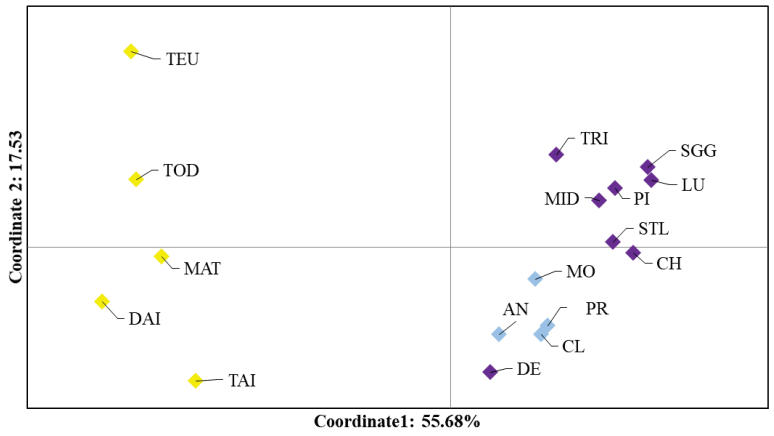
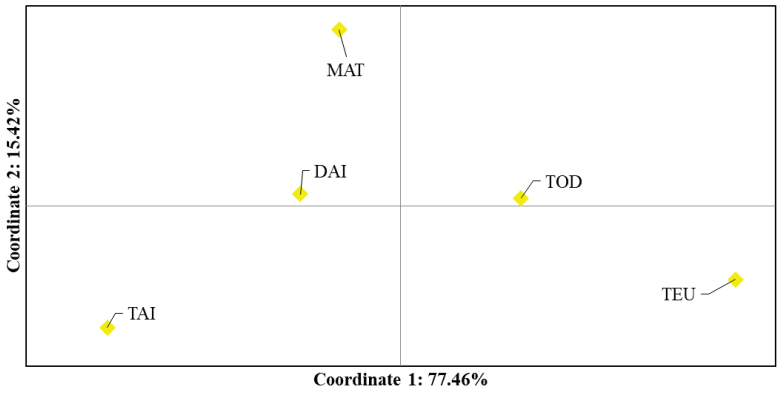


Figure 2.6: Hierarchical analysis of 13 eastern North Pacific Ocean rhinoceros auklet breeding colonies for ten microsatellite loci as inferred by STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003). Histogram plot shows ancestry coefficient (Q) for each individual. Populations are listed as they occur from Alaska to California (see Table 2.1 for population abbreviations). Substructure was found for the 13 eastern breeding colonies, and supported by mean lnPr(X|K) value and delta K (ΔK) at K=2 (Appendix 2.7b). Substructure includes one cluster of CH, MID, STL, LU, SGG, TRI, PI, DE, (purple average Q > 60%) with 67% and 64% of the individuals in the SEF and MID populations with Q > 60% for the purple cluster; the second cluster of MO, CL, & PR, & AN (light blue Q > 60%). No additional substructure was found.

a)



b)



c)

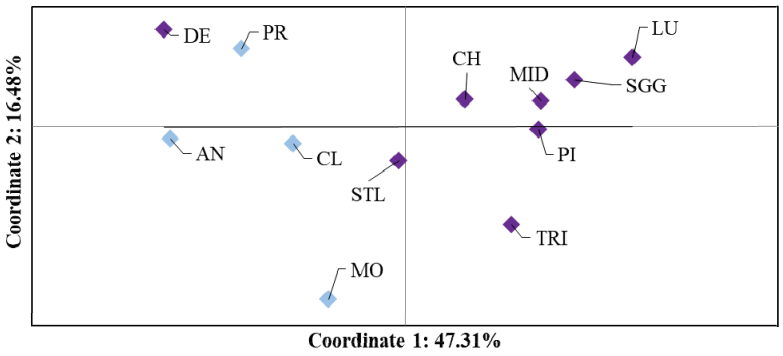


Figure 2.7: PCoA analysis conducted in GenAlEx v6.5 (Peakall & Smouse, 2006, 2012) based on pairwise F'_{ST} values for a) the western and eastern, b) the western, and c) the eastern North Pacific rhinoceros auklet breeding colonies. Colours correspond to STRUCTURE plots (Figures 2.5 & 2.6). Plot a) coordinates 1 and 2 explain 55.68% and 17.53% of the variation (not shown: coordinate 3 at 8.38%). b) Coordinates 1 and 2 explain 77.46% and 15.42% of the variation (not shown: coordinate 3 at 6.80%). Plot c) coordinates 1 and 2 explain 47.31% and 16.48% of the variation (not shown: coordinate 3 at 13.15%). See Table 2.1 for population abbreviations.

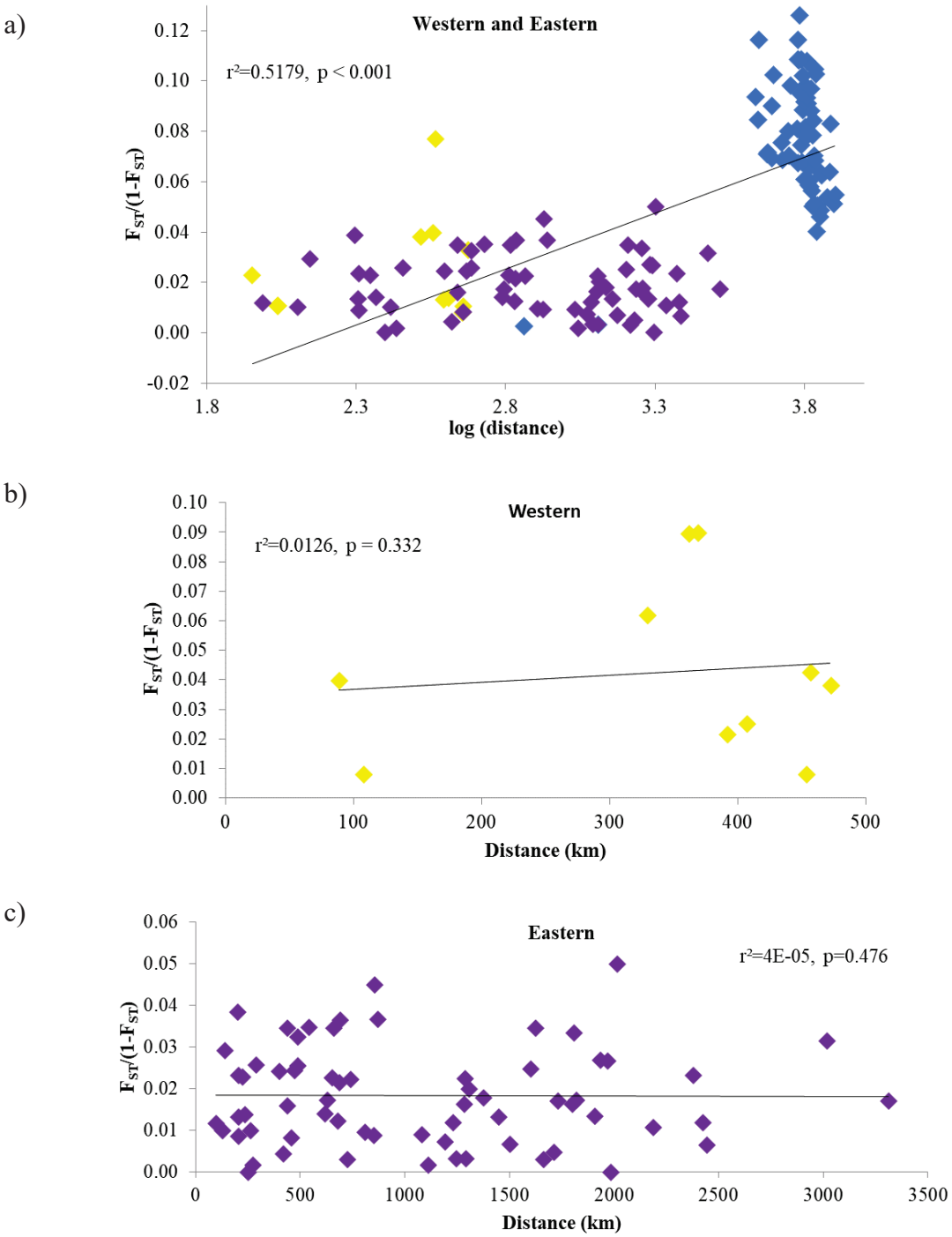


Figure 2.8: Plots of the Mantel test for IBD for a) western and eastern b) western, and c) eastern North Pacific Ocean rhinoceros auklet breeding colonies. Western populations are DAI, TAI, MAT, TEU, TOD (n=5; yellow). Eastern populations are CH, MID, STL, LU, SGG, MO, TRI, PI, CL, DE, PR, AN (n=12; purple). a) values comparing east and west populations denoted in blue. Mantel test calculated in GenAlEx v6.5 (Peakall & Smouse, 2006, 2012) using linearised F_{ST} vs. a) log or b & c) regular Euclidean distance.

CHAPTER 3:

Genetic assignment of eastern North Pacific Ocean rhinoceros auklets

3.1 Introduction

Knowledge of marine species' distribution is fundamental to ocean conservation and management. For highly mobile species, movements can depend on the temporal and spatial aspects of an environment (e.g. time of year, foraging locations) which can make population boundaries unclear (Cegelski et al., 2003; Lewallen et al., 2007). Many oceanic species migrate across regional, national, and international boundaries (e.g. sea turtles, whales, seabirds; Bowen et al., 1989; Fitzsimmons & Warburton, 1992; Etnoyer et al., 2006; Rayner et al., 2011; Stewart et al., 2013). This means multiple jurisdictions are responsible for protecting a species, with some responsible for managing breeding populations and others for managing non-breeding groups. Thus, conserving species that disperse over numerous jurisdictions can be complicated and requires communication from multiple parties (Wolf et al., 2006; Weimerskirch et al., 2012).

Assignment methods can be combined with genetic data to help determine species' dispersal when individuals move away from their natal breeding site (Hall et al., 2009; Saenz-Agudelo et al., 2009; Faria et al., 2010). These methods compare genotypes of individuals with unknown origins to those from reference (source) populations, allowing individuals to be assigned to a population of their natal origin. Methods to conduct assignment tests include likelihood estimates based on genetic distance, frequency, or partial-Bayesian assignment criteria (Paetkau et al., 1995; Rannala & Mountain, 1997;

Cornuet et al., 1999). Assignments can also be assessed *a posterior* using fully Bayesian clustering programs (e.g. STRUCTURE; Pritchard et al., 2000). Cornuet et al. (1999) showed partial Bayesian methods perform slightly better compared to the frequency-based methods and with $F_{ST} \sim 0.1$, ten microsatellites, and 30-50 individuals per population, 100% correct assignment could be achieved using partial-Bayesian methods. In contrast, fully Bayesian methods can have higher performance compared to partial-Bayesian methods (Manel et al., 2002; Dalvit et al., 2008). In weakly differentiated populations ($F_{ST} < 0.1$), the ability of the assignment to accurately classify individuals to populations declines (Maudet et al., 2002; Berry et al., 2004; Ogden & Linacre, 2015). Thus, these factors can limit the accuracy and performance of assignment tests and should be considered in the assessment of the results.

Here we will evaluate the feasibility of using genetic markers to identify the genetic origin of individual rhinoceros auklets found at sea. This seabird breeds in colonies throughout the North Pacific Ocean and populations are highly vulnerable to oiling events (Page et al., 1990; Oka & Okuyama, 2000; Henkel et al., 2014) and have high bycatch mortality in net-associated fishery activities (Thompson et al., 1998; Smith & Morgan, 2005; Hamel et al., 2009). Genetic methods can assess the genetic origin of birds located at sea when populations are genetically structured (e.g. albatross; Abbott et al., 2006; Burg, 2007; Burg et al., 2017; petrels; Techow et al., 2016). The effectiveness of assignment methods depends on the amount of genetic differentiation between subpopulations, if the population of origin has been sampled, and the number of samples and loci. As population genetic structure is present among eastern North Pacific rhinoceros auklet breeding colonies (Abbott et al., 2014; Chapter 2), we will evaluate if assignment tests can be used

to assign eastern North Pacific Ocean bycatch rhinoceros auklets back to their breeding population.

3.2 Methods

3.2.1 Sampling and DNA extraction

Tissue samples (muscle or feather) were collected from 124 rhinoceros auklet bycatch carcasses (123 birds from BC locations and one from Oregon; Figure 3.1 & 3.2; Appendix 3.1). Collection dates ranged from June-December from 2005-2016 (one sample unknown) with 94% of the samples collected from June-August. With the exception of five samples, a geographical location (e.g. closest island; Appendix 3.1) was provided for each bird. Tissue samples were stored in ethanol at -20°C while in the lab. DNA was extracted using a modified Chelex protocol (Walsh et al., 1991; Burg & Croxall, 2001).

3.2.2 Microsatellite genotyping

Samples were genotyped with the ten microsatellite loci used in the rhinoceros auklet breeding colonies population assessments (Table 2.4). Microsatellite genotyping protocols are described in Chapter 2, Section 2.2.2 of this thesis.

3.2.3 Assignment test analyses

After excluding individuals missing three or more loci, a total of 69 bycatch samples remained for analyses: closest breeding island LU [n=33], PI [n=20], PR [n=10], DE [n=1],

unknown [n=5] (Figure 3.2). To assess the accuracy of assignment, individuals were arranged by location (e.g. marine waters, nearest breeding island) and collection date (Figure 3.1; Appendix 3.1). Individuals collected in June and July were considered birds from the breeding period when birds would be feeding chicks near their breeding colony (n=43; Figure 3.2). Birds collected from Aug-Nov were considered post-chick rearing (post-breeding) and these individuals have a higher potential to disperse (n=26; Figure 3.2). Baseline genetic information for source populations included the 336 individuals of the 13 eastern North Pacific Ocean breeding colonies used in the population studies (Chapter 2 of this thesis; Figure 2.1b) unless otherwise noted.

3.2.3.1 Assignment analyses

The CMms26 locus and the SEF source population were excluded from likelihood assignment tests because of missing data. WHICHRUN v4.1 (Banks & Eichert, 2000) and GENECLASS2 (Piry et al., 2004) were used to assign individuals using likelihood methods. WHICHRUN assigns individuals to populations with the greatest probability of occurrence based on maximum likelihood. GENECLASS2 was used with the partial-Bayesian criterion of Rannala & Mountain (1997) with the probability computation of Cornuet et al. (1999). These probabilities are developed from exclusion-based simulations with the likelihood of a genotype compared to a distribution of genotypes, generated by Monte Carlo resampling methods. Individuals are given a probability, with confidence intervals, of belonging to a list of potential source populations. Under the exclusion based simulation in GENECLASS2 certainty of assignment can be measured by the number of

populations an individual is assigned to. High levels of certainty occur when individuals can only be assigned to one population.

To measure accuracy, self assignment was performed on individuals of known origin (i.e. reference samples). In WHICHRUN, reference files can be self assigned using the jackknife option. In GENECLASS2, self assignment was completed under the model from Cornuet et al. (1999) using a statistical threshold of 0.01 with 10 000 Monte Carlo simulated individuals per sample. For each algorithm, assignment was performed using individuals of known origin (329 individuals) from the 12 source populations and individuals in groups created based on genetic similarity (F_{ST} values). The four groups include: North (CH, MID, STL, LU, SGG, PI); TRI; MO & CL; and South (DE, PR, AN).

3.2.3.2 Bayesian clustering analyses

STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003) was run with the POPFLAG option, admixture ancestry model, correlated allele frequencies, and locpriors. When a POPFLAG is applied, STRUCTURE uses this to identify individuals of known origin (POPFLAG=1) or unknown origin (POPFLAG=0). STRUCTURE then utilizes these "learning samples" and compares the ancestry of unknown individuals to the baseline dataset. This provides a probability of origin for each unknown sample. As the program uses individual genotypes to cluster the data, all 13 breeding colonies were used for assignment as the baseline reference (Figure 2.1b). The 13 breeding populations were assigned POPFLAG=1 and the bycatch individuals assigned POPFLAG=0. STRUCTURE was run for ten independent runs over a range of K (1-3) with a burn-in of 60,000 and 70,000 Markov chain Monte Carlo (McMC) repetitions. A range of K (1-3) was completed

to confirm the accuracy of K when individuals were assigned using POPFLAG. The ancestry of the unknown individuals was assessed at K=2, the number genetic clusters shown to occur for eastern North Pacific Ocean rhinoceros auklet breeding populations (Figure 2.6; Appendix 2.7).

3.3 Results

3.3.1 Assignment analyses

The accuracy of self assignment for birds in both WHICHRUN and GENECLASS2 was low. In WHICHRUN with the 12 source populations, the breeding colony with the highest assignment was MO (44%) followed by AN (41%). The remaining colonies had < 25% of individuals correctly assigned to the colony of origin (Table 3.1). In GENECLASS2 using the partial Bayesian method, the overall assignment quality index with 12 breeding colonies was low at 12.5% with only 65 out of the 329 individuals (19.8%) being correctly assigned to their sampled colony of origin. Of the 12 breeding colonies, MID had the highest correct assessment rate at 46% followed by DE and SGG at 28%, and CL at 23%. The remaining eight populations had < 20% of the individuals correctly assigned (Table 3.2).

Self assignment with the four groups based on genetic similarity varied depending on the software. For WHICHRUN the highest correct assignment was for MO & CL (35%) followed by TRI (31%). In comparison, GENECLASS2 showed a relativity high assignment for the North genetic group (72%). The remaining groups had < 50% correct assignment, with no individuals correctly assigned to TRI (Table 3.3).

3.3.2 Fully Bayesian analyses

Results from the hierarchical STRUCTURE analysis (Chapter 2, Section 2.3.2.2 of this thesis) show the eastern North Pacific Ocean rhinoceros auklet populations splitting into two clusters: 1) CH, MID, STL, LU, SGG, TRI, PI, DE, SEF (Q > 60%; with 67% and 64% of the individuals in the SEF and MID having Q > 60%) and 2) MO, CL, PR, & AN have (Q > 60%; Figure 2.6).

