UNRAVELLING POPULATION GENETIC STRUCTURE OF BLACK OYSTERCATCHER (*HAEMATOPUS BACHMANI*) IN NORTH AMERICA

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DEDICATION

To my late grandmother, whose unwavering motivation and belief in me, gave me the courage to pursue my dreams. Even if you are not here physically, I have always felt your love and support throughout my journey. In this wonderful achievement of my life and my further endeavors, you will always be remembered and cherished.

Thank you for your love, Aama.

ABSTRACT

This study analyzed the genetic structure of the black oystercatcher (*Haematopus bachmani*) across its range using an improved version of genotype by sequencing (GBS) to understand the genetic variation, gene flow, and population differentiation. I used Bayesian clustering and principal coordinate analysis (PCoA) to identify the population genetic structure of the black oystercatcher. Population-level analyses with PCoA and pairwise F_{ST} showed moderate to high connectivity and gene flow among most sampled populations, with some subtle north-south structuring. I also employed connectivity modeling approaches, such as isolation by distance and the least-cost corridor model, to understand the pattern of gene flow. The moderate isolation by distance implied that gene flow decreases with increasing geographical distance. The least-cost corridor analyses provided additional spatial context by showing pathways as dispersal corridors and highlighting potential isolation between distant populations. Additionally, I conducted a redundancy analysis, examining the relationship between environmental and spatial factors and genetic variation, which revealed a weak association between environment and genetics, but also supported the isolation by distance model to some extent. My thesis demonstrates how a species' genetic structure is shaped by geographic distance and how behaviors, such as breeding site fidelity, play a significant role.

CONTRIBUTIONS OF AUTHORS

I, Anisha Neupane, affirm that I am solely responsible for formulating the research objectives, designing the study, conducting all analyses, interpreting the findings, and drafting this thesis. This data chapter has not been submitted for publication during the preparation of the thesis. Any future manuscript derived from this work may involve revisions, and the associated author contribution statement may be modified accordingly.

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List of abbreviations, acronyms and symbols

AUC	Area under curve
bam	Binary alignment map
BLOY	Black oystercatcher
bp	Base pairs
Bwa	Burrows-wheeler alignment tools
DNA	Deoxyribonucleic acid
ECCC	Environment and Climate Change Canada
ESRI	Environment System Research Institute
F_{ST}	Fixation index
GBIF	Global Biodiversity Information Facility
GBS	Genotype by sequencing
GIS	Geographical information system
H_e	Expected heterozygosity
H_o	Observed heterozygosity
IBD	Isolation by distance
km	Kilometers
LCC	Least cost corridor
lcWGS	Low-coverage whole genome sequencing
Maxent	Maximum entropy
mg	Milligram
NGS	Next generation sequencing
PCA	Principal component analysis
PCoA	Principal coordinate analysis
RDA	Redundancy analysis
ROC	Receiver operating characteristics
SDM	Species distribution modelling
SNP	Single nucleotide polymorphisms
vcf	Variant call file
WGS	Whole genome sequencing

Abbreviations for Populations

Aiktak_Chowiet	Aiktak and Chowiet
ECVI	East Coast of Vancouver Island
HG	Haida Gwaii
LUCY	LUCY
St. Laz	St. Lazaria
TRI	Triangle Island
VAN	Vancouver
WCVI	West Coast of Vancouver Island

Chapter 1: General Introduction

1.1 Population genetics

Population genetics is a discipline within evolutionary biology that studies the distribution and frequency of alleles within and between population, and the influence of evolutionary processes including gene flow, genetic drift, selection, and mutation on alleles (Chen, 2015; Hedrick, 2009). Studies using population genetics help us to identify factors driving population connectivity, predict the capacity of species to adapt in dynamic environments and understand how evolutionary processes shape biodiversity across landscapes (Allendorf et al., 2012; Hohenlohe et al., 2021; Rieseberg & Burke, 2001). For nearly all species, some degree of genetic variation exists among populations because of microevolutionary processes (Hedrick, 2009) that drive genetic differentiation between breeding groups (Freeland, 2020). Genetic variation, essential for species to adapt in a changing environment, is key to track gene flow, determine genetic diversity and population structure, and infer evolutionary history of the species (Kardos, 2021; Woodruff, 2004).

1.1.1 Gene flow and population connectivity

Gene flow, the transfer of genetic material among populations, is a fundamental process in evolution that influences the genetic diversity and adaptability of species (Feder et al., 2012; López-Goldar & Agrawal, 2021; Slatkin, 1987; Wang et al., 2025). In species with high dispersal potential and continuous habitats, gene flow is typically sufficient to prevent substantial genetic differentiation and maintain population connectivity countering the effects of drift and local adaptation (Galindo et al., 2006; Tigano & Friesen, 2016). The exchange of genes through migration or dispersal between population maintain genetic connections and reduce population differentiation. For instance, dispersal in roe deer (*Capreolus caprelous*) resulted in genetic homogeneity among populations despite their habitat fragmentation in France (Coulon et al., 2006). However, when movements between populations are restricted by geographical, ecological, or behavioral barriers, exchange of genes are limited and can lead to increased genetic differentiation possibly leading to speciation over evolutionary time (Pilot et al., 2006;

Slatkin, 1987). Since the evolutionary trajectories of populations are strongly influenced by gene flow, quantifying the factors that restrict gene flow is critical to our understanding on evolution.