STRUCTURE results indicated that bycatch individuals have ancestry coefficient ranging between 55-80% to one genetic group (Figure 3.3). Thus, most individuals were correctly assigned to their correct genetic cluster using the POPFLAG option in STRUCTURE. The exception is birds from the PR(BP) population that were assigned to genetic cluster one versus genetic cluster two (Figure 3.3; Figure 2.6).

3.4 Discussion

3.4.1 Assignment tests

Performance of assignment tests is strongly influenced by the level of population differentiation (Cornuet et al., 1999). Results from simulated (Cornuet et al., 1999; Paetkau et al. 2004) and empirical (Maudet et al., 2002; Berry et al., 2004) studies have shown that the success of assignment tests can drop when F_{ST} is ≤ 0.05. Our results suggest that assignments based on the current nine microsatellite loci using likelihood assignment methods are limited (Tables 3.1-3.3). Assignment tests have shown to be limited for some seabirds including common guillemots (*Uria aalge*) as a result of low levels of genetic

differentiation among populations (average F_{ST}=0.004; Cadiou et al., 2004). Predicting the ability to assign individuals based on F_{ST} values alone can be inaccurate. Cegelski et al. (2003) demonstrated that the exclusion method was not able to assign wolverines (*Gulo gulo*) from Montana to source populations, although populations show moderate genetic differentiation (F_{ST}=0.08-0.10). In contrast, steelhead (*Oncorhynchus mykiss*) from Washington could be assigned with high accuracy (90%) in populations with limited genetic differences (F_{ST}=0.02; Hauser et al., 2006).

Assignment success can improve when the number of individuals genotyped is increased (e.g. 30-50) and when additional loci are used (Cornuet et al., 1999). Bjørnstad & Røed (2002) showed horse breeds with F_{ST} between 0.08 and 0.14 could be correctly assigned using six microsatellites. In comparison, horse breed-crosses with F_{ST} 0.05-0.07 could be identified using 12 loci. As well, the accuracy of horse breed assignments increased with larger sample sizes (Bjørnstad & Røed, 2002). Thus, due to genetic differentiation among rhinoceros auklet populations, future investigations could increase the number of loci and the number of individuals genotyped to help improve assignment accuracy.

Results of the fully Bayesian STRUCTURE analysis showed bycatch individuals had ancestry coefficients between 55-80% (Figure 3.3). Thus, STRUCTURE was able to correctly assign most of the bycatch birds available in this study to their correct genetic cluster. The exception to this was the birds from PR(PB) population, which clustered with group one versus the correct cluster of group two (Figure 3.3; Figure 2.6). This could be because these birds were collected during the post-breeding period, when birds may have moved away from the breeding colony. For comparison, the five bycatch birds from unknown locations clustered into group one (Figure 3.3). Our study was unable to

determine if bycatch birds belonging to MO or CL would be assigned to the second genetic cluster.

3.4.2 Conservation and Management

Knowledge that assignment tests do not provide an adequate method to determine the origin of at sea rhinoceros auklets has important implications for future research necessary to manage the species. Rhinoceros auklets are highly vulnerable to oil pollution from oil seepage (e.g. from natural sources, shipwrecks, oil extraction, waste water) or random oil spills. Rhinoceros auklets were the second most common species to be oiled and found washed ashore from the *Apex Houston* oil spill off the central California Coast in February 1986 (Page et al., 1990). As assignment methods are limited using genetic data from the nine microsatellite loci used for this study, observational methods, including ring recoveries from banded birds, could be a potential option to help determine the geographic origin of birds killed at sea during an oil spill (Cadiou et al., 2004).

Henkel et al. (2014) determined that between 2005 and 2010 a major cause of seabird morality off the coast of California was the result of offshore oil-extraction platforms and that the highest peak seabird mortalities occurred during the winter months. Rhinoceros auklets are known to winter in large numbers off central California (Briggs et al., 1987) and for many populations we have limited understanding as to their distribution during the non-breeding season (Gaston & Dechesne, 1996; Abbott et al., 2014). As this species only breeds on a few islands throughout the eastern North Pacific (Gaston & Dechesne, 1996), additional research is needed to understand pre- and post-breeding season movements. This knowledge can be used to help mitigate population losses as a result of stochastic oil spill

events. Monitoring post-breeding movements (e.g. geolocators) would provide knowledge as to the distribution of breeding groups when individuals disperse away from their colonies, and a reference for breeding populations under threat from oil pollution when at sea.

Rhinoceros auklets have high mortality in net-associated fishery activities because they dive underwater in pursuit of fish. Rhinoceros auklets have the second highest seabird bycatch rate in BC (~2800 birds/year out of 12,085 or ~23% from 1995-2001; Smith & Morgan, 2005) and WA (25% of total entanglement in 1996 Puget Sound sockeye test fishery; Melvin et al., 1997; Thompson et al., 1998; Hamel et al., 2009). Active fishing grounds operate near breeding islands (e.g. Lucy & Pine, BC, and Protection, WA; Smith & Morgan, 2005) in the summer and fall (Thompson et al., 1998; Hamel et al., 2009). Thus, the at sea morality caused by net-associated fishing activities can impact both adult and young-of-the-year survival.

There is limited understanding of the movement of juveniles among rhinoceros colonies (Gaston & Dechesne, 1996; Abbott et al., 2014). This can impact the yearly breeding potential of rhinoceros auklets under both Canadian and US jurisdictions. As indicated by Thompson et al. (1998) in Puget Sound, from 1993-1994, 63% of rhinoceros auklets found in gillnets were hatch-year birds. With the uncertainty as to what levels of bycatch pose a threat to the long-term viability of breeding populations (Thompson et al., 1998), future investigation should include research into understanding juvenile dispersal among rhinoceros auklet colonies to aid in the long-term management for the species throughout the eastern North Pacific Ocean.

3.5 Conclusions

Our research indicates that using assignment tests to determine the genetic origin for eastern North Pacific Ocean rhinoceros auklets is limited with the current set of nine microsatellites. Increasing the number of loci and the number of individuals genotyped can help improve assignment accuracy (Cornuet et al., 1999). Thus future investigation could include the use of additional individuals or microsatellite loci with assignment-based methods as this could improve assignment accuracy. Likewise, as this species is highly susceptible to mortality from oil pollution and net-associated fishing activities, and research to understand breeding and non-breeding movements of individuals could assist in recovery efforts or mitigation initiatives for populations that have high mortality when at sea.

Table 3.1: Self-assignment tests for rhinoceros auklets of known origin from WHICHRUN based on maximum likelihood analysis. Comparison is based on 12 source breeding populations and nine microsatellite loci. Samples originating from one area (row) are assigned to one of 12 populations (columns) based on the highest probability. Grey cells show the number and overall percentage of individuals correctly assigned to their colony of origin. See Table 2.1 for population abbreviations.

	CH	MID	STL	LU	SGG	MO	TRI	PI	CL	DE	PR	AN	Total/ per colony
CH	1 (6%)	0	3	2	1	0	3	1	0	2	5	0	18
MID	5	5 (10%)	2	5	2	7	7	2	4	5	4	2	50
STL	5	0	1 (5%)	1	0	4	2	2	2	3	2	0	22
LU	3	1	1	6 (23%)	7	2	2	0	1	1	1	1	26
SGG	3	1	1	9	7 (13%)	3	8	3	0	7	8	3	53
MO	1	2	0	0	2	8 (44%)	1	1	1	1	0	1	18
TRI	4	1	3	1	3	4	4 (15%)	1	0	4	1	0	26
PI	5	0	1	2	1	2	6	2 (7%)	0	0	5	3	27
CL	1	0	0	2	0	6	4	2	2 (7%)	2	7	3	30
DE	2	1	1	2	1	0	4	0	1	4 (22%)	0	2	18
PR	4	1	1	2	2	2	0	0	1	2	4 (21%)	0	19
AN	0	1	1	0	2	2	0	2	1	3	1	9 (41%)	22

Table 3.2: Self-assignment tests for rhinoceros auklets of known origin from GENECLASS2 based on partial-Bayesian method and the probability computation of Cornuet et al. (1999). Comparison is based on 12 source breeding populations and nine microsatellite loci. Samples originating from one area (row) are assigned to one of 12 populations (columns) based on the highest probability. Grey cells show the number and overall percentage of individuals correctly assigned to their colony of origin. See Table 2.1 for population abbreviations.

	CH	MID	STL	LU	SGG	MO	TRI	PI	CL	DE	PR	AN	Not assigned	Total/ per colony
CH	1 (5.6%)	7	5	1	0	0	0	1	0	0	2	0	1	18
MID	1	23 (46%)	7	1	6	0	0	2	4	3	1	0	2	50
STL	0	4	2 (9%)	1	1	0	0	6	2	1	1	0	4	22
LU	0	9	5	3 (12%)	5	0	0	1	2	0	0	1	0	26
SGG	1	16	7	1	15 (28%)	0	1	6	1	4	0	1	0	53
MO	0	7	2	0	1	1 (6%)	0	2	2	0	0	2	1	18
TRI	0	7	7	0	7	1	0 (0%)	1	2	1	0	0	0	26
PI	0	6	9	1	2	0	0	3 (11%)	2	2	0	2	0	27
CL	0	7	6	0	0	1	0	6	7 (23%)	1	0	1	1	30
DE	0	4	3	1	1	0	0	1	1	5 (28%)	0	2	0	18
PR	2	7	4	0	2	0	0	1	2	0	1 (5%)	0	0	19
AN	0	3	4	0	1	0	0	2	2	3	0	4 (18%)	3	22

Table 3.3: Self-assignment tests rhinoceros auklets of known origin based on genetic groupings. Results are based on nine microsatellite loci. Samples originating from one area (row) are assigned to one of four groups (columns) based on the highest probability. Grey cells show the number and overall percentage of individuals correctly assigned to their colony of origin. Genetic groupings are based on genetic similarity and F_{ST} values (Table 2.3) and include: North (CH, MID, STL, LU, SGG, PI), South (DE, PR, AN), MO & CL and TRI. Results are shown for a) WHICHRUN and b) GENECLASS2.

a)

	NORTH	SOUTH	TRI	MO/CL	Total/ per colony
NORTH	53 (27%)	28	90	26	196
SOUTH	15	14 (24%)	17	13	59
TRI	12	2	8 (31%)	4	26
MO/CL	6	13	16	17 (35%)	48

b)

	NORTH	SOUTH	TRI	MO/CL	Not assigned	Total/ per colony
NORTH	142 (72%)	36	1	12	5	196
SOUTH	29	20 (34%)	0	7	3	59
TRI	21	2	0 (0%)	3	0	26
MO/CL	17	10	0	21 (44%)	0	48

Figure 3.1: Map of coastal regions from AK to CA (inset BC & WA; Appendix 3.1). Waterways (e.g. straits) are denoted in italics and geographical landmarks (e.g. cities) are shown with red stars and regular font. Map was visualised in ArcMap 10.2 (ESRI®) in the North Pole Lambert Azimuthal Equal Area projection. Provinces/states and ocean shapefiles courtesy of Natural Earth (2017).

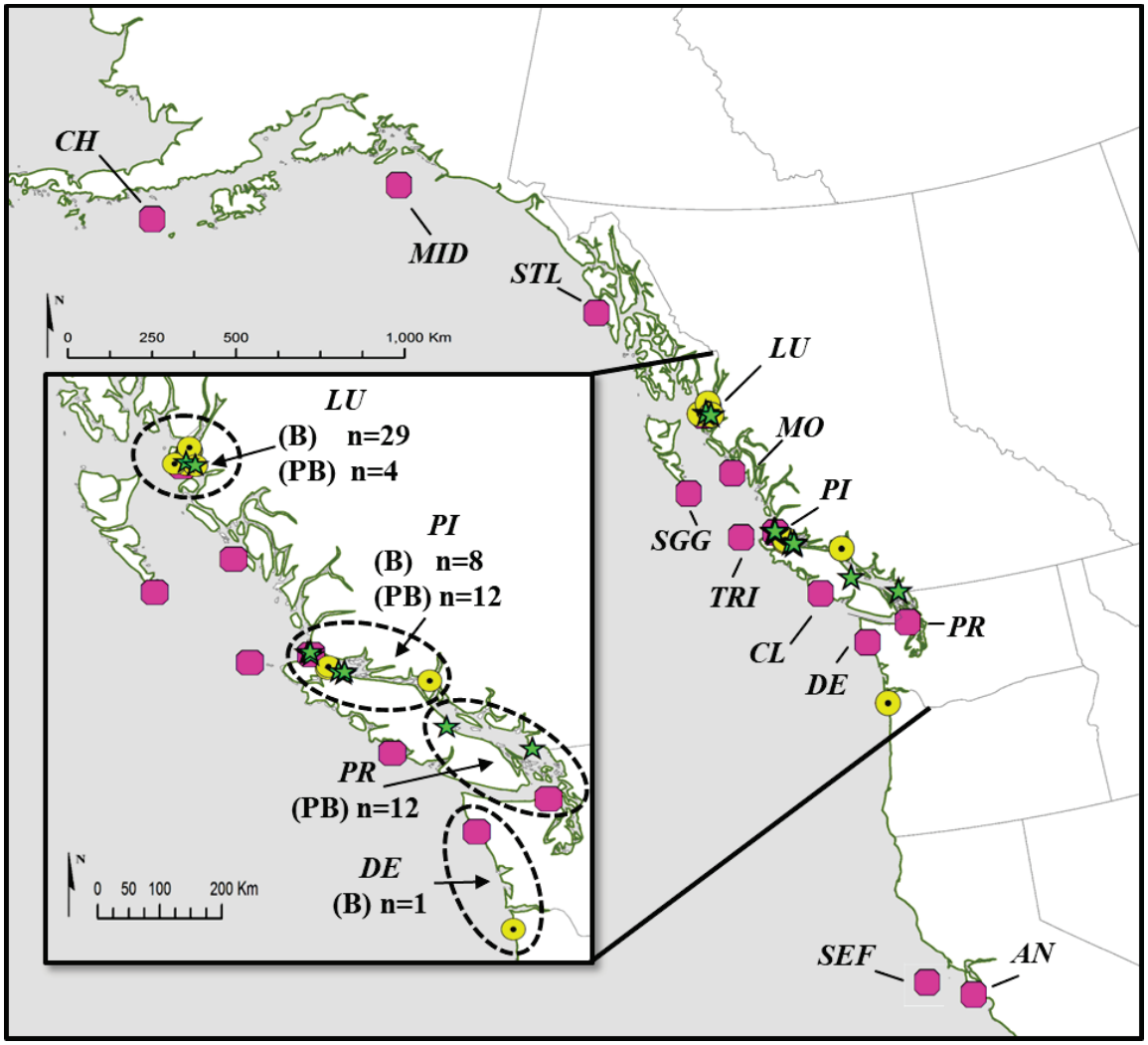


Figure 3.2: Locations of rhinoceros auklet breeding colonies (pink soft-edge squares) and bycatch samples (stars and circles) used in analyses for the breeding period (June-July) and post-breeding period (Aug-Nov). See Appendix 2.1 for breeding colonies abbreviations. Insert shows the location of bycatch samples, referenced to their closest breeding colony (dashed ovals). Samples collected during the breeding period pinpointed with yellow circles with black centres; nearest colonies are labeled with (B) and (n) for the number of bycatch samples collected. The collection location for five samples collected during June-July are unknown and not shown in the totals. Samples collected during the post-breeding period pinpointed with green stars; nearest colonies are labeled with (PB) and (n) for number of bycatch samples collected. Map was visualised in ArcMap 10.2 (ESRI®) in the North Pole Lambert Azimuthal Equal Area projection. Provinces/states and ocean shapefiles courtesy of Natural Earth (2017).

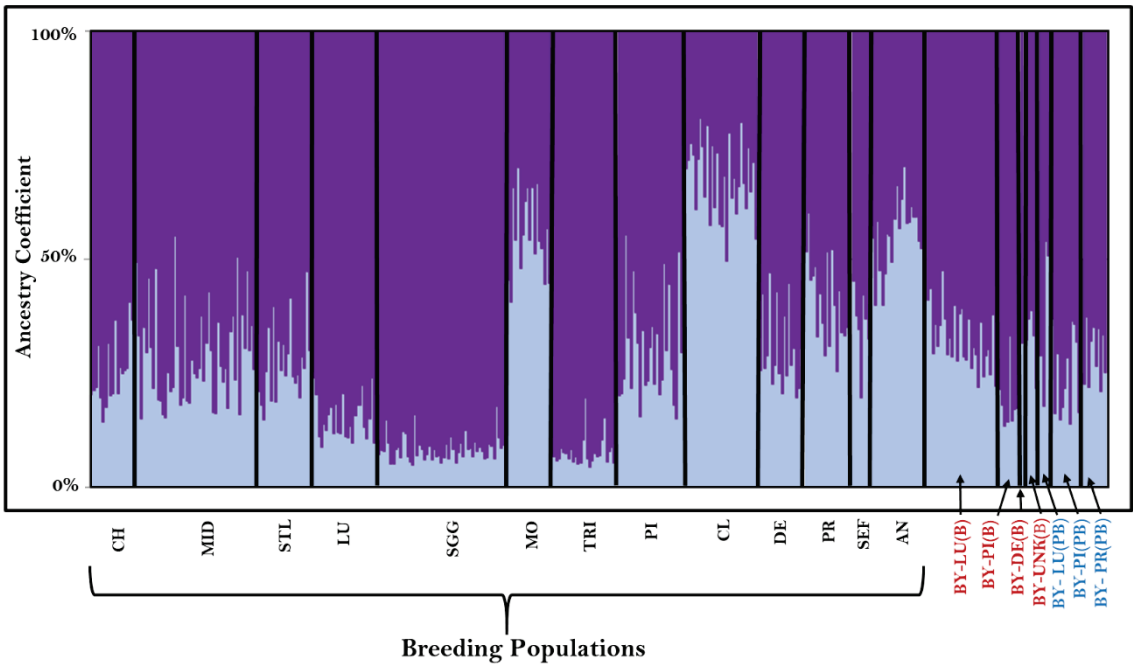


Figure 3.3: Assignment of 69 bycatch rhinoceros auklets in STRUCTURE v2.3.4 (Pritchard et al., 2000; Falush et al., 2003) using the POPFLAG and locpriors options and ten microsatellites. Samples were collected at sea or on beaches in the eastern North Pacific Ocean. Source populations included 13 eastern North Pacific rhinoceros auklet breeding colonies. Breeding populations are ordered along the coastline from Alaska to California. Bycatch individuals collected during the breeding season (June-July) abbreviated with (B) in red; bycatch individuals post-breeding season (Aug-Nov) abbreviated with (PB) in light blue. See Table 2.1 and Figure 3.2 for population abbreviations. Two genetic groups occur among the eastern North Pacific breeding populations: population 1 (purple) and population 2 (light blue). All bycatch samples have ancestry coefficients (Q) between 55%-80% for population 1 (purple) with the exception of two birds from LU(PB) that have 51% and 53% ancestry coefficient for group 2 (light blue).

Chapter 4:

General Discussion

4.1 General discussion

It is often assumed high mobility correlates to genetic homogeneity across populations (Hedgecock, 1994; Crochet, 2000). However, many highly mobile avian species, including seabirds, show population genetic structure (Burg & Croxall, 2001; Burg & Croxall, 2004). Our study on the contemporary population genetic structure for rhinoceros auklets finds support that seabirds with high dispersal capabilities can have genetic divergence among populations. Our research shows that rhinoceros auklets have significant genetic differentiation both between and among the western and eastern North Pacific breeding groups. Our results indicate isolation by distance (IBD) and ocean barriers promote contemporary genetic structure between the western and eastern rhinoceros auklet North Pacific Ocean metapopulations. Among the western and eastern breeding islands, we found that genetic differences are likely due to a combination of factors with behavioural and ecological variables providing intrinsic barriers to gene flow among breeding islands. Knowledge of genetic differentiation for rhinoceros auklets improves our overall understanding of the species, thus benefiting the long-term management of rhinoceros auklets throughout the North Pacific Ocean.

4.1.1 Barriers to gene flow

4.1.1.1 Isolation by distance and oceanic barriers

Geographic distance has been found to promote genetic divergence for various seabirds (Steeves et al., 2003; Morris-Pocock et al., 2011). Similarly, IBD is an important factor that limits gene flow between the western and eastern North Pacific rhinoceros auklets (Figure 2.8a). In our study the large expanse of deep ocean between Japan and North America restricts dispersal (Figure 2.3). Thus, physical barriers, including the edge of the continental shelf and water depth, help to limit dispersal and gene flow between the western and eastern North Pacific Ocean metapopulations. However, neither IBD or oceanic environmental variables are shown to limit movement for either the Japanese or North America breeding islands (Figures 2.3, 2.4, & 2.8b, c). Therefore, we suggest intrinsic behaviours and ecological factors could be promoting the genetic divergence among islands within both the eastern and western Pacific.

4.1.1.2 Site fidelity and foraging segregation

Site fidelity to breeding site is known to promote genetic structure for various marine species (Bowen et al., 1992; Bowen et al., 1993; Encalada et al., 1996; Hellberg et al., 2002; Dearborn et al., 2003) and considered an adaptive strategy for many groups of birds (Cézilly et al., 2000; Bried et al., 2003; Vergara et al., 2006; Blums et al., 2018). Nest site fidelity has many advantages including familiarity to the feeding resources, social neighbourhood (e.g. social status, mate retention, competition), and physical characteristics of a territory (Greenwood & Harvey, 1982; Koivula et al., 1993; Cézilly et al., 2000). The

rhinoceros auklet is a colonial seabird that nests in a soil burrow (Gaston & Dechesne, 1996). Nest site fidelity would reduce the need for rhinoceros auklet breeding pairs to develop nesting burrows each season and improve a pair's understanding of social competition within a colony.

Our study shows significant genetic differentiation between Teuri Island and three (Daikoku, Matsumae-Kojima, and Tai) of the four western North Pacific breeding islands (Chapter 2). For birds in the western North Pacific, genetic differentiation among colonies could be a result of nest site fidelity. In particular, because Teuri island is considered the largest rhinoceros auklet breeding colony of Japan (with approximately 0.3 million breeding pairs; Osa & Watanuki, 2002; Watanuki & Ito, 2012), nest site fidelity in this population is highly likely due to the number of rhinoceros auklets. Thus, this factor could promoting the significant genetic difference shown between Teuri Island and three of the four western North Pacific Ocean populations.

For the eastern North Pacific Ocean colonies, there is no clear spatial pattern to the genetic structure among rhinoceros auklets and islands in close proximity show significant genetic differences. Along with site fidelity, foraging segregation among colonies could promote this spatial genetic pattern. Foraging segregation in rhinoceros auklets could result from birds remaining close to the nesting colony during the breeding season to forage (Wahl & Speich, 1994) or differences in diet such as provisioning their young with different species of epipelagic fish (Davoren, 2000; Ito et al., 2009; Deguchi et al., 2010). Adults from different colonies have been shown to provision their young with different fish, even when the colonies are in close proximity to one another (~90 km; Año Nuevo & Southeast Farallon Islands, CA; Thayer & Sydeman, 2007). These behaviours could provide the

pattern of population genetic structure shown for rhinoceros auklets, with the genetic difference confined to colonies.

4.1.1.3 Environmental conditions and divergent breeding times

Environmental conditions are known to promote genetic structure for numerous marine organism (Perez-Enriquez & Taniguchi, 1999; Withler et al., 2001; Yoshida et al., 2001; Bekkevold et al., 2005; Jørgensen et al., 2005; Gaggiotti et al., 2009; Siegle et al., 2013). For rhinoceros auklets, environmental conditions have been found to influence foraging and breeding success among colonies. Specifically, for birds on Triangle Island, BC, fine-scale environmental conditions have been shown to influence breeding success (Borstad et al., 2011). Breeding performance among BC colonies is influenced by local fish populations (Bertram et al., 2002). Prey provisioned to nestlings have annual, latitudinal, and inter-colony differences resulting in differences in chick growth due to the type of prey, and bill load amount provisioned to nestlings (Wilson, 1986; Bertram et al., 2002; Thayer & Sydeman, 2007). For colonies in the eastern North Pacific Ocean, the primary type of forage fish collected by rhinoceros auklet was correlated to sea surface temperature, however, this pattern was not as highly correlated for birds in western North Pacific populations (Thayer et al., 2008).

Reductions in gene flow can arise because of differences in breeding times among populations (Burg & Croxall, 2004; Overeem et al., 2008), and for birds, differences in egg laying synchrony can be attributed to food availability (Veen, 1977; Wilson, 1986; Sydeman et al., 1991; Visser et al., 1998). Asynchronies in egg laying have been found to occur among Washington rhinoceros auklet colonies (Smith vs. Destruction & Protection

Islands, WA), with food availability suggested as an explanation of egg laying variability among the colonies (Wilson, 1986). Oceanic conditions and prey availability have been found to differ between a number of inshore and offshore islands (e.g. Protection vs. Destruction, WA, Wilson, 1986; Triangle vs. Pine Island, BC, Hedd et al., 2006; Año Nuevo & Southeast Farallon Islands, CA; Thayer & Sydeman, 2007) with our study showing genetic differences between some of these islands (Chapter 2; Triangle vs. Pine Island, BC; Destruction vs. Protection Islands, WA). Thus, we suggest several factors including local oceanic conditions, and temporal differences among egg laying, help to explain the genetic differentiation occurring for islands in close proximity (e.g. ~ 100 km Triangle and Pine Islands, BC; Chapter 2; Abbott et al., 2014).

4.2 Assignment tests

Our research also examined the feasibility of using molecular markers and assignment tests to help identify the genetic origin of individual rhinoceros auklets found at sea. Our findings indicate that the current nine microsatellites do not have adequate resolution to assign individuals to populations or groups. As a result of low levels of genetic differentiation among populations, assignment tests have been shown to be limited for some seabirds including common guillemots (*Uria aalge*; Cadiou et al., 2004). Due to the genetic differentiation shown among rhinoceros auklet colonies, increasing the number of loci and number of individuals used in the source groups may improve the resolution of the assignments. Because assignment tests are limited for rhinoceros auklets, future research should be conducted to understand the at sea movements (e.g. geolocators). This research could be used to detect differences among foraging patterns, movements of non-breeding

individuals, and adult/juvenile dispersal among colonies. This information can be used to help manage rhinoceros auklets and reduce the high morality when at sea (Melvin et al., 1997; Thompson et al., 1998; Smith & Morgan, 2005; Hamel et al., 2009).

4.3 Future research and directions

We were able to clarify that oceanic variables limit gene flow between western and eastern North Pacific rhinoceros auklets using a species distribution model (SDM) and seascape resistance model (Figure 2.3 & 2.4). Resistance for rhinoceros auklets movements corresponds the edge of the continental shelf, and water depth, as physical barriers to dispersal. Although, oceanic conditions were not found limit dispersal within either the western or eastern North Pacific Ocean rhinoceros auklet colonies (Figure 2.4). For marine organisms in BC or Japan, ocean conditions promote population genetic structure (Perez-Enriquez & Taniguchi, 1999; Withler et al., 2001; Yoshida et al., 2001; Siegle et al., 2013). In SDM analyses, relevant spatial information can get muted when populations of a widespread organism are grouped and analysed as a single entity (Gonzalez et al., 2011). Thus, future investigation could include examining the western and eastern metapopulations at a finer scale, as separate entities in SDM analyses.

As oceanic conditions and current movements have been found to promote genetic structure among marine organisms in North Pacific, additional study is needed to help understand rhinoceros auklets dispersal and foraging movements. In particular, post-breeding population movement and segregation during the non-breeding season can promote genetic structure among seabirds (Friesen et al., 2007; Rayner et al., 2011). There is limited understanding of the distribution of rhinoceros auklet populations during the non-

breeding season (Gaston & Dechesne, 1996; Abbott et al., 2014). Thus, future research on understanding rhinoceros auklet breeding and post-breeding dispersal and population foraging patterns could help determine if local prey resources and their availability are promoting population genetic structure among colonies.

Of the Japanese colonies, much of the research has focused on birds from Teuri Island, with limited understanding of rhinoceros auklet nesting, behaviour, and movement among the other Japanese islands. In the western North Pacific, oceanic conditions were not as highly correlated to the primary type of forage fish (Japanese anchovy, *Engraulis japonicus*; Pacific sand lance, *Ammodytes personatus*; or juvenile greenling *Pleurogrammus azonus*) for rhinoceros auklets (Thayer et al., 2008; Watanuki et al., 2009). However, seabird populations separated by ocean currents show genetic differences among populations (Levy et al., 2016). Similarity, ocean currents surrounding Japan could be spatially separating rhinoceros auklet populations. To help clarify genetic population patterns among Japanese colonies, future research should examine the dispersal and behaviours of multiple rhinoceros auklet colonies of Japan. This information could be used to help clarify if ocean currents influence dispersal and gene flow in the western North Pacific Ocean.

4.4 General Conclusions

Our research indicates that population genetic structure exists among rhinoceros auklet breeding colonies. Both IBD and oceanic variables are barriers to gene flow between western and eastern North Pacific Ocean colonies, with genetic structure among the two metapopulations potentially a result of different mechanisms operating on each breeding

group. Mechanisms including site fidelity, foraging segregation, oceanic conditions, and temporal differences in egg laying are potential factors that limit gene flow among colonies. To help clarify these findings, future research should focus on understanding the dispersal and foraging movements for the populations to determine if local climatic conditions are promoting genetic structure among colonies, as a result of local prey resources and their availability. This research is also necessary as rhinoceros auklets found at sea cannot currently be assigned back to their colony of origin with the current suite of molecular markers. Thus, clarifying movement is critical to help in the long-term management and conservation of rhinoceros auklets throughout the North Pacific Ocean.

References

Abbott, C. L., Double, M. C., Gales, R., Baker, G. B., Lashko, A., Robertson, C. J. R., & Ryan, P. G. (2006). Molecular provenance analysis for shy and white-capped albatrosses killed by fisheries interactions in Australia, New Zealand, and South Africa. *Conservation Genetics*, *7*(4), 531–542.

Abbott, C. L., Millikin, R. L., Hipfner, M. J., Hatch, S., Ito, M., Watanuki, Y., & Burg, T. M. (2014). Genetic structure of rhinoceros auklets, *Cerorhinca monocerata*, breeding in British Columbia, Alaska, and Japan. *Marine Biology*, *161*(2), 275–283.

Adams, J., & Flora, S. (2010). Correlating seabird movements with ocean winds: linking satellite telemetry with ocean scatterometry. *Marine Biology*, *157*(4), 915–929.

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of "least-cost" modelling as a functional landscape model. *Landscape and Urban Planning*, *64*(4), 233–247.

Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Boutov, D., Freitas, L., Robertson, K.M., Sequeira, M., et al. (2012). Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (Genus *Delphinus*). *PLoS ONE*, *7*(2), e31482.

Anderson, C. D., Epperson, B. K., Fortin, M. J., Holderegger, R., James, P. M. A., Rosenberg, M. S., Scribner, K. T., et al. (2010). Considering spatial and temporal scale in landscape-genetic studies of gene flow. *Molecular Ecology*, *19*(17), 3565–3575.

Andersson, A. J., Mackenzie, F. T., & Bates, N. R. (2008). Life on the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers. *Marine Ecology Progress Series*, *373*, 265–273.

Assis, J., Tyberghein, L., Bosh, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2017). Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277–284.

Awade, M., & Metzger, J. P. (2008). Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology*, *33*(7), 863–871.

Baker, C. S., Medrano-Gonzalez, L., Calambokidis, J., Perry, A., Pichler, F., Rosenbaum, H., Straley, J. M., et al. (1998). Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. *Molecular Ecology*, *7*(6), 695–707.

Banks, M. A., & Eichert, W. (2000). WHICHRUN: a computer program for population assignment of individuals based on multilocus genotype data. *Journal of Heredity*, *91*(1), 87–89.

Banks, S. C., Piggott, M. P., Williamson, J. E., Bové, U., Holbrook, N. J., & Beheregaray, L. B. (2007). Oceanic variability and coastal topography shape genetic structure in a

long-dispersing sea urchin. *Ecology*, *88*(12), 3055–3064.

Barbraud, C., & Weimerskirch, H. (2006). Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences*, *103*(16), 6248–6251.

Barker, A. M., Nosal, A. P., Lewallen, E. A., & Burton, R. S. (2015). Genetic structure of leopard shark (*Triakis semifasciata*) populations along the Pacific coast of North America. *Journal of Experimental Marine Biology and Ecology*, *472*, 151–157.

Barrandeguy, M. E., & García, M. V. (2014). Quantifying genetic diversity: the starting point for population genetic studies using molecular markers. *Journal of Genetics*, *93*(2), 587–589.

Bartholomew, G. A., & Collias, N. E. (1962). The role of vocalization in the social behaviour of the northern elephant seal. *Animal Behaviour*, *10*(1), 7–14.

Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics*, *19*, 10–15.

Becker, B. H., Peery, M. Z., & Beissinger, S. R. (2007). Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Marine Ecology Progress Series*, *329*, 267–279.

Benestan, L., Quinn, B. K., Maaroufi, H., Laporte, M., Clark, F. K., Greenwood, S. J., Rochette, R., et al. (2016). Seascape genomics provides evidence for thermal adaptation and current-mediated population structure in American lobster (*Homarus americanus*). *Molecular Ecologycology*, *25*(20), 5073–5092.

Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *Annals of Statistics*, *29*(4), 1165–1188.

Bernardi, G., Sordino, P., & Powers, D. A. (1993). Concordant mitochondrial and nuclear DNA phylogenies for populations of the teleost fish *Fundulus heteroclitus*. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(20), 9271–9274.

Berry, O., Tocher, M. D., & Sarre, S. D. (2004). Can assignment tests measure dispersal? *Molecular Ecology*, *13*(3), 551–561.

Bertram, D. F., Golumbia, T., Davoren, G. K., Harfenist, A., & Brown, J. (2002). Short visits reveal consistent patterns of interyear and intercolony variation in seabird nestling diet and performance. *Canadian Journal of Zoology*, *80*(12), 2190–2199.

Bhargava, A., & Fuentes, F. F. (2010). Mutational dynamics of microsatellites. *Molecular Biotechnology*, *44*(3), 250–266.

BirdLife International. (2017). Rhinoceros auklet (*Cerorhinca monocerata*)-BirdLife species factsheet. Retrieved December 18, 2017, from http://datazone.birdlife.org/species/factsheet/Rhinoceros-Auklet

Bjørnstad, G., & Røed, K. H. (2002). Evaluation of factors affecting individual

assignment precision using microsatellite data from horse breeds and simulated breed crosses. *Animal Genetics*, *33*(4), 264–270.

Blums, P., Nichols, J. D., & Hines, J. E. (2018). Sources of variation in survival and breeding site fidelity in three species of European ducks. *Journal of Animal Ecology*, *71*(3), 438–450.

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, *275*, 73–77.

Borstad, G., Crawford, W., Hipfner, J. M., Thomson, R., & Hyatt, K. (2011). Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. *Marine Ecology Progress Series*, *424*, 285–302.

Bowen, B., Avise, J. C., Richardson, J. I., Meylan, A. B., Margaritoulis, D., & Hopkinsmurphy, S. R. (1993). Population structure of loggerhead turtles (*Caretta-caretta*) in the northwestern Atlantic ocean and Mediterranean sea. *Conservation Biology*, *7*(4), 834–844.

Bowen, B. W., Meylan, A. B., & Avise, J. C. (1989). An odyssey of the green sea turtle: Ascension Island revisited. *Source: Proceedings of the National Academy of Sciences, USA*, *86*(2), 573–576.