1.1.2 Barriers to gene flow

Barrier including physical features (e.g. water bodies), environment (e.g. climate gradients), ecology (e.g. competition), and behavior (e.g. mate choice) (Jha, 2015; Pilot et al., 2006; Ross, 2001; Slatkin, 1987) can limit gene flow between populations. Habitat loss, climate-driven shifts in species distributions, and anthropogenic pressures alter patterns of population connectivity and dispersal, potentially leading to changes in genetic structure and reduced gene flow over time (Bay et al., 2018; Razgour et al., 2019). Species with specialized habitat requirements, restricted ranges, or strong site fidelity are particularly vulnerable, as disruptions to key habitats and movement corridors may compromise adaptive potential and population viability (Brooks et al., 2002; Smith et al., 2015; Smith et al., 2023). Each barrier is dependent on how organisms interact or perceive their environment. For example, Burney & Brumfield, (2009) showed that bird populations of Neotropical canopy rainforest separated by the Andes and Amazon River had greater potential to disperse compared to populations of birds inhabiting the lower forest levels. Physical features can influence movements of species with high dispersal capability. For instance, several forest-dwelling birds (Awade & Metzger, 2008) and insects (yellow- faced bumblebee (*Bombus vosnesenskii*)) (Jha, 2015) showed decreased movement between areas with limited canopy cover and over anthropogenic features respectively. Environmental and ecological factors, such as, regional differences in the timing of precipitation and availability of vegetation promoted genetic divergence among giraffe population (Richard et al., 2013). Similarly, behaviors influencing mate selection, breeding location, and habitat preference also influence gene flow (Kobayashi et al., 2024; Ruegg et al., 2014). Breeding site fidelity, known as individuals returning to same breeding site every year, limits gene flow among colonies or breeding grounds. This behavioral tendency promotes genetic differentiation because mating occurs primarily among individuals within the same site, preserving distinct genetic composition (Liu et al., 2012). In both birds and fish, such behaviors have been linked to fine-scale population structure despite the absence of obvious geographic barrier (Greenwood, 1980; Greenwood &

Harvey, 1982; Knope et al., 2017; Lowther et al., 2012; Shitikov et al., 2012; Storfer et al., 2010).

Consequently, understanding the spatial genetic structure of a species provides insights on barriers that are limiting gene flow among populations, thus providing information on how populations are evolving (Manel et al., 2005; Ravinet et al., 2017; Smouse & Peakall, 1999).

1.1.3 Population structure

Population structure is the non-random distribution of genetic variation within and among populations, typically a consequence of genetic drift, selection, barriers to gene flow, and historical events (Allendorf et al., 2012; Coulon et al., 2006; Lowther et al., 2012; Slatkin, 1987). The relationship among abiotic and biotic factors, historical traits, habitat fragmentation, and behavioral tendencies of species influences the degree of population genetic structure. Studying this structure provides valuable insights into a species' demographic history, evolutionary dynamics, and conservation needs (Chen, 2015; Galindo et al., 2006; Slatkin, 1987).

Population genetic structure is often studied using statistical methods such as Bayesian clustering, principal component analysis (PCA), principal coordinate analysis (PCoA), and landscape genetic models including isolation by distance and isolation by resistance, which collectively enable researchers to detect patterns of genetic similarity, differentiation, and connectivity (Catchen et al., 2013). For example, Row et al., (2015) demonstrated strong genetic structure in greater sage-grouse (*Centrocercus urophasianus*) caused by natural barriers such as mountain ranges and unsuitable habitat. Isolation by resistance has also been documented in bird species; (Miller et al., 2018) showed that forest fragmentation reduced connectivity in the spotted owl (*Strix occidentalis*), illustrating the role of landscape features in shaping gene flow. Beyond spatial and environmental factors, behavioral traits such as site fidelity can also restrict genetic exchange (Barr et al. 2023), as seen in Galapagos Nazca booby (*Sula granti*) colonies due to natal philopatry (Levin & Parker, 2012).

In applied ecology and conservation, assessing population structure is essential for identifying management units, evaluating population resilience, and informing species recovery strategies (Palsbøll et al., 2007). For example, genetic analyses of marine mammals and seabirds have revealed cryptic population subdivisions undetectable through traditional ecological methods,

which carry important implications for conservation planning (Friesen et al., 2007; Hoelzel et al., 1998). Furthermore, understanding how landscape features, ecological traits, and human-induced changes influence gene flow helps predict population responses to habitat fragmentation, climate change, and exploitation pressures (Manel et al., 2003; Mimura et al., 2017).