Bowen, B. W., Meylan, A. B., Ross, J. P., Limpus, C. J., Balazs, G. H., & Avise, J. C. (1992). Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution*, *46*(4), 865–881.

Bried, J., Pontier, D., & Jouventin, P. (2003). Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. *Animal Behaviour*, *65*(1), 235–246.

Briggs, K. T., Tyler, W. B., Lewis, D. B., & Carlson, D. R. (1987). Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology*, *11*, 1–74.

Brown, J. L. (2014). SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution*, *5*(7), 694–700.

Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ.*, *5*, e4095.

Brownstein, M. J., Carpten, J. D., & Smith, J. R. (1996). Modulation of non-templated nucleotide addition by Taq DNA polymerase: primer modifications that facilitate genotyping. *BioTechniques*, *20*(6), 1004–1010.

Burg, T. M. (2007). Genetic analysis of wandering albatrosses killed in longline fisheries off the east coast of New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *17*(S1), S93–S101.

Burg, T. M., Catry, P., Ryan, P. G., & Phillips, R. A. (2017). Genetic population structure of black-browed and Campbell albatrosses, and implications for assigning

provenance of birds killed in fisheries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(6), 1156–1163.

Burg, T. M., & Croxall, J. P. (2001). Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology*, *10*(11), 2647–2660.

Burg, T. M., & Croxall, J. P. (2004). Global population structure and taxonomy of the wandering albatross species complex. *Molecular Ecology*, *13*(8), 2345–2355.

Burney, C. W., & Brumfield, R. T. (2009). Ecology predicts levels of genetic differentiation in Neotropical birds. *The American Naturalist*, *174*(3), 358–368.

Caballero, A., & García-Dorado, A. (2013). Allelic diversity and its implications for the rate of adaptation. *Genetics*, *195*(4), 1373–1384.

Cadiou, B., Riffaut, L., McCoy, K. D., Cabelguen, J., Matthieu, F., Gélinaud, G., Le Roch, A., et al. (2004). Ecological impact of the "Erika" oil spill: determination of the geographic origin of the affected common guillemots. *Aquatic Living Resources*, *17*, 369–377.

Cao, Y., DeWalt, R. E., Robinson, J. L., Tweddale, T., Hinz, L., & Pessino, M. (2013). Using Maxent to model the historic distributions of stonefly species in Illinois streams: the effects of regularization and threshold selections. *Ecological Modelling*, *259*, 30–39.

Carlsson, J. (2008). Effects of microsatellite null alleles on assignment testing. *Journal of Heredity*, *99*(6), 616–623.

Cegelski, C. C., Waits, L. P., & Anderson, N. J. (2003). Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-based approaches. *Molecular Ecology*, *12*(11), 2907–2918.

Cézilly, F., Dubois, F., & Pagel, M. (2000). Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiforms. *Animal Behaviour*, *59*(6), 1143–1152.

Chapuis, M. P., & Estoup, A. (2007). Microsatellite null alleles and estimation of population differentiation. *Molecular Biology and Evolution*, *24*(3), 621–631.

Choupina, A., & Martins, I. (2014). Molecular markers for genetic diversity, gene flow and genetic population structure of freshwater mussel species. *Brazilian Journal of Biology*, *74*(3), s167–s170.

Christie, M. R., Meirmans, P. G., Gaggiotti, O. E., Toonen, R. J., & White, C. (2017). Disentangling the relative merits and disadvantages of parentage analysis and assignment tests for inferring population connectivity. *ICES Journal of Marine Science*, *74*(6), 1749–1762.

Colonna, V., Nutile, T., Ferrucci, R. R., Fardella, G., Aversano, M., Barbujani, G., & Ciullo, M. (2009). Comparing population structure as inferred from genealogical versus genetic information. *European Journal of Human Genetics*, *17*(12), 1635–1641.

Cornuet, J. M., Piry, S., Luikart, G., Estoup, A., & Solignac, M. (1999). New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics*, *153*(4), 1989–2000.

Crochet, P. A. (2000). Genetic structure of avian populations--allozymes revisited. *Molecular Ecology*, *9*(10), 1463–1469.

Crow, J. F. (1987). Population genetics history: a personal view. *Annual Review of Genetics*, *21*, 1–22.

Dalvit, C., De Marchi, M., Dal Zotto, R., Gervaso, M., Meuwissen, T., & Cassandro, M. (2008). Breed assignment test in four Italian beef cattle breeds. *Meat Science*, *80*(2), 389–395.

Davoren, G. K. (2000). Variability in foraging in response to changing prey distributions in rhinoceros auklets. *Marine Ecology Progress Series*, *198*, 283–291.

Davoren, G. K., & Burger, A. E. (1999). Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour*, *58*(4), 853–863.

Dawson, D. A., Hunter, F. M., Pandhal, J., Buckland, R., Parham, A., Jones, I. L., Bradshaw, M., et al. (2005). Assessment of 17 new whiskered auklet (*Aethia pygmaea*) microsatellite loci in 42 seabirds identifies 5-15 polymorphic markers for each of nine Alcinae species. *Molecular Ecology Notes*, *5*(2), 289–297.

Dearborn, D. C., Anders, A. D., Schreiber, E. A., Adams, R. M. M., & Mueller, U. G. (2003). Inter-island movements and population differentiation in a pelagic seabird. *Molecular Ecology*, *12*(10), 2835–2843.

Deguchi, T., Wada, A., Watanuki, Y., & Osa, Y. (2010). Seasonal changes of the at-sea distribution and food provisioning in rhinoceros auklets. *Ecological Research*, *25*(1), 123–137.

Desrochers, A., & Hannon, S. J. (1997). Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology*, *11*(5), 1204–1210.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46.

Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, *4*(2), 359–361.

Ehrlich, P. R., & Raven, P. H. (1969). Differentiation of populations. *Science*, *165*(3899), 1228–1232.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342.

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical

hypothesis for flightlessness in penguins. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(23), 9380–9384.

Encalada, S. E., Lahanas, P. N., Bjorndal, K. A., & Bolten, A. B. (1996). Phylogeography and population structure of the Atlantic and Mediterranean green turtle *Chelonia mydas*: a mitochondrial DNA control region sequence assessment. *Molecular Ecology*, *5*(4), 473–483.

Engler, J. O., Stiels, D., Schidelko, K., Strubbe, D., & Quillfeldt, P. (2017). Avian SDMs: current state, challenges, and opportunities. *Journal of Avian Biology*, *48*(12), 1483–1504.

Etnoyer, P., Canny, D., Mate, B. R., Morgan, L. E., Ortega-Ortiz, J. G., & Nichols, W. J. (2006). Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *53*(3–4), 340–358.

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, *14*(8), 2611–2620.

Excoffier, L., & Heckel, G. (2006). Computer programs for population genetics data analysis: a survival guide. *Nature Reviews Genetics*, *7*(10), 745–758.

Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics*, *164*(4), 1567–1587.

Faria, P. J., Campos, F. P., Branco, J. O., Musso, C. M., Morgante, J. S., & Bruford, M. W. (2010). Population structure in the South American tern *Sterna hirundinacea* in the South Atlantic: two populations with distinct breeding phenologies. *Journal of Avian Biology*, *41*(4), 378–387.

FitzSimmons, N. N., Moritz, C., Limpus, C. J., Pope, L., & Prince, R. (1997). Geographic structure of mitochondrial and nuclear gene polymorphisms in Australian green turtle populations and male-biased gene flow. *Genetics*, *147*(4), 1843–1854.

Fitzsimmons, S. D., & Warburton, K. (1992). Fish movement behaviour: variability within and between groups. *Behavioural Processes*, *26*(2–3), 211–216.

Francis, R. C., Hare, S. R., Hollowed, A. B., & Wooster, W. S. (1998). Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, *7*(1), 1–21.

François, O., Ancelet, S., & Guillot, G. (2006). Bayesian clustering using hidden Markov random fields in spatial population genetics. *Genetics*, *174*(2), 805–816.

François, O., & Durand, E. (2010). Spatially explicit Bayesian clustering models in population genetics. *Molecular Ecology Resources*, *10*(5), 773–784.

Freeland, J. R., Gillespie, J., Ciotir, C., & Dorken, M. E. (2010). Conservation genetics of Hill's thistle (*Cirsium hillii*). *Botany*, *88*(12), 1073–1080.

Freeland, J. R., Kirk, H., & Petersen, S. (2011). Molecular Ecology: 2nd ed. *Molecular Ecology: 2nd ed.* (pp. 1–449). Chichester, UK: John Wiley & Sons, Ltd.

Friesen, V. L. (2015). Speciation in seabirds: why are there so many species…and why aren't there more? *Journal of Ornithology*, *156*(S1), S27–S39.

Friesen, V. L., Birt, T. P., Piatt, J. F., Golightly, R. T., Newman, S. H., Hébert, P. N., Congdon, B. C., et al. (2005). Population genetic structure and conservation of marbled murrelets (*Brachyramphus marmoratus*). *Conservation Genetics*, *6*(4), 607–614.

Friesen, V. L., Burg, T. M., & McCoy, K. D. (2007). Mechanisms of population differentiation in seabirds: invited review. *Molecular Ecology*, *16*(9), 1765–1785.

Fullard, K. J., Early, G., Heide-Jørgensen, M. P., Bloch, D., Rosing-Asvid, A., & Amos, W. (2000). Population structure of long-finned pilot whales in the North Atlantic: a correlation with sea surface temperature? *Molecular Ecology*, *9*(7), 949–958.

Galindo, H. M., Olson, D. B., & Palumbi, S. R. (2006). Seascape genetics: a coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology*, *16*(16), 1622–1626.

Gaston, A. J., & Dechesne, S. B. C. (1996). Rhinoceros auklet (*Cerorhinca monocerata*). (A. Poole & F. Gill, Eds.) *The Birds of North America Online*.

Gauffre, B., Estoup, A., Bretagnolle, V., & Cosson, J. F. (2008). Spatial genetic structure of a small rodent in a heterogeneous landscape. *Molecular Ecology*, *17*(21), 4619–4629.

Gilbert, K., Andrew, R., Bock, D., Franklin, M., Kane, N., Moore, J., Moyers, B., et al. (2012). Recommendations for utilizing and reporting population genetic analyses: the reproducibility of genetic clustering using the program STRUCTURE. *Molecular Ecology*, *21*(20), 4925–4930.

Gilbert, K. J. (2016). Identifying the number of population clusters with structure: problems and solutions. *Molecular Ecology Resources*, *16*(3), 601–603.

Giordano, A. R., Ridenhour, B. J., & Storfer, A. (2007). The influence of altitude and topography on genetic structure in the long-toed salamander (*Ambystoma macrodactulym*). *Molecular Ecology*, *16*(8), 1625–1637.

Goetze, E. (2005). Global population genetic structure and biogeography of the oceanic copepods *Eucalanus hyalinus* and *E. spinifer*. *Evolution*, *59*(11), 2378–2398.

Gomez-Diaz, E., & Gonzalez-Solis, J. (2007). Geographic assignment of seabirds to their origin: combining morphology, genetic, and biochemical analyses. *Ecological Applications*, *17*(5), 1484–1498.

Gómez-Díaz, E., González-Solís, J., & Peinado, M. A. (2009). Population structure in a highly pelagic seabird, the Cory's shearwater *Calonectris diomedea*: an examination of genetics, morphology and ecology. *Marine Ecology Progress Series*, *382*, 197–209.

Gonzalez, S. C., Soto-Centeno, J. A., & Reed, D. L. (2011). Population distribution models: species distributions are better modeled using biologically relevant data partitions. *BMC Ecology*, *11*(1), 20–30.

Gottelli, D., Marino, J., Sillero-Zubiri, C., & Funk, S. M. (2004). The effect of the last glacial age on speciation and population genetic structure of the endangered Ethiopian wolf (*Canis simensis*). *Molecular Ecology*, *13*(8), 2275–2286.

Grant, W. S., & Utter, F. M. (1984). Biochemical population genetics of Pacific herring (*Clupea pallasi*). *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(6), 856–864.

Grapputo, A., Boman, S., Lindström, L., Lyytinen, A., & Mappes, J. (2005). The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. *Molecular Ecology*, *14*(14), 4207–4219.

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*(3), 650–667.

Green, M. L., Manjerovic, M. B., Mateus-Pinilla, N., & Novakofski, J. (2014). Genetic assignment tests reveal dispersal of white-tailed deer: implications for chronic wasting disease. *Journal of Mammalogy*, *95*(3), 646–654.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*(4), 1140–1162.

Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, *13*, 1–21.

Grünwald, N. J., Everhart, S. E., Knaus, B. J., & Kamvar, Z. N. (2017). Best practices for population genetic analyses. *Papers in Plant Pathology*, *107*(9), 1000–1010.

Grünwald, N. J., & Goss, E. M. (2011). Evolution and population genetics of exotic and re-emerging pathogens: novel tools and approaches. *Annual Review of Phytopathology*, *49*, 249–267.

Guillot, G. (2008). Inference of structure in subdivided populations at low levels of genetic differentiation—the correlated allele frequencies model revisited. *Bioinformatics*, *24*(19), 2222–2228.

Gustafson, K. D., Vickers, T. W., Boyce, W. M., & Ernest, H. B. (2017). A single migrant enhances the genetic diversity of an inbred puma population. *Royal Society Open Science*, *4*(5), 170115.

Hall, L. A., Palsbøll, P. J., Beissinger, S. R., Harvey, J. T., Bérubé, M., Raphael, M. G., Nelson, S. K., et al. (2009). Characterizing dispersal patterns in a threatened seabird with limited genetic structure. *Molecular Ecology*, *18*(24), 5074–5085.

Hamel, N. J., Burger, A. E., Charleton, K., Davidson, P., Lee, S., Bertram, D. F., & Parrish, J. K. (2009). Bycatch and beached birds: assessing mortality impacts in

coastal net fisheries using marine bird strandings. *Marine Ornithology*, *37*(1), 41–60.

Hardy, G. H. (1908). *Mendelian proportions in a mixed population*. *Science* (Vol. 28).

Hasegawa, O., Ishibashi, Y., & Abe, S. (2005). Polymorphic microsatellite DNA markers for the rhinoceros auklet (*Cerorhinca monocerata*). *Molecular Ecology Notes*, *5*(3), 637–638.

Hauser, L., Seamons, T. R., Dauer, M., Naish, K. A., & Quinn, T. P. (2006). An empirical verification of population assignment methods by marking and parentage data: hatchery and wild steelhead (*Oncorhynchus mykiss*) in Forks Creek, Washington, USA. *Molecular Ecology*, *15*(11), 3157–3173.

Hedd, A., Bertram, D. F., Ryder, J. L., & Jones, I. L. (2006). Effects of interdecadal climate variability on marine trophic interactions: rhinoceros auklets and their fish prey. *Marine Ecology Progress Series*, *309*, 263–278.

Hedgecock, D. (1994). Temporal and spatial genetic structure of marine animal populations in the California current. *California Cooperative Oceanic Fisheries Investigations*, *35*, 73–81.

Hedrick, P. W. (2011). *Genetics of Populations: 4th ed.* Sudbury, Massachusetts: Jones and Bartlett Publishers.

Hellberg, M. E., Burton, R. S., Neigel, J. E., & Palumbi, S. R. (2002). Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science*, *70*(S1), 273–290.

Hendry, A. P., & Day, T. (2005). Population structure attributable to reproductive time: isolation by time and adaptation by time. *Molecular Ecology*, *14*(4), 901–916.

Henkel, L. A., Nevins, H., Martin, M., Sugarman, S., Harvey, J. T., & Ziccardi, M. H. (2014). Chronic oiling of marine birds in California by natural petroleum seeps, shipwrecks, and other sources. *Marine Pollution Bulletin*, *79*(1–2), 155–163.

Hoelzel, A. R. (2009). Evolution of population genetic structure in marine mammal species. In G. Bertorelle, M. W. Bruford, H. C. Hauffe, A. Rizzoli, & C. Vernesi (Eds.), *Population Genetics for Animal Conservation* (pp. 294–318). Cambridge: Cambridge University Press.

Hoelzel, A. R., Dahlheim, M., & Stern, S. J. (1998). Low genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific and genetic differentiation between foraging specialists. *Journal of Heredity*, *89*(2), 121–128.

Hoffmann, A. A., & Merilä, J. (1999). Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution*, *14*(3), 96–101.

Holderegger, R., Kamm, U., & Gugerli, F. (2006). Adaptive vs. neutral genetic diversity: implications for landscape genetics. *Landscape Ecology*, *21*(6), 797–807.

Holderegger, R., & Wagner, H. H. (2008). Landscape Genetics. *BioScience*, *58*(3), 199–207.

Hubisz, M. J., Falush, D., Stephens, M., & Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, *9*(5), 1322–1332.

Ito, M., Minami, H., Tanaka, Y., & Watanuki, Y. (2009). Seasonal and inter-annual oceanographic changes induce diet switching in a piscivorous seabird. *Marine Ecology Progress Series*, *393*, 273–284.

Ito, S.-I., Sugisaki, H., Tsuda, A., Yamamura, O., & Okuda, K. (2004). Contributions of the VENFISH program: meso-zooplankton, Pacific saury (*Cololabis saira*) and walleye pollock (*Theragra chalcogramma*) in the northwestern Pacific. *Fisheries Oceanography*, *13*(S1),1–9.

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*(14), 1801–1806.

Jha, S. (2015). Contemporary human-altered landscapes and oceanic barriers reduce bumble bee gene flow. *Molecular Ecology*, *24*(5), 993–1006.

Johnson, M., & Black, R. (2006). Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. *Evolution*, *60*(12), 2498–2506.

Johnson, M. S., & Black, R. (1982). Chaotic genetic patchiness in an intertidal Limpet, *Siphonaria* sp. *Marine Biology*, *70*(2), 157–164.

Jombart, T., Pontier, D., & Dufour, A.-B. (2009). Genetic markers in the playground of multivariate analysis. *Heredity*, *102*(4), 330–341.

Kalinowski, S. T. (2002). How many alleles per locus should be used to estimate genetic distances? *Heredity*, *88*(1), 62–65.

Kalinowski, S. T. (2004). Counting alleles with rarefaction: private alleles and hierarchical sampling designs. *Conservation Genetics*, *5*(4), 539–543.

Kalinowski, S. T. (2005). HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes*, *5*(1), 187–189.

Kalinowski, S. T. (2011). The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulations and implications for human population structure. *Heredity*, *106*(4), 625–632.

Keller, A., Rödel, M. O., Linsenmair, K. E., & Grafe, T. U. (2009). The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. *Journal of Animal Ecology*, *78*(2), 305–314.

Kerth, G., & Melber, M. (2009). Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation*, *142*(2), 270–279.

Kirk, H., & Freeland, J. R. (2011). Applications and implications of neutral versus non-neutral markers in molecular ecology. *International Journal of Molecular Sciences*,

12(6), 3966–3988.

Knope, M. L., Tice, K. A., & Rypkema, D. C. (2017). Site fidelity and homing behaviour of intertidal sculpins revisited. *Journal of Fish Biology*, *90*(1), 341–355.

Knowlton, N., Weight, L. A., Solórzano, L. A., Mills, D. K., Knowlton, N., Weigt, L. A., Solorzano, L. A., et al. (1993). Divergence in proteins, mitochondrial DNA, and reproductive compatibility across the Isthmus of Panama. *Science*, *260*(5114), 1629–1632.

Koivula, K., Lahti, K., Orell, M., & Rytkönen, S. (1993). Prior residency as a key determinant of social dominance in the willow tit (*Parus montanus*). *Behavioral Ecology and Sociobiology*, *33*(4), 283–287.

Kolding, S. (1985). Genetic adaptation to local habitats and speciation processes within the genus *Gammarus* (Amphipoda: Crustacea). *Marine Biology*, *89*(3), 249–255.

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. *Molecular Ecology Resources*, *15*(5), 1179–1191.

Krebs, J., Ashcroft, R., & Webber, M. (1978). Song repertoires and territory defence in the great tit. *Nature*, *271*(5645), 539–542.

Kuroki, M., Kato, A., Watanuki, Y., Niizuma, Y., Takahashi, A., & Naito, Y. (2003). Diving behavior of an epipelagically feeding alcid, the rhinoceros auklet (*Cerorhinca monocerata*). *Canadian Journal of Zoology*, *81*(7), 1249–1256.

Lal, M. M., Southgate, P. C., Jerry, D. R., Bosserelle, C., & Zenger, K. R. (2017). Swept away: ocean currents and seascape features influence genetic structure across the 18,000 km Indo-Pacific distribution of a marine invertebrate, the black-lip pearl oyster *Pinctada margaritifera*. *BMC Genomics*, *18*(1), 66.

Lande, R., & Shannon, S. (1996). The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*, *50*(1), 434–437.

Landguth, E. L., Fedy, B. C., Oyler-Mccance, S. J., Garey, A. L., Emel, S. L., Mumma, M., Wagner, H. H., et al. (2012). Effects of sample size, number of markers, and allelic richness on the detection of spatial genetic pattern. *Molecular Ecology Resources*, *12*(2), 276–284.

Latch, E. K., Dharmarajan, G., Glaubitz, J. C., & Rhodes, O. E. (2006). Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. *Conservation Genetics*, *7*(2), 295–302.

Latham, A. D. M., Latham, M. C., Boyce, M. S., & Boutin, S. (2011). Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications*, *21*(8), 2854–2865.

Lewallen, E. A., Anderson, T. W., & Bohonak, A. J. (2007). Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. *Marine Biology*,

152(3), 599–609.

Lewis, S., Benvenuti, S., Dall-Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S., et al. (2002). Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society B: Biological Sciences*, *269*(1501), 1687–1693.

Lieske, D. J., Fifield, D. A., & Gjerdrum, C. (2014). Maps, models, and marine vulnerability: assessing the community distribution of seabirds at-sea. *Biological Conservation*, *172*, 15–28.

Liu, Y., Webber, S., Bowgen, K., Schmaltz, L., Bradley, K., Halvarsson, P., Abdelgadir, M., et al. (2013). Environmental factors influence both abundance and genetic diversity in a widespread bird species. *Ecology and Evolution*, *3*(14), 4683–4695.

Louzao, M., Bécares, J., Rodríguez, B., Hyrenbach, K., Ruiz, A., & Arcos, J. (2009). Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Marine Ecology Progress Series*, *391*, 183–197.

Lowther, A. D., Harcourt, R. G., Goldsworthy, S. D., & Stow, A. (2012). Population structure of adult female Australian sea lions is driven by fine-scale foraging site fidelity. *Animal Behaviour*, *83*(3), 691–701.

Manel, S., Berthier, P., & Luikart, G. (2002). Detecting wildlife poaching: identifying the origin of individuals with Bayesian assignment tests and multilocus genotypes. *Conservation Biology*, *16*(3), 650–659.

Manel, S., Gaggiotti, O. E., & Waples, R. S. (2005). Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution*, *20*(3), 136–142.

Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution*, *18*(4), 189–197.

Martien, K. K., Givens, G. H., & Archer, E. (2007). A note on the ability of STRUCTURE to correctly infer the number of populations for Bering-Chukchi-Beaufort Seas bowhead whales. *(SC/59/BRG34) presented to the Scientific Committee of the International Whaling Commission, Cambridge*, 1–8.

Maudet, C., Miller, C., Bassano, B., Breitenmoser-Würsten, C., Gauthier, D., Obexer-Ruff, G., Michallet, J., et al. (2002). Microsatellite DNA and recent statistical methods in wildlife conservation management: applications in Alpine ibex [*Capra ibex (ibex)*]. *Molecular Ecology*, *11*(3), 421–436.

Meirmans, P. G., & Hedrick, P. W. (2011). Assessing population structure: FST and related measures. *Molecular Ecology Resources*, *11*(1), 5–18.

Melvin, E. F., Conquest, L. L., & Parrish, J. (1997). *Seabird bycatch reduction: new tools for Puget Sound drift gillnet salmon fisheries*. *WSG-AS 97-01, Washington Sea Grant*. Seattle.

Møller Nielsen, M., Paulino, C., Neiva, J., Krause-Jensen, D., Bruhn, A., & Serrão, E. A. (2016). Genetic diversity of *Saccharina latissima* (Phaeophyceae) along a salinity gradient in the North Sea–Baltic Sea transition zone. *Journal of Phycology*, *52*(4), 523–531.

Morris-Pocock, J. A., Anderson, D. J., & Friesen, V. L. (2011). Mechanisms of global diversification in the brown booby (*Sula leucogaster*) revealed by uniting statistical phylogeographic and multilocus phylogenetic methods. *Molecular Ecology*, *20*(13), 2835–2850.

Munro, K. J., & Burg, T. M. (2017). A review of historical and contemporary processes affecting population genetic structure of Southern Ocean seabirds. *Emu Austral Ornithology*, *117*(1), 4–18.

Nagasawa, K. (2001). Long-term variations in abundance of Pacific herring (*Clupea pallasi*) in Hokkaido and Sakhalin related to changes in environmental conditions. *Progress in Oceanography*, *49*(1–4), 551–564.

Naish, K. A., & Hard, J. J. (2008). Bridging the gap between the genotype and the phenotype: linking genetic variation, selection and adaptation in fishes. *Fish and Fisheries*, *9*(4), 396–422.

Natural Earth. (2017). Retrieved September 15, 2017, from http://www.naturalearthdata.com/

Navarrete, S. A., Broitman, B. R., & Menge, B. A. (2008). Interhemispheric comparison of recruitment to intertidal communities: pattern persistence and scales of variation. *Ecology*, *89*(5), 1308–1322.

Noto, M., & Yasuda, I. (1999). Population decline of the Japanese sardine *Sardinops melanostictus* in relation to sea surface temperature in the Kuroshio Extension. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(6), 973–983.

Oberg, P. R. (2001). *Responses of mountain caribou to linear features in a west-central Alberta landscape*. MSc Thesis, University of Alberta.

Ogden, R. (2008). Fisheries forensics: the use of DNA tools for improving compliance, traceability and enforcement in the fishing industry. *Fish and Fisheries*, *9*(4), 462–472.

Ogden, R., & Linacre, A. (2015). Wildlife forensic science: a review of genetic geographic origin assignment. *Forensic Science International: Genetics*, *18*, 152–159.

Oka, N., & Okuyama, M. (2000). Nutritional status of dead oiled rhinoceros auklets (*Cerorhinca monocerata*) in the southern Japan Sea. *Marine Pollution Bulletin*, *40*(4), 340–347.

Osa, Y., & Watanuki, Y. (2002). Status of seabirds breeding in Hokkaido. *Journal of the Yamashina Institute for Ornithology*, *33*, 107–141.

Ouborg, N. J., Piquot, Y., & Van Groenendael, J. M. (1999). Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology*, *87*(4), 551–568.

Overeem, R. L., Peucker, A. J., Austin, C. M., Dann, P., & Burridge, C. P. (2008). Contrasting genetic structuring between colonies of the World's smallest penguin, *Eudyptula minor* (Aves: Spheniscidae). *Conservation Genetics*, *9*(4), 893–905.

Paetkau, D., Calvert, W., Stirling, I., & Strobeck, C. (1995). Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology*, *4*(3), 347–354.

Paetkau, D., Slade, R., Burden, M., & Estoup, A. (2004). Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology*, *13*(1), 55–65.

Page, G. W., Carter, H. R., & Ford, R. G. (1990). Numbers of seabirds killed or debilitated in the 1986 Apex Houston oil spill in central California. *Studies in Avian Biology*, *14*, 164–174.

Paliy, O., & Shankar, V. (2016). Application of multivariate statistical techniques in microbial ecology. *Molecular Biology and Evolution*, *25*(5), 1032–1057.

Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, *25*, 547–572.

Parker, P. G., Snow, A. A., Schug, M. D., Booton, G. C., & Fuerst, P. A. (1998). What molecules can tell us about populations: choosing and using a molecular marker. *Ecology*, *79*(2), 361–382.

Patterson, N., Price, A. L., & Reich, D. (2006). Population structure and eigenanalysis. *PLoS Genetics*, *2*(12), 2074–2093.

Peakall, R., & Smouse, P. E. (2006). GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, *6*(1), 288–295.

Peakall, R., & Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics*, *28*(19), 2537–2539.

Pepper, M., Fujita, M. K., Moritz, C., & Keogh, J. S. (2011). Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone. *Molecular Ecology*, *20*(7), 1529–1545.

Perez-Enriquez, R., & Taniguchi, N. (1999). Genetic structure of red sea bream (*Pagrus major*) population off Japan and the Southwest Pacific, using microsatellite DNA markers. *Fisheries Science*, *65*(1), 23–30.

Pérez-Ortega, M., & İsfendiyaroğlu, S. (2017). Predicting foraging hotspots for Yelkouan Shearwater in the Black Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *141*, 237–247.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259.

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161–175.

Phillips, S. J., Dudik, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., Ferrier, S., et al. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, *19*(191), 181–197.

Pilot, M., Jedrzejewski, W., Branicki, W., Sidorovich, V. E., Jedrzejewska, B., Stachura, K., & Funk, S. M. (2006). Ecological factors influence population genetic structure of European grey wolves. *Molecular Ecology*, *15*(14), 4533–4553.

Piry, S., Alapetite, A., Cornuet, J. M., Paetkau, D., Baudouin, L., & Estoup, A. (2004). GENECLASS2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity*, *95*(6), 536–539.

Pometti, C. L., Bessega, C. F., Saidman, B. O., & Vilardi, J. C. (2014). Analysis of genetic population structure in *Acacia caven* (Leguminosae, Mimosoideae), comparing one exploratory and two Bayesian-model-based methods. *Genetics and Molecular Biology*, *37*(1), 64–72.

Porras-Hurtado, L., Ruiz, Y., Santos, C., Phillips, C., Carracedo, A., & Lareu, M. V. (2013). An overview of STRUCTURE: applications, parameter settings, and supporting software. *Frontiers in Genetics*, *4*(98), 1–13.

Primmer, C. R., Møller, A. R., & Ellegren, H. (1996). A wide-range survey of cross-species microsatellite amplification in birds. *Molecular Ecology*, *5*(3), 365–378.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959.

Putman, A. I., & Carbone, I. (2014). Challenges in analysis and interpretation of microsatellite data for population genetic studies. *Ecology and Evolution*, *4*(22), 4399–4428.

Quillfeldt, P., Masello, J. F., Navarro, J., & Phillips, R. A. (2013). Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. *Journal of Biogeography*, *40*(3), 430–441.

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, *41*(4), 629–643.

Ramírez, F., Tarroux, A., Hovinen, J., Navarro, J., Afán, I., Forero, M. G., & Descamps, S. (2017). Sea ice phenology and primary productivity pulses shape breeding success in Arctic seabirds. *Scientific Reports*, *7*(1), 1–9.

Rannala, B., & Mountain, J. L. (1997). Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(17), 9197–9201.

Raymond, M., & Rousset, F. (1995). GENEPOP (Version 1.2): population genetics

software for exact tests and ecumenicism. *Journal of Heredity*, *86*(3), 248–249.

Rayner, M. J., Hauber, M. E., Steeves, T. E., Lawrence, H. A., Thompson, D. R., Sagar, P. M., Bury, S. J., et al. (2011). Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations. *Nature Communications*, *2*(332), 1–7.

Reich, D., Price, A. L., & Patterson, N. (2008). Principal component analysis of genetic data. *Nature Genetics*, *40*(5), 491–492.

Renner, M., Hunt, G. L., Piatt, J. F., & Byrd, G. V. (2008). Seasonal and distributional patterns of seabirds along the Aleutian Archipelago. *Marine Ecology Progress Series*, *357*, 301–311.

Richardson, F. (1961). Breeding biology of the rhinoceros auklet on Protection Island, Washington. *The Condor*, *63*(6), 456–473.

Riffaut, L., McCoy, K. D., Tirard, C., Friesen, V. L., & Boulinier, T. (2005). Population genetics of the common guillemot *Uria aalge* in the North Atlantic: geographic impact of oil spills. *Marine Ecology Progress Series*, *291*, 263–273.

Riginos, C., & Liggins, L. (2013). Seascape genetics: populations, individuals, and genes marooned and adrift. *Geography Compass*, *7*(3), 197–216.

Robinson, L. M., Elith, J., Hodday, A. J., Pearson, R. G., Kendall, B. E., Possingham, H. P., & Richardson, A. J. (2011). Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, *20*(6), 789–802.

Ross, K. G. (2001). Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Molecular Ecology*, *10*(2), 265–284.

Roughgraden, J., Gaines, S., & Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science*, *241*(4872), 1460–1466.

Rousset, F. (2008). GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources*, *8*(1), 103–106.

Rueness, E. K., Stenseth, N. C., O'Donoghue, M., Boutin, S., Ellegren, H., & Jakobsen, K. S. (2003). Ecological and genetic spatial structuring in the Canadian lynx. *Nature*, *425*(6953), 69–72.

Russell, A., Hunt, R., Coyle, G., Russell, R. W., Hunt, G. L., Coyle, K. O., & Cooney, T. R. (1992). Foraging in a fractal environment: spatial patterns in a marine predator-prey system. *Landscape Ecology*, *7*(3), 195–209.

Saenz-Agudelo, Jones, G. P., Thorrold, S. R., & Planes, S. (2009). Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. *Molecular Ecology*, *18*(8), 1765–1776.

Sagarin, R. D., Gaines, S. D., & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology*

and Evolution, *21*(9), 524–530.

Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: ocean climate layers for marine spatial ecology. *Ecology*, *94*(4), 979.

Schlötterer, C. (2000). Evolutionary dynamics of microsatellite DNA. *Chromosoma*, *109*(6), 365–371.

Seidel, R. A., Lang, B. K., & Berg, D. J. (2010). Salinity tolerance as a potential driver of ecological speciation in amphipods (*Gammarus* spp.) from the northern Chihuahuan Desert. *Journal of the North American Benthological Society*, *29*(3), 1161–1169.

Selkoe, K. A., Gaines, S. D., Caselle, J. E., Warner, R. R., Caselle, E., & Warner, R. (2006). Current shifts and kin aggregation explain genetic patchiness in fish recruits. *Ecology*, *87*(12), 3082–3094.

Selkoe, K. A., & Toonen, R. J. (2006). Microsatellites for ecologists: A practical guide to using and evaluating microsatellite markers. *Ecology Letters*, *9*(5), 615–629.

Selkoe, K. A., Watson, J. R., White, C., Horin, T. Ben, Iacchei, M., Mitarai, S., Siegel, D. A., et al. (2010). Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology*, *19*(17), 3708–3726.

Selwyn, J. D., Hogan, J. D., Downey-Wall, A. M., Gurski, L. M., Portnoy, D. S., & Heath, D. D. (2016). Kin-aggregations explain chaotic genetic patchiness, a commonly observed genetic pattern, in a marine fish. *PLoS ONE*, *11*(4), e0153381.

Shanks, A. L., & Eckert, G. L. (2005). Population persistence of California current fishes and benthic crustaceans: a marine drift paradox. *Ecological Monographs*, *75*(4), 505–524.

Shitikov, D., Fedotova, S., Gagieva, V., Fedchuk, D., Dubkova, E., & Vaytina, T. (2012). Breeding-site fidelity and dispersal in isolated populations of three migratory passerines. *Ornis Fennica*, *89*(1), 53–62.

Siegle, M. R., Taylor, E. B., Miller, K. M., Withler, R. E., & Yamanaka, K. L. (2013). Subtle population genetic structure in yelloweye rockfish (*Sebastes ruberrimus,*) is consistent with a major oceanographic division in British Columbia, Canada. *PLoS ONE*, *8*(8), e71083.

Skov, H., & Durinck, J. (1998). Constancy of frontal aggregations of seabirds at the shelf break in the Skagerrak. *Journal of Sea Research*, *39*(3–4), 305–311.