1.2 Landscape genetics or seascape genetics

Understanding the patterns of gene flow within a landscape is important for evaluating and predicting vulnerability of organisms under rapid environmental change (Klinga et al., 2019; Sexton et al., 2014). Landscape genetics, an evolving interdisciplinary field that integrates approaches from population genetics and landscape ecology (Holderegger & Wagner, 2008), helps to determine the effect of landscape features on gene flow and genetic structure (Epps & Keyghobadi, 2015; Holderegger & Wagner, 2008; Manel & Holderegger, 2013). With advanced genetic techniques and use of high-resolution landscape data from Geographical Information System (GIS) technology allows researchers to address questions of gene flow, natural selection, behavior, and evolutionary history through integrative, landscape-informed approaches (Charlesworth & Charlesworth, 2017; Kozak et al., 2008; Manel & Holderegger, 2013; Storfer et al., 2010).

Seascape genetics uses similar theoretical and analytical approaches as landscape genetics (Riginos et al., 2016; Riginos & Liggins, 2013), the main difference is seascape genetics focus on aquatic landscapes, not terrestrial environments. Both landscape and seascape genetics utilize concepts from landscape ecology to assess the influence of habitat configuration and environmental variables on genetic connectivity and differentiation (Amaral et al., 2012; Galindo et al., 2006; Lal et al., 2017; Riginos et al., 2016; White et al., 2010). Resistance surfaces, generated by inverting species distribution models (SDM), can help identify how environmental variables habitat, and dispersal resistance influence connectivity and genetic differentiation among populations (Wilcox et al., 2023).

1.3 Genomic techniques

1.3.1 Next generation sequencing

Next generation sequencing (NGS) is a powerful tool used in genomics research which sequence millions of deoxyribose nucleic acid (DNA) fragments at once, providing detailed information about the structure of genomes, genetic variations, gene activity, and changes in gene behavior (Behjati & Tarpey, 2013; Satam et al., 2023). NGS includes various sequencing protocols, sequence large fragments of DNA molecules simultaneously (De Ronne et al., 2023; Satam et al., 2023). With the advance in sequencing technology, NGS facilities are expanding the scope and intensity of sequencing coverage through various sequencing methods (Lou et al., 2021).
As a cost-effective, high-throughput method for generating genome-wide SNP data across large sample sizes, GBS (genotype by sequencing) is now widely used in population genomics, making robust analyses of genetic diversity, structure, and evolutionary history possible (De Ronne et al., 2023; Lou et al., 2021). 3D-GBS, an improved version of GBS, uses three restriction enzymes (*PstI, NsiI,* and *MspI*) to target specific genomic regions for SNP (Single Nucleotide Polymorphism) discovery and genotyping (De Ronne et al., 2023).

1.3.2 Molecular markers

Molecular markers, which are DNA sequences, are common tools for studying population genetics (Al-Samarai & Al-Kazaz, 2015; Duran et al., 2009; Grover & Sharma, 2016). They are used to assess genetic diversity, evolutionary relationships, and demographic processes in natural populations (Duran et al., 2009). Their evolution progressed from early markers, like allozymes, to advanced genomic tools such as microsatellite and SNP, enhancing fine-scale resolution (Allendorf, 2017; Allendorf et al., 2012). Molecular markers help detect population structure and provide insights into gene flow (Ruegg et al., 2014; Zink & Barrowclough, 2008).
SNPs are single base-pair variations in DNA sequence. They have emerged as a powerful molecular marker because of their abundance across the genome, stability due to low mutation rates, and suitability for high-throughput genotyping (Elshire et al., 2011; Morin et al., 2004). SNPs are particularly valuable in population genetics, where they provide estimates of gene flow, relatedness, and population structure. In mammals, SNP discovery approaches have expanded

their use beyond model species, such as the identification of informative SNPs across loci derived from conserved genomic sequences (Morin et al., 2004), and the application SNPs in the gopher tortoise (*Gopherus polyphemus*) to accurately estimate population parameters with reduced SNP panel sizes (Elbers et al., 2017). Similarly, in the critically endangered swift parrot (*Lathamus discolor*), genome-wide SNP data produced consistent estimates of genetic diversity and low spatial structure, supporting their application in conservation management (Olah et al., 2024). The collective results of these studies illustrate SNPs' role as the molecular markers for modern population genetics offering insights into genetic structure, evolution, and conservation needs.

1.4 Study species

Globally, shorebirds are declining more rapidly than other avian groups (Rogers et al., 2025; Smith et al., 2023). Their reliance on a relatively small and widely scattered habitats such as intertidal mudflats, estuaries, wetlands and sandy beaches exposes shorebirds to a wide range of threats including habitat loss or degradation in the habitat, mortality from harvest, disease, pollution, climate-driven pressures such as sea-level rise and altered prey availability (Smith et al., 2023; Stroud et al., 2006). As a result, their populations are especially susceptible to decline. Furthermore, because shorebirds respond quickly to environmental changes across broad geographic ranges, they are widely considered sensitive indicators of global environmental change, reflecting the cumulative effects of habitat alteration, ecosystem health, and climate-driven shifts. (Piersma & Lindström, 2004; Smith et al., 2023).