Slatkin, M. (1985). Gene flow in natural populations. *Annual Review of Ecology & Systematics*, *16*(1), 393–430.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, *236*(4803), 787–792.

Smith, J. L., & Morgan, K. H. (2005). *An assessment of seabird bycatch in longline and net fisheries in British Columbia*. *Canadian Wildlife Service Technical Report Series*. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia,

Canada.

Smouse, P. E., & Peakall, R. (1999). Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity*, *82*(5), 561–573.

Sokal, R. R. (1979). Testing statistical significance of geographic variation. *Systematic Zoology*, *28*(2), 227–232.

Sorensen, M. C., Hipfner, J. M., Kyser, T. K., & Norris, D. R. (2010). Pre-breeding diet influences ornament size in the rhinoceros auklet *Cerorhinca monocerata*. *Ibis*, *152*(1), 29–37.

Spear, S. F., Balkenhol, N., & Scribner, K. (2010). Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology*, *19*(17), 3576–3591.

Stanley, H. F., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J., & Wayne, R. K. (1996). Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). *Molecular Biology and Evolution*, *13*(2), 368–382.

Steeves, T. E., Anderson, D. J., & Friesen, V. L. (2005). A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the masked booby (*Sula dactylatra*). *Molecular Ecology*, *14*(12), 3877–3887.

Steeves, T. E., Anderson, D. J., McNally, H., Kim, M. H., & Friesen, V. L. (2003). Phylogeography of *Sula*: the role of physical barriers to gene flow in the diversification of tropical seabirds. *Journal of Avian Biology*, *34*(2), 217–223.

Stewart, K. R., James, M. C., Roden, S., & Dutton, P. H. (2013). Assignment tests, telemetry and tag-recapture data converge to identify natal origins of leatherback turtles foraging in Atlantic Canadian waters. *Journal of Animal Ecology*, *82*(4), 791–803.

Storfer, A., Murphy, M. A., Spear, S. F., Holderegger, R., & Waits, L. P. (2010). Landscape genetics: where are we now? *Molecular Ecology*, *19*(17), 3496–3514.

Sunday, J. M., Popovic, I., Palen, W. J., Foreman, M. G. G., & Hart, M. W. (2014). Ocean circulation model predicts high genetic structure observed in a long-lived pelagic developer. *Molecular Ecology*, *23*(20), 5036–5047.

Sunnucks, P. (2000). Efficient genetic markers for population biology. *Trends in Ecology & Evolution*, *15*(5), 199–203.

Takahashi, A., Ito, M., Suzuki, Y., Watanuki, Y., Thiebot, J. B., Yamamoto, T., Iida, T., et al. (2015). Migratory movements of rhinoceros auklets in the northwestern Pacific: connecting seasonal productivities. *Marine Ecology Progress Series*, *525*, 229–243.

Takahashi, A., Kuroki, M., Niizuma, Y., Kato, A., Saitoh, S., & Watanuki, Y. (2001). Importance of the Japanese anchovy (*Engraulis japonicus*) to breeding rhinoceros auklets (*Cerorhinca monocerata*) on Teuri Island, Sea of Japan. *Marine Biology*, *139*(2), 361–371.

Techow, N. M. S. M., O'Ryan, C., Robertson, C. J. R., & Ryan, P. G. (2016). The origins of white-chinned petrels killed by long-line fisheries off South Africa and New Zealand. *Polar Research*, *35*, 1–5.

Thaxter, C. B., Lascelles, B., Sugar, K., Cook, A. S. C. P., Roos, S., Bolton, M., Langston, R. H. W., et al. (2012). Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*, *156*, 53–61.

Thayer, J. A., Bertram, D. F., Hatch, S. A., Hipfner, M. J., Slater, L., Sydeman, W. J., & Watanuki, Y. (2008). Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(8), 1610–1622.

Thayer, J. A., & Sydeman, W. J. (2007). Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. *Marine Ecology Progress Series*, *329*, 253–265.

Thomassen, H. A., Freedman, A. H., Brown, D. M., Buermann, W., & Jacobs, D. K. (2013). Regional differences in seasonal timing of rainfall discriminate between genetically distinct east African giraffe taxa. *PLoS ONE*, *8*(10), e77191.

Thompson, C. W., Wilson, M. L., Pierce, D. J., & DeGhetto, D. (1998). Population characteristics of common murres and rhinoceros auklets entangled in gillnets in Puget Sound, Washington, from 1993 to 1994, *79*(3), 77–91.

Tinnert, J., Hellgren, O., Lindberg, J., Koch-Schmidt, P., & Forsman, A. (2016). Population genetic structure, differentiation, and diversity in *Tetrix subulata* pygmy grasshoppers: roles of population size and immigration. *Ecology and Evolution*, *6*(21), 7831–7846.

Tremblay, M. A., & St. Clair, C. C. (2009). Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *Journal of Applied Ecology*, *46*(6), 1314–1322.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272–281.

Valsecchi, E., Palsboll, P., Hale, P., Glockner-Ferrari, D., Ferrari, M., Clapham, P., Larsen, F., et al. (1997). Microsatellites genetic distances between oceanic populations of the humpback whale (*Megaptera novaeangliae*). *Molecular Biology and Evolution*, *14*(4), 355–362.

van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., & Shipley, P. (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, *4*(3), 535–538.

Veen, J. (1977). Functional and causal aspects of nest distribution in colonies of the sandwich tern (*Sterna S. Sandvicencis* Lath.). *Behaviour. Supplement*, *20*, 1–193.

Vergara, P., Aguirre, J. I., Fargallo, J. A., & Dávila, J. A. (2006). Nest-site fidelity and breeding success in white stork *Ciconia ciconia*. *Ibis*, *148*(4), 672–677.

Vidya, T. N. C., Fernando, P., Melnick, D. J., & Sukumar, R. (2005). Population differentiation within and among Asian elephant (*Elephas maximus*) populations in southern India. *Heredity*, *94*(1), 71–80.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*, 1867–1870.

Wahl, T. R., & Speich, S. M. (1994). Distribution of foraging rhinoceros auklets in the Strait of Juan de Fuca, Washington. *Northwestern Naturalist*, *75*(2), 63–69.

Wallace, S. J., Wolf, S. G., Bradley, R. W., Harvey, L. L., & Friesen, V. L. (2015). The influence of biogeographical barriers on the population genetic structure and gene flow in a coastal Pacific seabird. *Journal of Biogeography*, *42*(2), 390–400.

Walsh, P. S., Metzger, D. A., & Higuchi, R. (1991). Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques*, *10*(4), 506–513.

Wan, Q. H., Wu, H., Fujihara, T., & Fang, S. G. (2004). Which genetic marker for which conservation genetics issue? *Electrophoresis*, *25*(14), 2165–2176.

Wandeler, P., Smith, S., Morin, P. A., Pettifor, R. A., & Funk, S. M. (2003). Patterns of nuclear DNA degeneration over time-a case study in historic teeth samples. *Molecular Ecology*, *12*(4), 1087–1093.

Wang, J. (2017). The computer program structure for assigning individuals to populations: easy to use but easier to misuse. *Molecular Ecology Resources*, *17*(5), 981–990.

Wang, Y. H., Yang, K. C., Bridgman, C. L., & Lin, L. K. (2008). Habitat suitability modelling to correlate gene flow with landscape connectivity. *Landscape Ecology*, *23*(8), 989–1000.

Waples, R. S. (2015). Testing for Hardy-Weinberg proportions: have we lost the plot? *Journal of Heredity*, *106*(1), 1–19.

Waples, R. S., & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, *15*(6), 1419–1439.

Ward, E. J., Holmes, E. E., & Balcomb, K. C. (2009). Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology*, *46*(3), 632–640.

Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, *33*(3), 607–611.

Watanuki, Y., & Ito, M. (2012). Climatic effects on breeding seabirds of the northern Japan Sea. *Marine Ecology Progress Series*, *454*, 183–196.

Watanuki, Y., Ito, M., Deguchi, T., & Minobe, S. (2009). Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of

anchovy. *Marine Ecology Progress Series*, *393*, 259–271.

Wattier, R., Engel, C. R., Saumitou-Laprade, P., & Valero, M. (1998). Short allele dominance as a source of heterozygote deficiency at microsatellite loci: experimental evidence at the dinucleotide locus Gv1CT in *Gracilaria gracilis*. *Molecular Ecology*, *7*(11), 1569–1573.

Weimerskirch, H., Louzao, M., Delord, K., & Garcı, D. (2012). Protecting persistent dynamic oceanographic features: transboundary conservation efforts are needed for the critically endangered Balearic shearwater. *PLoS ONE*, *7*(5), e35728.

Weinberg, W. (1908). *On the demonstration of heredity in man*. In: Boyer SH, editor, Papers on human genetics. Englewood Cliffs, NJ: Prentice Hall. Translated, 1963.

White, C., Selkoe, K. A., Watson, J., Siegel, D. A., Zacherl, D. C., & Toonen, R. J. (2010). Ocean currents help explain population genetic structure. *Proceedings. Biological Sciences*, *277*(1688), 1685–1694.

Whitlock, M. C., & McCauley, D. E. (1999). Indirect measures of gene flow and migration: FST≠1/(4Nm+1). *Heredity*, *82*(2), 117–125.

Wiley, A. E., Welch, A. J., Ostrom, P. H., James, H. F., Strieker, C. A., Fleischer, R. C., Gandhi, H., et al. (2012). Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia*, *168*(1), 119–130.

Wilson, C. C., Liskauskas, A. P., & Wozney, K. M. (2016). Pronounced genetic structure and site fidelity among native muskellunge populations in Lake Huron and Georgian Bay. *Transactions of the American Fisheries Society*, *145*(6), 1290–1302.

Wilson, U. W. (1986). Breeding biology of the rhinoceros auklet in Washington. *The Condor*, *88*(2), 143–155.

Withler, R. E., Beacham, T. D., Schulze, A. D., Richards, L. J., & Miller, K. M. (2001). Co-existing populations of Pacific Ocean perch, *Sebastes alutus*, in Queen Charlotte Sound, British Columbia. *Marine Biology*, *139*(1), 1–12.

Wolf, S., Keitt, B., Aguirre-Muñoz, A., Tershy, B., Palacios, E., & Croll, D. (2006). Transboundary seabird conservation in an important North American marine ecoregion. *Environmental Conservation*, *33*(4), 294–305.

Wright, S. (1931). Evolution in Mendelian Populations. *Genetics*, *16*(2), 97–159.

Wright, S. (1943). Isolation by distance. *Genetics*, *28*(2), 114–138.

Wright, S. (1951). Genetical structure of populations. *Annals of Eugenics*, *15*(4), 323–354.

Wright, S. (1965). The interpretation of population structure by F-Statistics with special regard to systems of mating. *Evolution*, *19*(3), 395–420.

Yoshida, H., Yoshioka, M., Shirakihara, M., & Chow, S. (2001). Population structure of finless porpoises (*Neophocaena phocaenoides*) in coastal waters of Japan based on

mitochondrial sequences. *Journal of Mammalogy*, *82*(1), 123–130.

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecology*, *27*(6), 777–797.

Appendix 2.1: Rhinoceros auklet samples used in the analyses with location and sample information. Sample IDs in grey were removed from analyses.

Population	Breeding Island	Sample ID	Sample	Latitude °N	Longitude °W
DAI	Daikoku Island, Japan	RHAUDAI-001	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-002	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-003	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-004	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-005	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-006	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-007	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-008	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-009	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-010	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-011	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-012	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-013	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-014	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-015	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-016	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-017	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-018	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-019	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-020	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-021	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-022	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-023	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-024	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-025	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-026	extracted DNA	42.954744	144.866057

DAI	Daikoku Island, Japan	RHAUDAI-027	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-028	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-029	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-030	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-031	extracted DNA	42.954744	144.866057
DAI	Daikoku Island, Japan	RHAUDAI-032	extracted DNA	42.954744	144.866057
TAI	Tai Islet, Japan	RHAUTAI-001	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-002	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-003	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-004	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-005	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-006	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-007	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-008	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-009	extracted DNA	41.135258	140.761813
TAI	Tai Islet, Japan	RHAUTAI-010	extracted DNA	41.135258	140.761813
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-001	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-002	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-003	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-004	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-005	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-006	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-007	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-008	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-009	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-010	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-011	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-012	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-013	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-014	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-015	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-016	extracted DNA	41.360155	139.818113

MAT	Matsumae-Kojima Island, Japan	RHAUMAT-017	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-018	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-019	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-020	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-021	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-022	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-023	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-024	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-025	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-026	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-027	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-028	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-029	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-030	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-031	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-032	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-033	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-034	extracted DNA	41.360155	139.818113
MAT	Matsumae-Kojima Island, Japan	RHAUMAT-035	extracted DNA	41.360155	139.818113
TEU	Teuri Island, Japan	RHAUTEU/09-001	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-002	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-003	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-004	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-005	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-006	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-007	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-008	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-009	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-010	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-011	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-012	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-013	blood	44.417646	141.312281

TEU	Teuri Island, Japan	RHAUTEU/09-014	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-015	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-016	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-017	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-018	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-019	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-020	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-021	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-022	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-023	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-024	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-025	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-026	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-027	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-028	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-029	blood	44.417646	141.312281
TEU	Teuri Island, Japan	RHAUTEU/09-030	blood	44.417646	141.312281
TOD	Todo Islet, Japan	RHAUTOD-001	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-002	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-003	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-004	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-005	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-006	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-007	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-008	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-009	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-010	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-011	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-012	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-013	extracted DNA	45.366808	141.035141
TOD	Todo Islet, Japan	RHAUTOD-014	extracted DNA	45.366808	141.035141
CH	Chowiet Island, Alaska	RHAUCHOW-001	blood	56.015513	-156.740272

CH	Chowiet Island, Alaska	RHAUCHOW-002	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-003	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-004	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-005	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-006	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-007	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-008	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-009	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-010	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-011	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-012	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-013	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-014	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-015	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-016	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-017	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-018	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-019	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-020	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-021	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-022	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-023	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-024	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-025	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAUCHOW-026	blood	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAU(MS)CH14-001	feather	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAU(MS)CH14-002	feather	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAU(MS)CH14-003	feather	56.015513	-156.740272
CH	Chowiet Island, Alaska	RHAU(MS)CH14-004	feather	56.015513	-156.740272
MID	Middleton Island, Alaska	RHAUMID/09-001	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-002	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-003	blood	59.415254	-146.345472

MID	Middleton Island, Alaska	RHAUMID/09-004	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-005	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-006	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-007	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-008	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-009	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-010	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-011	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-012	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-013	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-014	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-015	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-016	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-017	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-018	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-019	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-020	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-021	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-022	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-023	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-024	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-025	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-026	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-027	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-028	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-029	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-030	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-031	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-032	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-033	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-034	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-035	blood	59.415254	-146.345472

MID	Middleton Island, Alaska	RHAUMID/09-036	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-037	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-038	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-039	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-040	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-041	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-042	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-043	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-044	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-045	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-046	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-047	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-048	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-049	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-050	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-051	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-052	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-053	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-054	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-055	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-056	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-057	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-058	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-059	blood	59.415254	-146.345472
MID	Middleton Island, Alaska	RHAUMID/09-060	blood	59.415254	-146.345472
STL	St. Lazaria Island, Alaska	RHAUStL/09-001	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-002	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-003	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-004	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-005	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-006	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-007	blood	56.986502	-135.710838

STL	St. Lazaria Island, Alaska	RHAUStL/09-008	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-009	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-010	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-011	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-012	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-013	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL/09-014	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-001	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-002	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-003	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-004	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-005	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-006	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-007	blood	56.986502	-135.710838
STL	St. Lazaria Island, Alaska	RHAUStL-008	blood	56.986502	-135.710838
LU	Lucy Island, British Columbia	RHAULI/08-001	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-002	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-003	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-004	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-005	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-006	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-007	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-008	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-009	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-010	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-011	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-012	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-013	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-014	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-015	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-016	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-017	blood	54.297282	-130.614581

LU	Lucy Island, British Columbia	RHAULI/08-018	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-019	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-020	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-021	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-022	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-023	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-024	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-025	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-026	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-027	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-028	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-029	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/08-030	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-001	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-002	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-003	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-004	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-005	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-006	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-007	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-008	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-009	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-010	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-011	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-012	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-013	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-014	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-015	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-016	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-017	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-018	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-019	blood	54.297282	-130.614581

LU	Lucy Island, British Columbia	RHAULI/09-020	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-021	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-022	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-023	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-024	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-025	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-026	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-027	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-028	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-029	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-030	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-031	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-032	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-033	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-034	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-035	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-036	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-037	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-038	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-039	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-040	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-041	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-042	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-043	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-044	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-045	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-046	blood	54.297282	-130.614581
LU	Lucy Island, British Columbia	RHAULI/09-047	blood	54.297282	-130.614581
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-001	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-002	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-003	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-004	blood	52.092634	-131.225633

SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-005	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-006	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-007	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-008	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-009	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-010	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-011	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-012	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-013	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-014	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-015	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-016	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-017	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-018	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-019	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-020	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-021	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-022	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-023	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-024	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-025	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-026	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-027	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-028	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-029	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-030	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-031	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-032	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-033	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-034	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-035	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-036	blood	52.092634	-131.225633

SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-037	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-038	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-039	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-040	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-041	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-042	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-043	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-044	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-045	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-046	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-047	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-048	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-049	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-050	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-051	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-052	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-053	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-054	blood	52.092634	-131.225633
SGG	SG̲aang Gwaii Island, British Columbia	SPG/09-055	blood	52.092634	-131.225633
MO	Moore Island, British Columbia	RHAUMI-001	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-002	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-003	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-004	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-005	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-006	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-007	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-008	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-009	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-010	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-011	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-012	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-013	blood	52.678344	-129.418847

MO	Moore Island, British Columbia	RHAUMI-014	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-015	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-016	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-017	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAUMI-018	blood	52.678344	-129.418847
MO	Moore Island, British Columbia	RHAU(MS)M14-001	feather	52.678344	-129.418847
TRI	Triangle Island, British Columbia	RHAUTRI/08-001	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-002	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-003	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-004	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-005	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-006	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-007	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-008	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-009	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-010	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-011	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-012	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-013	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-014	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-015	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-016	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-017	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-018	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-019	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-020	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-021	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-022	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-023	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-024	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-025	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-026	blood	50.851023	-129.066292

TRI	Triangle Island, British Columbia	RHAUTRI/08-027	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-028	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-029	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-030	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-031	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-032	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-033	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-034	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-035	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-036	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-037	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-038	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-039	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-040	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-041	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-042	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-043	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-044	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-045	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-046	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-047	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-048	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-049	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-050	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-051	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-052	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-053	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-054	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-055	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-056	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-057	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-058	blood	50.851023	-129.066292

TRI	Triangle Island, British Columbia	RHAUTRI/08-059	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/08-060	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-001	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-002	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-003	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-004	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-005	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-006	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-007	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-008	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-009	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-010	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-011	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-012	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-013	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-014	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-015	blood	50.851023	-129.066292
TRI	Triangle Island, British Columbia	RHAUTRI/09-016	blood	50.851023	-129.066292
PI	Pine Island, British Columbia	RHAUPI/08-001	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-002	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-003	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-004	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-005	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-006	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-007	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-008	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-009	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-010	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-011	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-012	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-013	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-014	blood	50.976062	-127.729909

PI	Pine Island, British Columbia	RHAUPI/08-015	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-016	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-017	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-018	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-019	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-020	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-021	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-022	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-023	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-024	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-025	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-026	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-027	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-028	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-029	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-030	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/08-031	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-001	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-002	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-003	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-004	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-005	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-006	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-007	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-008	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-009	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-010	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-011	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-012	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-013	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-014	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-015	blood	50.976062	-127.729909

PI	Pine Island, British Columbia	RHAUPI/09-016	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-017	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-018	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-019	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-020	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-021	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-022	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-023	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-024	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-025	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-026	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-027	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-028	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-029	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-030	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-031	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-032	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-033	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-034	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-035	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-036	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-037	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-038	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-039	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-040	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-041	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-042	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-043	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-044	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-045	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-046	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-047	blood	50.976062	-127.729909

PI	Pine Island, British Columbia	RHAUPI/09-048	blood	50.976062	-127.729909
PI	Pine Island, British Columbia	RHAUPI/09-049	blood	50.976062	-127.729909
CL	Cleland Island, British Columbia	RHAUCL-001	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-002	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-003	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-004	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-005	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-006	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-007	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-008	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-009	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-010	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-011	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-012	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-013	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-014	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-015	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-016	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-017	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-018	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-019	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-020	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-021	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-022	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-023	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-024	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-025	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-026	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-027	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-028	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-029	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-030	blood	49.171516	-126.091075

CL	Cleland Island, British Columbia	RHAUCL-031	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-032	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-033	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-034	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-035	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-036	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-037	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-038	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-039	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-040	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-041	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-042	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-043	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-044	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAUCL-045	blood	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAU(MS)CL14-001	feather	49.171516	-126.091075
CL	Cleland Island, British Columbia	RHAU(MS)CL14-002	feather	49.171516	-126.091075
DE	Destruction Island, Washington	RHAUDEST-001	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-002	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-003	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-004	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-005	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-006	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-007	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-008	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-009	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-010	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-011	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-012	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-013	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-014	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-015	blood	47.674599	-124.484817

DE	Destruction Island, Washington	RHAUDEST-016	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-017	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-018	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-019	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-020	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-021	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-022	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-023	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-024	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-025	blood	47.674599	-124.484817
DE	Destruction Island, Washington	RHAUDEST-026	blood	47.674599	-124.484817
PR	Protection Island, Washington	RHAUPROT-001	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-002	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-003	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-004	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-005	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-006	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-007	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-008	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-009	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-010	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-011	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-012	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-013	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-014	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-015	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-016	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-017	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-018	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-019	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-020	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-021	blood	48.126341	-122.930289

PR	Protection Island, Washington	RHAUPROT-022	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-023	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-024	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-025	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-026	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-027	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-028	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAUPROT-029	blood	48.126341	-122.930289
PR	Protection Island, Washington	RHAU(MS)MPW15-001	feather	48.126341	-122.930289
PR	Protection Island, Washington	RHAU(MS)MPW15-002	feather	48.126341	-122.930289
PR	Protection Island, Washington	RHAU(MS)MPW15-003	feather	48.126341	-122.930289
PR	Protection Island, Washington	RHAU(MS)MPW15-004	feather	48.126341	-122.930289
PR	Protection Island, Washington	RHAU(MS)MPW15-005	feather	48.126341	-122.930289
SEF	Southeast Farallon Islands, California	RHAUSEF-001	blood	37.695357	-123.000752
SEF	Southeast Farallon Islands, California	RHAUSEF-002	blood	37.695357	-123.000752
SEF	Southeast Farallon Islands, California	RHAUSEF-003	blood	37.695357	-123.000752
SEF	Southeast Farallon Islands, California	RHAUSEF-004	blood	37.695357	-123.000752
SEF	Southeast Farallon Islands, California	RHAUSEF-005	blood	37.695357	-123.000752
SEF	Southeast Farallon Islands, California	RHAUSEF-006	blood	37.695357	-123.000752
SEF	Southeast Farallon Islands, California	RHAUSEF-007	blood	37.695357	-123.000752
AN	Año Nuevo Island, California	RHAUAN-001	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-002	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-003	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-004	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-005	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-006	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-007	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-008	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-009	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-010	blood	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-011	extracted DNA	37.107584	-122.337026

AN	Año Nuevo Island, California	RHAUAN-012	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-013	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-014	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-015	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-016	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-017	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-018	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-019	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-020	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-021	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-022	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-023	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-024	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-025	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-026	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-027	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-028	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-029	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-030	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-031	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-032	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-033	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-034	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-035	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-036	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-037	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-038	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-039	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-040	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-041	extracted DNA	37.107584	-122.337026

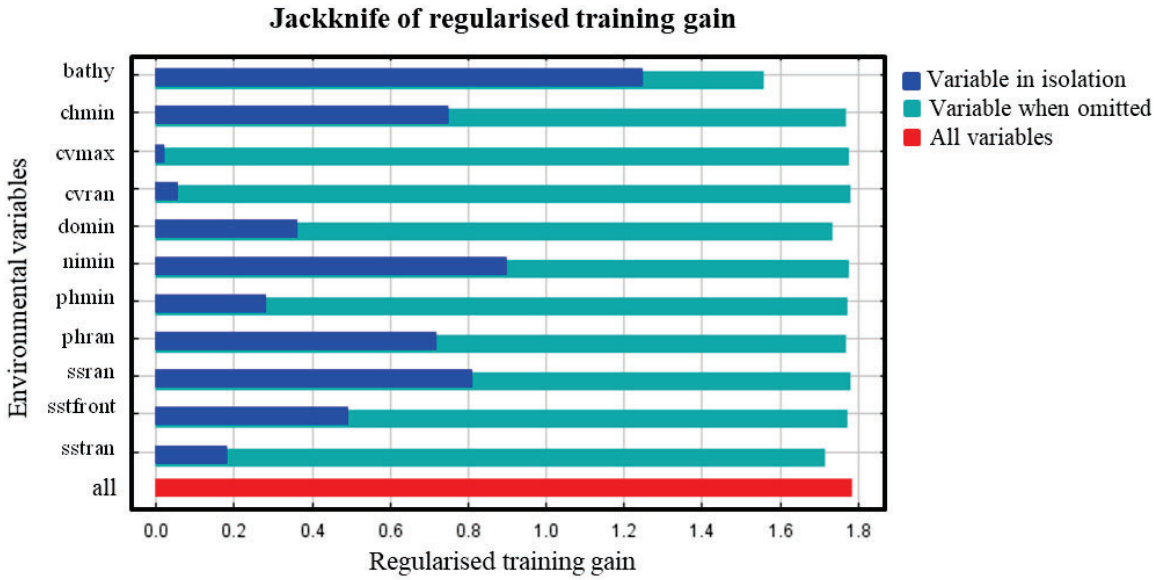
AN	Año Nuevo Island, California	RHAUAN-042	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-043	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-044	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-045	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-046	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-047	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-048	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-049	extracted DNA	37.107584	-122.337026
AN	Año Nuevo Island, California	RHAUAN-050	extracted DNA	37.107584	-122.337026

Appendix 2.2: Environmental GIS rasters obtained from the MARSEC* and Bio-ORACLE (max, min, mean & range) datasets. Pearson's correlation coefficient was used to check all variables for correlation. Variables $r > 0.7$ were considered to be highly correlated and removed from further analysis. In total 11 variables were retained.

Available environmental layers	Retained variable(s)
Bathymetry*: depth to seafloor	depth in m
Sea surface temperature: max, min, mean, range & front	front, range
Nitrate: max, min, mean & range	min
Dissolved molecular oxygen: max, min, mean & range	min
Phosphate: max, min, mean & range	min, range
Chlorophyll: max, min, mean & range	min
Currents velocity: max, min, mean & range	max, range
Salinity: max, min, mean & range	range
Silicate: max, min, mean & range	removed
Iron: max, min, mean & range	removed
Phytoplankton: max, min, mean & range	removed
Primary productivity: max, min, mean & range	removed

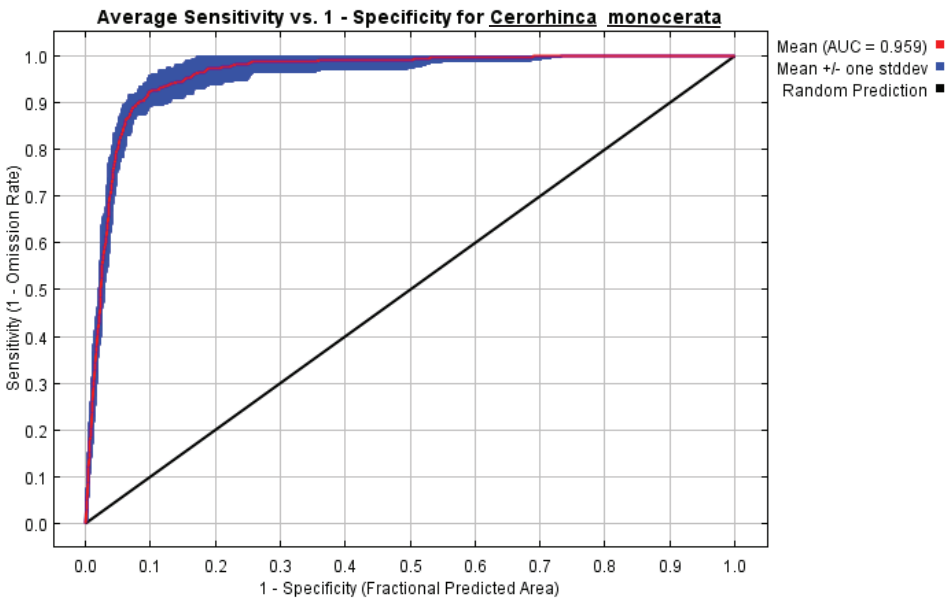
Appendix 2.3: Environmental layers used to develop the SDM for rhinoceros auklet. Contribution to the model values are determined using a heuristic approach that depends on the path of the Maxent code. Permutation importance is determined by values being randomly permutated along training points and measurements for the decrease in training AUC. Variables with a higher influence have a larger percent value.

Layer	Description	Unit	Contribution to model (%)	Permutation importance (%)
bathy	bathymetry - depth to seafloor	m	64.3	59.8
sstran	sea surface temperature (SST) - range	^{o}C	10.4	8.9
nimin	nitrate - min	$\mu mol.m^{-3}$	8.4	3.1
domin	dissolved molecular oxygen - min	$\mu mol.m^{-3}$	6.1	11.4
phran	phosphate - range	$\mu mol.m^{-3}$	5.5	5
chmin	chlorophyll - min	$mg.m^{-3}$	2.6	8.1
sstfront	ocean fronts - (sd SST range, °C, over 3x3 grid)	-	0.9	0.2
phmin	phosphate - min	$\mu mol.m^{-3}$	0.8	1.6
cvmax	currents velocity - max	$m \bullet s^{-1}$	0.5	1.2
cvran	currents velocity - range	$m \bullet s^{-1}$	0.3	0
ssran	salinity - range	PSS	0.1	0.7

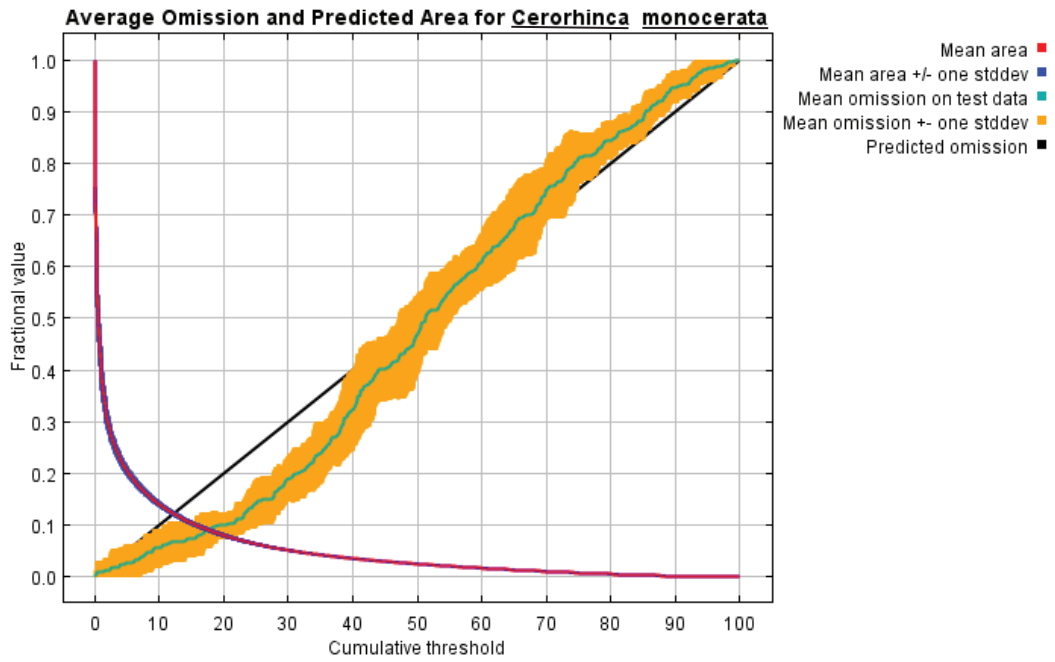


Appendix 2.4: Jackknife test of variable importance showing regularised training gain of the model with and without each environmental variable for rhinoceros auklet SDM. Dark blue bar shows amount of gain a variable has when used in isolation with bathy showing the most useful information, for model performance, when used by itself. Aqua-green bars show how much gain is lost when a variable is excluded from the model. Bathy shows to have the most gain lost when this variable is omitted from the model, thus, bathy has the most information that is not present in the other variables. See Appendix 2.3 for environmental variables abbreviations.

a)

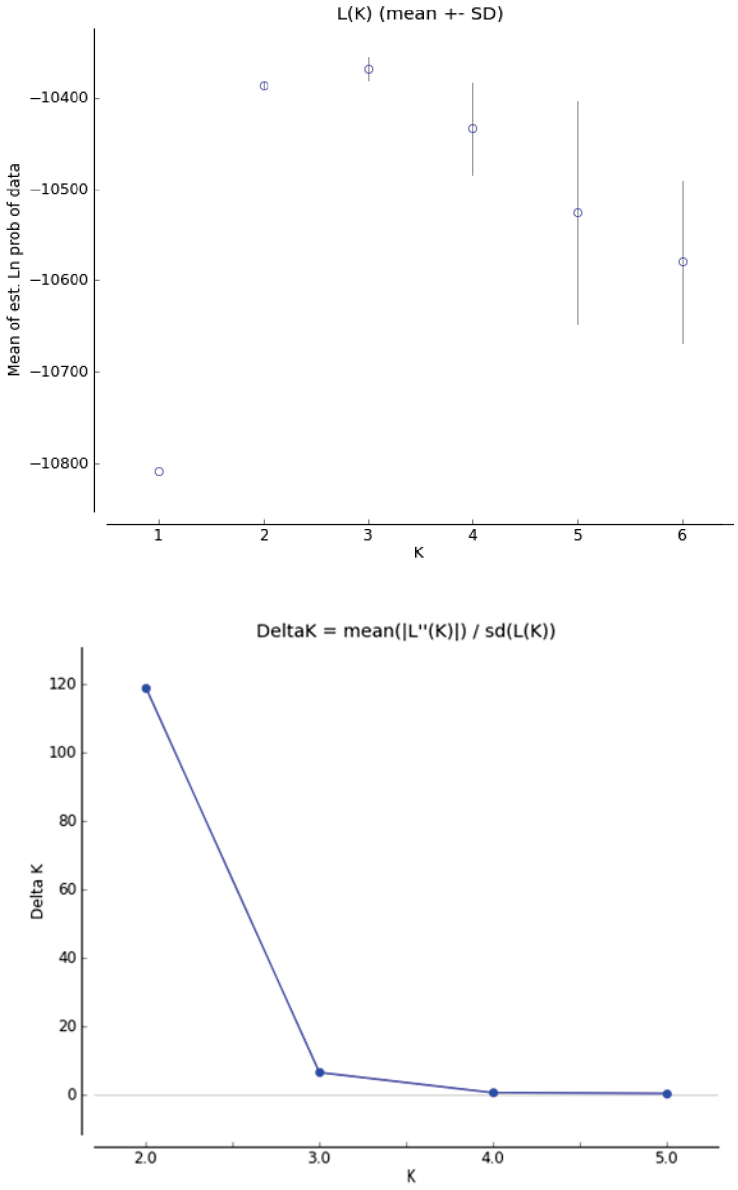


b)