The black oystercatcher (*Haematopus bachmani*) is a large and partially migratory shorebird with global population estimation of 8900-12,000 individuals scattered unevenly along the North American Pacific Ocean Coast from the Aleutian Islands in Alaska to Baja California, Mexico (Andres, 2020; Tessler et al., 2014). Approximately 80% of the global population of the species lives in north range of species in Alaska and British Columbia (Roodenrijs et al., 2024; Tessler et al., 2014). In Alaska, at least 50% of breeding birds go south for the nonbreeding season (Johnson et al., 2010; Rankin, 2023), whereas birds breeding in British Columbia, are thought to be almost entirely resident (Johnson et al., 2010; Ware et al., 2023). Favouring rocky shorelines in areas of high tidal variation, they forage exclusively on intertidal invertebrates such as limpets

and mussels (Tessler et al., 2014). It is a species of management interest because of its limited geographic range, small global population size, and reliance on intertidal habitat, which is experiencing ongoing threats related to human development and sea level rise (Meehan et al., 2018; Tessler et al., 2014).

In the absence of migration, populations can become reproductively isolated from each other and acquire allelic differences through mutation and genetic drift (Burney & Brumfield, 2009), which can ultimately lead to the divergence of populations and the eventual formation of distinct species over evolutionary time scales (Naciri & Linder, 2020). Examining partial migratory species (where some population migrate and others don't) allows us to validate comparative findings by connecting traits to migration over ecological periods (Boyle, 2008). Partial migration can impact a species' genetic structure and evolution by shaping patterns of gene flow and local adaptation. While mutation is the primary source of new genetic variation, gene flow distributes this variation among populations, contributing to overall genetic diversity and evolutionary change (Berthold, 1999; Boyle, 2008; Chapman et al., 2011).

Understanding the spatial genetic structure of a species provides information into what barriers are limiting gene flow among populations (Manel et al., 2005; Silva & Gardner, 2016; Smouse & Peakall, 1999). My research will determine the population genetic structure of black oystercatcher populations in North America by assessing patterns of genetic diversity and population differentiation along with identifying the potential barriers to gene flow.

1.5 Thesis objectives

The primary objective of this thesis is to investigate the population genetic structure and connectivity of black oystercatcher populations along the Pacific coast of North America. Specifically, this research aims to:

1. Assess the genetic diversity and differentiation among black oystercatcher populations across their breeding range.
2. Identify potential geographic, environmental, and ecological barriers to gene flow.

By integrating genomic analyses with ecological, spatial, and environmental data, this study will contribute to a broader understanding of population genetics in coastal bird species and inform

evidence-based conservation strategies for one of North America's most important intertidal shorebirds.

1.6 Thesis overview

This thesis is organized into three chapters. Chapter 1 provides a general introduction, general background on population genetics, gene flow, barriers to gene flow, population structure, landscape genetics, genomics techniques and outlining the ecological significance of the black oystercatcher, and the study objectives. Chapter 2 presents the data chapter, which addresses the objectives by assessing genetic diversity and differentiation (PCoA, F_{ST}), identifying geographic and ecological barriers to gene flow (isolation by distance, least-cost corridor analysis), and examining the influence of contemporary environmental gradients on genetic variation through redundancy analysis (RDA). Chapter 3 synthesizes these findings in a general discussion, highlighting their implications for population connectivity and conservation with directions for future research.

1.7 References

Al-Samarai, F. R., & Al-Kazaz, A. A. (2015). Molecular markers: an introduction and applications. *European Journal of Molecular Biotechnology*, *9*(3), 118-130.

Allendorf, F. W. (2017). Genetics and the conservation of natural populations: allozymes to genomes. *Molecular Ecology 26*(2), 420-430.

Allendorf, F. W., Luikart, G. H., & Aitken, S. N. (2012). Conservation and the genetics of populations. *John Wiley & Sons*.

Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Boutov, D., Freitas, L., Robertson, K. M., Sequeira, M., Stockin, K. A., Coelho, M. M., & Möller, L. M. (2012). Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (genus *Delphinus*). *PloS One*, *7*(2), e31482.

Andres, B. A. F., G.A. (2020). *Black Oystercatcher (Haematopus bachmani), version 1.0.*

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.

Bay, R. A., Harrigan, R. J., Underwood, V. L., Gibbs, H. L., Smith, T. B., & Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science*, *359*(6371), 83-86.

Behjati, S., & Tarpey, P. S. (2013). What is next generation sequencing? *Archives of Disease in Childhood-Education and Practice*, *98*(6), 236-238.

Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich*, *70*(1), 1-11.

Boyle, W. A. (2008). Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology*, *77*(6), 1122-1128.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., & Magin, G. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909-923.

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

Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: an analysis tool set for population genomics. *Molecular Ecology*, *22*(11), 3124-3140.

Chapman, B. B., Brönmark, C., Nilsson, J. Å., & Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos*, *120*(12), 1764-1775.

Charlesworth, B., & Charlesworth, D. (2017). Population genetics from 1966 to 2016. *Heredity*, *118*(1), 2-9.

Chen, H. (2015). Population genetic studies in the genomic sequencing era. *Zoological Research 36*(4), 223-232. https://doi.org/10.13918/j.issn.2095-8137.2015.4.223

Coulon, A., Guillot, G., Cosson, J. F., Angibault, J., Aulagnier, S., Cargnelutti, B., Galan, M., & Hewison, A. (2006). Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Molecular Ecology*, *15*(6), 1669-1679.

De Ronne, M., Légaré, G., Belzile, F., Boyle, B., & Torkamaneh, D. (2023). 3D-GBS: A universal genotyping-by-sequencing approach for genomic selection and other high-throughput low-cost applications in species with small to medium-sized genomes. *Plant Methods*, *19*(1), 13.

Duran, C., Appleby, N., Edwards, D., & Batley, J. (2009). Molecular genetic markers: discovery, applications, data storage and visualisation. *Current Bioinformatics*, *4*(1), 16-27.

Elbers, J. P., Clostio, R. W., & Taylor, S. S. (2017). Population genetic inferences using immune gene SNPs mirror patterns inferred by microsatellites. *Molecular Ecology Resources*, *17*(3), 481-491.

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PloS One*, *6*(5), e19379.

Epps, C. W., & Keyghobadi, N. (2015). Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. *Molecular Ecology*, *24*(24), 6021-6040.

Feder, J. L., Egan, S. P., & Nosil, P. (2012). The genomics of speciation-with-gene-flow. *Trends in Genetics*, *28*(7), 342-350.

Freeland, J. R. (2020). *Molecular Ecology*. John Wiley & Sons.

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

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.

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.

Grover, A., & Sharma, P. (2016). Development and use of molecular markers: past and present. *Critical Reviews in Biotechnology*, *36*(2), 290-302.

Hedrick, P. W. (2009). *Genetics of Populations*. Jones & Bartlett Publishers.

Hoelzel, A., Dahlheim, M., & Stern, S. (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.

Hohenlohe, P. A., Funk, W. C., & Rajora, O. P. (2021). Population genomics for wildlife conservation and management. *Molecular Ecology*, *30*(1), 62-82.

Holderegger, R., & Wagner, H. H. (2008). Landscape genetics. *Bioscience*, *58*(3), 199-207.

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

Johnson, M., Clarkson, P., Goldstein, M. I., Haig, S. M., Lanctot, R. B., Tessler, D. F., & Zwiefelhofer, D. (2010). Seasonal movements, winter range use, and migratory connectivity of the Black Oystercatcher. *The Condor*, *112*(4), 731-743.

Kardos, M. (2021). Conservation genetics. *Current Biology*, *31*(19), R1185-R1190.

Klinga, P., Mikoláš, M., Smolko, P., Tejkal, M., Höglund, J., & Paule, L. (2019). Considering landscape connectivity and gene flow in the Anthropocene using complementary landscape genetics and habitat modelling approaches. *Landscape Ecology*, *34*(3), 521-536.

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

Kobayashi, K. M., Bond, R. M., Reid, K., Garza, J. C., Kiernan, J. D., & Palkovacs, E. P. (2024). Genetic divergence and one-way gene flow influence contemporary evolution and ecology of a partially migratory fish. *Evolutionary Applications*, *17*(6), e13712.

Kozak, K. H., Graham, C. H., & Wiens, J. J. (2008). Integrating GIS-based environmental data into evolutionary biology. *Trends in Ecology & Evolution*, *23*(3), 141-148.

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.

Levin, I. I., & Parker, P. G. (2012). Philopatry drives genetic differentiation in an island archipelago: comparative population genetics of Galapagos Nazca boobies (*Sula granti*) and great frigatebirds (*Fregata minor*). *Ecology and Evolution*, *2*(11), 2775-2787.

Liu, Y., Keller, I., & Heckel, G. (2012). Breeding site fidelity and winter admixture in a long-distance migrant, the tufted duck (*Aythya fuligula*). *Heredity*, *109*(2), 108-116.

López-Goldar, X., & Agrawal, A. A. (2021). Ecological interactions, environmental gradients, and gene flow in local adaptation. *Trends in Plant Science*, *26*(8), 796-809.

Lou, R. N., Jacobs, A., Wilder, A. P., & Therkildsen, N. O. (2021). A beginner's guide to low-coverage whole genome sequencing for population genomics. *Molecular Ecology*, *30*(23), 5966-5993.

Lowther, A., Harcourt, R., Goldsworthy, S., & 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., Gaggiotti, O. E., & Waples, R. S. (2005). Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology & Evolution*, *20*(3), 136-142.

Manel, S., & Holderegger, R. (2013). Ten years of landscape genetics. *Trends in Ecology & Evolution*, *28*(10), 614-621.

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

Meehan, T. D., Harvey, A. L., Michel, N. L., Langham, G. M., & Weinstein, A. (2018). A population model exploring factors influencing black oystercatcher (*Haematopus bachmani*) population dynamics. *Waterbirds*, *41*(2), 115-221.