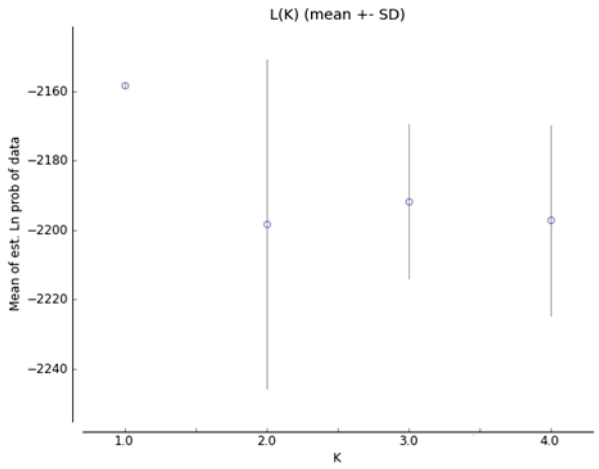
Appendix 2.5: a) Receiver operating curve (ROC) and AUC value and b) test omission data for both the SDM's training and test data. Training data was run using 25% of the occurrence records for testing over ten replicate runs. a) The ROC shown (red line) has a AUC of 0.959 indicative of an informative and accurate model. b) The test omission data (green line) and ± one standard deviation mean omission (yellow) is close to the predicted omission data (black line) indicative of an informative model.

a)

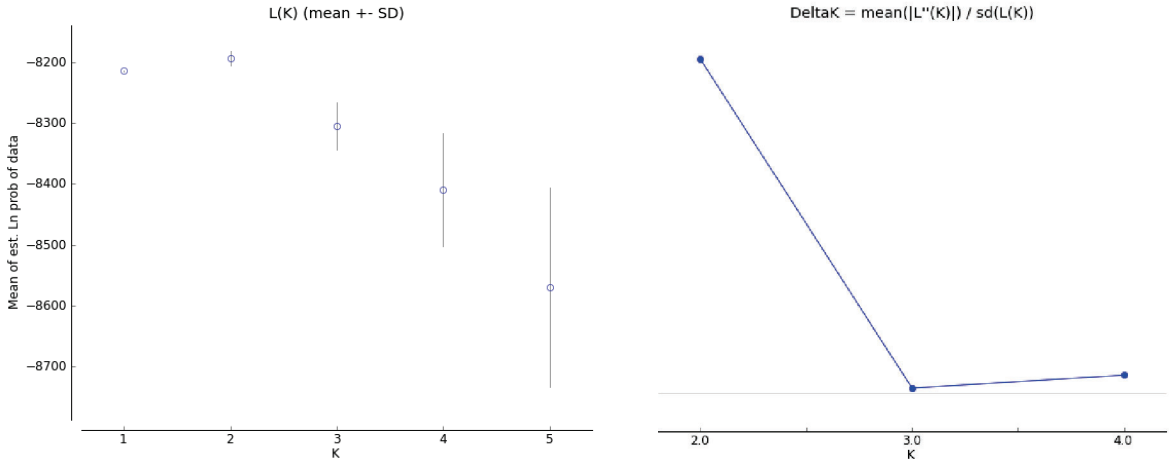


Appendix 2.6: Plots of a) log likelihood (ln(P(X|K)) and b) delta K (ΔK) over ten replicate runs with all 18 rhinoceros auklet breeding populations. Plots were created using STRUCTURE HARVESTER v0.6.94 (Earl & vonHoldt, 2012). The most likely number of K populations is measured by the highest estimated log probability and the highest delta K value.

a)



b)



Appendix 2.7: Plots for the hierarchical STRUCTURE results over ten replicate runs each K showing the a) log likelihood (ln(P(X|K)) for five western and b) log likelihood (ln(P(X|K)) and delta K (ΔK) for 13 eastern North Pacific Ocean rhinoceros auklet breeding colonies. Plots were created using STRUCTURE HARVESTER v0.6.94 (Earl & vonHoldt, 2012). a) As delta K cannot be evaluated only the log likelihood plot is shown for the western North Pacific breeding colonies. The most likely number of K populations is measured by the highest estimated log probability and the highest delta K value.

Appendix 3.1: Rhinoceros auklet bycatch samples used in analyses with location and sample information. Sampling dates in bold are from the post-breeding season (Aug.-Nov.). Abbreviations of age and sex of birds include: unknown (U), juvenile (J), subadult (SA), adult (A), male (M), female (F). Sample ID's in grey were removed from analyses.

Population	Region	Sampling Area	Sample ID	Sample Type	Date Collected	Sex	Age	Latitude (°N)	Longitude (°W)
Bycatch	Queen Charlotte Strait	Deer Island, BC	BYCBC(c)-001	web punch	14-Jul-05	U	U	50.714502	-127.371851
Bycatch	Storm Islands	Pine Island, BC	BYCBC(c)-002	web punch	**7-Aug-06**	U	U	51.024300	-127.795300
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-003	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-004	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-005	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-006	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-007	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-008	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-009	web punch	9-Jul-06	U	U	54.340300	-130.521800
Bycatch	Dixon Entrance/Hecate Strait	Parkin Islets, BC	BYCBC(n)-010	web punch	26-Jul-07	U	U	54.624500	-130.460900
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-011	web punch	**15-Aug-06**	U	U	54.380700	-130.542300
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-012	web punch	**15-Aug-06**	U	U	54.380700	-130.542300

Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-013	web punch	**15-Aug-06**	U	U	54.380700	-130.542300
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC	BYCBC(n)-014	web punch	2-Jul-07	U	U	54.574000	-130.484500
Bycatch	Dixon Entrance/Hecate Strait	Parkin Islets, BC	BYCBC(n)-015	web punch	25-Jun-07	U	U	54.619800	-130.460000
Bycatch	Dixon Entrance/Hecate Strait	Parkin Islets, BC	BYCBC(n)-016	web punch	26-Jun-07	U	U	54.624500	-130.460900
Bycatch	Dixon Entrance/Hecate Strait	Dundas Island, BC	BYCBC(n)-017	web punch	23-Jul-07	U	U	54.337400	-130.817900
Bycatch	Storm Islands	Pine Island, BC	BYCBC(c)-018	web punch	**7-Aug-06**	U	U	51.017000	-127.754100
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC	BYCBC(n)-019	web punch	14-Jul-06	U	U	54.578500	-130.478500
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC	BYCBC(n)-020	web punch	14-Jul-06	U	U	54.566200	-130.486200
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-021	web punch	13-Jul-06	U	U	54.321400	-130.540600
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC	BYCBC(n)-022	web punch	2-Jul-07	U	U	54.574000	-130.484500
Bycatch	Dixon Entrance/Hecate Strait	Parkin Islets, BC	BYCBC(n)-023	web punch	7-Jul-07	U	U	54.618100	-130.459000
Bycatch	Dixon Entrance/Hecate Strait	Georgetown Mills, BC	BYCBC(n)-024	web punch	13-Jul-06	U	U	54.436600	-130.513500

Bycatch	Queen Charlotte Strait/Johnstone Strait	Malcolm Island, BC	BYCBC(n)-025	web punch	**27-Aug-06**	U	U	50.673800	-127.134100
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-026	muscle	16-Jul-09	U	U	54.310922	-130.311178
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-027	muscle	16-Jul-09	U	U	54.310922	-130.311178
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-028	muscle	18-Jul-09	U	U	54.310922	-130.311178
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-029	muscle	9-Jul-10	U	U	54.310922	-130.311178
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-030	muscle	**10-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-031	muscle	**23-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-032	muscle	**23-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-033	muscle	**24-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-034	muscle	**26-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-035	muscle	**26-Aug-10**	**U**	**U**	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-036	muscle	**27-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-037	muscle	**29-Aug-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-038	muscle	**4-Sep-10**	U	U	49.056339	-123.117095
Bycatch	Strait of Georgia	Delta, BC	BYCBC(n)-039	muscle	**8-Sep-10**	U	U	49.056339	-123.117095
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-040	web punch	9-Jul-06	U	U	54.341332	-130.509262
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-041	web punch	9-Jul-06	U	U	54.341332	-130.509262
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-042	web punch	9-Jul-06	U	U	54.341332	-130.509262

Bycatch	Johnstone Strait/Strait of Georgia	Big Bay, BC	BYCBC(c)-043	web punch	2-Jul-07	U	U	50.396936	-125.152389
Bycatch	Johnstone Strait/Strait of Georgia	Big Bay, BC	BYCBC(c)-044	web punch	2-Jul-07	U	U	50.396936	-125.152389
Bycatch	Johnstone Strait/Strait of Georgia	Big Bay, BC	BYCBC(c)-045	web punch	25-Jun-07	U	U	50.396936	-125.152389
Bycatch	Johnstone Strait/Strait of Georgia	Big Bay, BC	BYCBC(c)-046	web punch	26-Jun-07	U	U	50.396936	-125.152389
Bycatch	Johnstone Strait/Strait of Georgia	Big Bay, BC	BYCBC(c)-047	web punch	26-Jun-07	U	U	50.396936	-125.152389
Bycatch	Johnstone Strait/Strait of Georgia	Big Bay, BC	BYCBC(c)-048	web punch	26-Jun-07	U	U	50.396936	-125.152389
Bycatch	Storm Islands	Roller Bay Area, BC	BYCBC(c)-049	web punch	**7-Aug-06**	U	U	51.036901	-127.735164
Bycatch	Storm Islands	Roller Bay Area, BC	BYCBC(c)-050	web punch	**8-Aug-06**	U	U	51.036901	-127.735164
Bycatch	Storm Islands	Roller Bay Area, BC	BYCBC(c)-051	web punch	**7-Aug-06**	U	U	51.036901	-127.735164
Bycatch	Storm Islands	Roller Bay Area, BC	BYCBC(c)-052	web punch	**17-Aug-06**	U	J	51.036901	-127.735164
Bycatch	Storm Islands	Roller Bay Area, BC	BYCBC(c)-053	web punch	**17-Aug-06**	U	J	51.036901	-127.735164
Bycatch	Storm Islands	Roller Bay Area, BC	BYCBC(c)-054	web punch	**19-Aug-06**	U	U	51.036901	-127.735164
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC	BYCBC(n)-055	web punch	11-Jul-07	U	U	54.535524	-130.471265

Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC	BYCBC(n)-056	web punch	11-Jul-05	U	U	54.535524	-130.471265
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC West	BYCBC(n)-057	web punch	14-Jul-06	U	U	54.535524	-130.471265
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC West	BYCBC(n)-058	web punch	11-Jul-05	U	U	54.535524	-130.471265
Bycatch	Dixon Entrance/Hecate Strait	Finlayson Island, BC West	BYCBC(n)-059	web punch	11-Jul-05	U	U	54.535524	-130.471265
Bycatch	Queen Charlotte Strait/Johnstone Strait	Round Island, BC	BYCBC-060	web punch	20-Jul-07	U	U	50.531708	-126.286930
Bycatch	Queen Charlotte Strait/Johnstone Strait	Malcolm Island, BC North	BYCBC-(c)061	web punch	**27-Aug-06**	U	U	50.664251	-126.999588
Bycatch	Storm Islands	Pine Island, BC	BYCBC-(c)062	web punch	**7-Aug-06**	U	U	50.974699	-127.722155
Bycatch	Queen Charlotte Strait/Johnstone Strait	Malcolm Island, BC Sointula	BYCBC-(c)063	web punch	**18-Aug-06**	U	J	50.625798	-127.028827
Bycatch	Dixon Entrance/Hecate Strait	Port Simpson. BC	BYCBC-(n)064	web punch	14-Jul-06	U	U	54.563386	-130.433076
Bycatch	California Current	Haystack Rock, Oregon	BYCOR-001	web punch	9-Jul-06	U	U	45.883957	-123.967961
Bycatch	Dixon Entrance/Hecate Strait	Parken Islet	BYCBC(n)-065	muscle	15-Jul-09	U	U	54.624500	-130.460900
Bycatch	Strait of Georgia	Union Bay, BC	BYCBC(s)-066	web punch	**7-Nov-05**	U	U	49.581556	-124.879314

Bycatch	Dixon Entrance/Hecate Strait	near Lucy Island	BYCBC-067	web punch	**unknown**	U	U	54.330695	-130.318720
Bycatch	unknown	no info	BYCBC-068	web punch	13-Jul-06	U	U	unknown	unknown
Bycatch	unknown	no info	BYCBC-069	web punch	14-Jul-05	U	U	unknown	unknown
Bycatch	unknown	no info	BYCBC-070	web punch	15-Jul-06	U	U	unknown	unknown
Bycatch	unknown	no info	BYCBC-071	web punch	9-Jul-07	U	U	unknown	unknown
Bycatch	unknown	no info	BYCBC-072	web punch	9-Jul-07	U	U	unknown	unknown
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-073	feather	15-Jul-09	M	A	54.313320	-130.514621
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-074	feather	16-Jul-09	F	A	54.313320	-130.514621
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-075	feather	16-Jul-09	M	A	54.313320	-130.514621
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-076	feather	16-Jul-09	M	A	54.313320	-130.514621
Bycatch	Hecate Strait	Tugwell Island, BC South	BYCBC(n)-077	feather	18-Jul-09	M	A	54.313320	-130.514621
Bycatch	Queen Charlotte Strait/Johnstone Strait	Port McNeill, BC	BYCBC(n)-078	muscle	20-Jul-11	M	A	50.752010	-127.352230
Bycatch	Queen Charlotte Strait/Johnstone Strait	Port McNeill, BC	BYCBC(n)-079	muscle	18-Jul-11	F	A	50.752010	-127.352230
Bycatch	Hecate Strait	Tugwell Island, BC	BYCBC(n)-080	muscle	**04-Aug-11**	F	A	54.324144	130.541767
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-081	muscle	28-Jul-11	F	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-082	muscle	28-Jul-11	M	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-083	muscle	28-Jul-11	F	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-084	muscle	28-Jul-11	M	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-085	muscle	28-Jul-11	M	A	54.663913	-130.392266

Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-086	muscle	28-Jul-11	M	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-087	muscle	28-Jul-11	M	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-088	muscle	28-Jul-11	F	A	54.663913	-130.392266
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-089	muscle	28-Jul-11	F	A	54.663913	-130.392266
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-090	muscle	**30-Sep-11**	F	A	50.610013	-126.741370
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-091	muscle	**30-Sep-11**	M	A	50.610013	-126.741370
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-092	muscle	**30-Sep-11**	F	A	50.610013	-126.741370
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-093	muscle	**30-Sep-11**	F	A	50.610013	-126.741370
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-094	muscle	**30-Sep-11**	M	A	50.610013	-126.741370
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-095	muscle	**30-Sep-11**	F	A	50.610013	-126.741370
Bycatch	Vancouver Island Shelf	Tofino, BC	BYCBC(s)-096	muscle	**07-Dec-11**	F	A	49.067931	-125.800016
Bycatch	Queen Charlotte Strait/Johnstone Strait	Round Island, BC	BYCBC(c)-097	muscle	**07-Aug-12**	F	A	50.752010	-127.352230
Bycatch	Queen Charlotte Strait	Port Hardy, BC	BYCBC(c)-098	muscle	**26-Aug-12**	M	J	50.590735	-130.857890
Bycatch	Hecate Strait	Prince Rupert, BC	BYCBC(n)-099	muscle	25-Jun-12	F	A	54.663913	-130.392266
Bycatch	Hecate Strait	Lucy Island, BC	BYCBC(n)-100	muscle	31-Jul-12	U	A	54.294693	-130.614578
Bycatch	Hecate Strait	Lucy Island, BC	BYCBC(n)-101	muscle	31-Jul-12	U	A	54.294693	-130.614578
Bycatch	Hecate Strait	Lucy Island, BC	BYCBC(n)-102	muscle	31-Jul-12	U	A	54.294693	-130.614578
Bycatch	Dixon Entrance	Masset, BC	BYCBC(n)-103	muscle	**01-Sep-12**	F	J	54.042092	-131.915473
Bycatch	Queen Charlotte Strait/Johnstone Strait	Port McNeill, BC	BYCBC(c)-104	muscle	**06-Aug-13**	F	A	50.749090	-127.369800
Bycatch	Queen Charlotte Strait/Johnstone Strait	Port McNeill, BC	BYCBC(c)-105	muscle	**08-Oct-13**	F	J	50.593780	-126.754000
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-106	muscle	**18-Aug-14**	M	A	50.517641	-126.694902

Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-107	muscle	**18-Aug-14**	M	A	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-108	muscle	**18-Aug-14**	M	A	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-109	muscle	**18-Aug-14**	M	A	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-110	muscle	**18-Aug-14**	M	A	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-111	muscle	**18-Aug-14**	M	A	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-112	muscle	**18-Aug-14**	F	SA	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-113	muscle	**18-Aug-14**	F	SA	50.517641	-126.694902
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-114	muscle	**18-Aug-14**	F	A	50.517641	-126.694902
Bycatch	Hecate Strait	Kitson Island, BC	BYCBC(n)-115	muscle	11-Jul-14	M	A	54.139583	-130.296417
Bycatch	Hecate Strait	Smith Island, BC	BYCBC(n)-116	muscle	11-Jul-14	F	A	54.130117	-130.291167
Bycatch	Hecate Strait	Smith Island, BC	BYCBC(n)-117	muscle	21-Jul-14	F	A	54.141167	-130.279000
Bycatch	Hecate Strait	Smith Island, BC	BYCBC(n)-118	muscle	11-Jul-14	M	A	54.153770	-130.301499
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-119	muscle	**18-Aug-14**	M	A	50.546775	-126.833965
Bycatch	Johnstone Strait	Telegraph Cove, BC	BYCBC(c)-120	muscle	**18-Aug-14**	F	A	50.517641	-126.694902
Bycatch	Haro Strait	Victoria, BC	BYCBC(s)-121	feather	12-Jul-16	U	U	48.406420	-123.354000
Bycatch	Haro Strait	Victoria, BC	BYCBC(s)-122	feather	12-Jul-16	U	U	48.406420	-123.354000
Bycatch	Haro Strait	Victoria, BC	BYCBC(s)-123	feather	12-Jul-16	U	U	48.406420	-123.354000