Miller, M. P., Davis, R. J., Forsman, E. D., Mullins, T. D., & Haig, S. M. (2018). Isolation by distance versus landscape resistance: Understanding dominant patterns of genetic

structure in northern spotted owls (*Strix occidentalis caurina*). *PloS One*, *13*(8), e0201720.

Mimura, M., Yahara, T., Faith, D. P., Vázquez-Domínguez, E., Colautti, R. I., Araki, H., Javadi, F., Núñez-Farfán, J., Mori, A. S., & Zhou, S. (2017). Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evolutionary Applications*, *10*(2), 121-139.

Morin, P. A., Luikart, G., Wayne, R. K., & Group, S. W. (2004). SNPs in ecology, evolution and conservation. *Trends in Ecology & Evolution*, *19*(4), 208-216.

Naciri, Y., & Linder, H. P. (2020). The genetics of evolutionary radiations. *Biological Reviews*, *95*(4), 1055-1072.

Olah, G., Waples, R. S., & Stojanovic, D. (2024). Influence of molecular marker type on estimating effective population size and other genetic parameters in a critically endangered parrot. *Ecology and Evolution*, *14*(3), e11102.

Palsbøll, P. J., Berube, M., & Allendorf, F. W. (2007). Identification of management units using population genetic data. *Trends in Ecology & Evolution*, *22*(1), 11-16.

Piersma, T., & Lindström, Å. (2004). Migrating shorebirds as integrative sentinels of global environmental change. *Ibis*, *146*, 61-69.

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.

Rankin, C. (2023). Migration strategies of black oystercatchers (*Haematopus bachmani*) breeding in the Gulf of Alaska. Simon Fraser University. Retrieved from https://summit.sfu.ca/item/36665.

Ravinet, M., Faria, R., Butlin, R., Galindo, J., Bierne, N., Rafajlović, M., Noor, M., Mehlig, B., & Westram, A. (2017). Interpreting the genomic landscape of speciation: a road map for finding barriers to gene flow. *Journal of Evolutionary Biology*, *30*(8), 1450-1477.

Razgour, O., Forester, B., Taggart, J. B., Bekaert, M., Juste, J., Ibáñez, C., Puechmaille, S. J., Novella-Fernandez, R., Alberdi, A., & Manel, S. (2019). Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proceedings of the National Academy of Sciences*, *116*(21), 10418-10423.

Richard, A., Dionne, M., Wang, J., & Bernatchez, L. (2013). Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar L.*)? *Molecular Ecology*, *22*(1), 187-200.

Rieseberg, L. H., & Burke, J. M. (2001). The biological reality of species: gene flow, selection, and collective evolution. *Taxon*, *50*(1), 47-67.

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., & Treml, E. A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. *Current Zoology*, *62*(6), 581-601.

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

Rogers, D. I., Piersma, T., Minton, C. D., Boyle, A. N., Hassell, C. J., Rogers, K. G., Silcocks, A., & Gutiérrez, J. S. (2025). Coastal shorebirds delay maturity more than inland ones. *Ecology and Evolution*, *15*(7), e71679.

Roodenrijs, H., Ware, L., Rankin, C., Maftei, M., Hipfner, J. M., Robinson, B. H., Esler, D., Coletti, H., & Green, D. J. (2024). Latitudinal gradients and sex differences in morphology of the black oystercatcher (*Haematopus bachmani*). *Ecology and Evolution*, *14*(9), e70115.

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

Row, J. R., Oyler-McCance, S. J., Fike, J. A., O'Donnell, M. S., Doherty, K. E., Aldridge, C. L., Bowen, Z. H., & Fedy, B. C. (2015). Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: A holistic modeling approach. *Ecology and Evolution*, *5*(10), 1955-1969.

Ruegg, K. C., Anderson, E. C., Paxton, K. L., Apkenas, V., Lao, S., Siegel, R. B., DeSante, D. F., Moore, F., & Smith, T. B. (2014). Mapping migration in a songbird using high-resolution genetic markers. *Molecular Ecology*, *23*(23), 5726-5739.

Satam, H., Joshi, K., Mangrolia, U., Waghoo, S., Zaidi, G., Rawool, S., Thakare, R., Banday, S., Mishra, A., & Das, G. (2023). Next-generation sequencing technology: current trends and advancements. *Biology, 12*(7), 997.

Sexton, J. P., Hangartner, S. B., & Hoffmann, A. A. (2014). Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution*, *68*(1), 1-15.

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.

Silva, C. N., & Gardner, J. P. (2016). Identifying environmental factors associated with the genetic structure of the New Zealand scallop: linking seascape genetics and ecophysiological tolerance. *ICES Journal of Marine Science*, *73*(7), 1925-1934.

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

Smith, A. C., Hudson, M.-A. R., Downes, C. M., & Francis, C. M. (2015). Change points in the population trends of aerial-insectivorous birds in North America: Synchronized in time across species and regions. *PloS One*, *10*(7), e0130768.

Smith, P., Smith, A., Andres, B., Francis, C., Harrington, B., Friis, C., Morrison, G., Paquet, J., Winn, B., & Brown, S. (2023). Accelerating declines of North America's shorebirds signal the need for urgent conservation action. *Ornithological Applications*, *125*(2), 1-14.

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

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.

Stroud, D. A., Baker, A., Blanco, D., Davidson, N. C., Delany, S., Ganter, B., Gill, R., González, P., Haanstra, L., & Morrison, R. (2006). The conservation and population status of the world's waders at the turn of the millennium. In *Waterbirds around the world: A global overview of the conservation, management and research of the world's waterbird flyways* (pp. 643-648). The Stationary Office.

Tessler, D. F., Johnson, J. A., Andres, B. A., Thomas, S., & Lanctot, R. B. (2014). A global assessment of the conservation status of the black oystercatcher *Haematopus bachmani*. *International Wader Studies*, *20*, 83-96.

Tigano, A., & Friesen, V. L. (2016). Genomics of local adaptation with gene flow. *Molecular Ecology*, *25*(10), 2144-2164.

Wang, J., Tang, L., Yu, X., Yu, C., Tang, X., Wang, D., Kong, F., Du, G., & Mao, Y. (2025). Gene flow enhances genetic diversity and local adaptation in *Pyropia yezoensis* populations. *Water Biology and Security*, 100411.

Ware, L., Hipfner, J. M., & Green, D. J. (2023). Satellite telemetry reveals habitat selection decisions by black oystercatchers across seasonal, diel, and tidal cycles. *Ecology and Evolution*, *13*(4), e9957.

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 of the Royal Society B: Biological Sciences*, *277*(1688), 1685-1694.

Wilcox, M. A., Jeffery, N. W., DiBacco, C., Bradbury, I. R., Lowen, B., Wang, Z., Beiko, R. G., & Stanley, R. R. (2023). Integrating seascape resistances and gene flow to produce area-based metrics of functional connectivity for marine conservation planning. *Landscape Ecology*, *38*(9), 2189-2205.

Woodruff, D. S. (2004). Populations, species, and conservation genetics. In *Encyclopedia of Biodiversity* (pp. 811).

Zink, R. M., & Barrowclough, G. F. (2008). Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology*, *17*(9), 2107-2121.

Chapter 2: Unravelling population genetic structure of black oystercatcher (*Haematopus bachmani*) in North America

Abstract

Studying population genetic structure enables us to evaluate genetic variation, gene flow, and population differentiation. It also helps us better understand evolution and develop conservation strategies. The black oystercatcher (*Haematopus bachmani*) is a resident bird, with partial migratory behavior, found in the North Pacific Coast, yet knowledge of its wintering grounds, migration routes, and connectivity remains limited. This study explores the genetic diversity and population structure of black oystercatcher across their breeding range in North America using genomic sequencing. Bayesian clustering and principal coordinates analyses were used to identify patterns of differentiation in 107 samples from Alaska, British Columbia, and the Pacific Northwest. Population structure and differentiation analyses with PCoA and pairwise F_{ST} indicated moderate to high connectivity and gene flow among most sampled populations, with some subtle north-south structuring. The moderate isolation-by-distance further supports this pattern, implying that gene flow decreases with increasing geographical distance. The least cost corridor analyses provided complementary spatial context, by identifying pathways as corridors for dispersal and highlighting potential isolation among distant island populations. Furthermore, the redundancy analysis supported isolation by distance and weak association between genetic variation and environmental variables such as temperature and topography driving the differentiation. However, environmental effects explained only a small fraction of total genetic variance, suggesting that processes such as isolation-by-distance and strong breeding site fidelity play more substantial roles in shaping genetic patterns.

2.1 Introduction

Population genetic techniques are crucial tools in understanding how ecological and evolutionary processes determine the genetic structure of natural populations. Population structure is a result

of evolutionary processes including mutation, genetic drift, natural selection, and gene flow (Burke, 2001; Slatkin, 1987; Tigano & Friesen, 2016). Among these forces, gene flow, the exchange of alleles among populations through dispersal, plays an important role in maintaining connectivity and preventing divergence for many species (Slatkin, 1987). Limited gene flow allows genetic drift and selection to act leading to genetic differentiation and, eventually, speciation (Feder et al., 2012; Ravinet et al., 2017). Knowledge of how the gene flow varies across the landscape and identifying the environmental and behavioral factors that regulate it are therefore key to understanding evolutionary dynamics and their implications (Barr et al., 2023; Kobayashi et al., 2024; López-Goldar & Agrawal, 2021).

Natural landscapes are spatially heterogeneous, and dispersal is typically uneven as a result. Landscape genetics combines population genetics with spatial data to understand how the environment affects gene flow and genetic structure (Epps & Keyghobadi, 2015; Manel et al., 2003). By modeling movement based on environmental resistance, landscape genetics approaches allow researchers to test theories on connectivity and find the mechanisms creating genetic patterns (McRae, 2006). Advances in genomic sequencing have further increased resolution of such research, allowing genome-wide assessments of population differentiation and connectivity across complex aquatic and terrestrial systems (Storfer et al., 2010; Wilcox et al., 2023). In many avian species, using these genomic approaches showed that highly mobile species often exhibit genetic structuring driven by behavioral, environmental, and landscape features (Friesen et al., 2007; Holderegger & Wagner, 2008). Landscape genomic approaches have highlighted how geographic barriers, habitat fragmentation, and climate gradients shape connectivity and adaptive potential for terrestrial species (Bay et al., 2018; Klinga et al., 2019; Row et al., 2015; Storfer et al., 2010) and that gene flow not only relies on dispersal but behavioral ecology and landscape features, which could be an important aspect in modern landscape and seascape genetics.

Within this broader framework, population genetics of shorebirds can be used to study how dispersal, behavior and landscape configuration lead to gene flow and connectivity. Shorebirds have different migratory strategies (Piersma, 2007; Piersma & Lindström, 2004) ranging from fully migratory species to partially migratory populations where only a small portion of individuals migrate, to resident species that remain in the same area year-round (Conklin et al., 2017; Piersma, 1988). Migratory behavior can influence genetic structure and connectivity. For

example, bar-tailed godwit (*Limosa lapponica*) and red knot (*Calidris canutus*) revealed weak genetic differentiation at a continental scale due to high connectivity along major flyways (Conklin et al., 2022; Conklin et al., 2024) whereas, Southern dunlin (*Calidris alpina schinzii*) exhibits population structure among breeding populations in the fragmented Baltic coastline as a result of reduced dispersal and strong site fidelity (Rönkä et al., 2021). Partial migratory behavior can induce differences between migratory and resident populations resulting in asymmetric gene flow (Barr et al., 2023) where migratory individuals link the populations while resident individuals promote differentiation; this pattern has been increasingly detected using the genomic approaches (Rönkä et al., 2021). Moreover, seascape features such as oceanic currents, velocity, intertidal habitat continuity and anthropogenic development can act as either corridors or barriers to movement, thereby shaping patterns of gene flow (Amaral et al., 2012; Riginos & Liggins, 2013; Silva & Gardner, 2016; Wilcox et al., 2023). Studies integrating seascape genetics with population genetic data are important to study the factors shaping population genetic structure.

The black oystercatcher (*Haematopus bachmani*) is an intertidal shorebird found along the Pacific Coast of North America, from the Aleutian Islands in Alaska to Baja California, Mexico (Andres, 2020; Tessler et al., 2014, Figure 1). Globally, it plays a critical ecological role in the rocky intertidal ecosystem as it depends exclusively on the rocky shoreline and intertidal zones for both nesting and foraging (Tessler et al., 2014) making it an indicator species of the overall health of the rocky intertidal environment (Carlson-Bremer et al., 2010; Tessler et al., 2014) and its decline can reflect broader ecological disruptions in intertidal ecosystems (Johnson et al., 2010; Rankin, 2023; Tessler et al., 2014). Although often considered largely sedentary, populations in Alaska and northern British Columbia exhibit partial migratory behavior, with some individuals overwintering near breeding sites while others disperse to more southerly latitudes (Andres, 2020; Tessler et al., 2014). The absence of genetic data constrains our understanding on how coastal landscape features, geographic distance, and migratory strategies shape gene flow in this species.

This study aims to elucidate the population genetic structure and connectivity of the black oystercatcher across its North American range by using reduced-representation genomic data (3D-GBS) to identify population structure, quantify levels of genetic differentiation, and test for isolation by distance and isolation by resistance. The study aims to answer (i) How do black

oystercatcher populations differ genetically across their distribution? and (ii) How do environmental variables and behavioral drivers shape the dispersal of black oystercatcher on the North Pacific Coast?

2.2 Methods

2.2.1 Sample collection and DNA extraction

I received tissue and eggshell samples from 107 individuals in collaboration with Environment and Climate Change Canada, Laskeek Bay Conservation Society, United States Fisheries and Wildlife Services representing, nine locations across North America (Figure 1, Table 1). I extracted DNA from eggshell membranes and feather samples using the DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia, CA, USA) and followed the manufacturer's protocol, with minor modifications to optimize yield from low-quality substrates. I rinsed eggshells with 70% ethanol to remove surface contaminants, carefully separated the membranes from the calcified shell and took approximately 20–30 mg of egg membrane in sterile 1.5 mL microcentrifuge tubes. For feathers, I trimmed the calamus (shaft) to ~5 mm in length, ensuring to include the basal portion that contains the highest concentration of nucleated cells.

I incubated samples overnight at 56 °C in 180 µL of ATL buffer with 0.4/mg of Proteinase K, 0.03/mg of RNase to achieve complete lysis. After the digestion of samples, I added 200 µL of AL buffer and 200 µL of 100% ethanol to each sample and transferred to DNeasy spin columns. I washed the columns sequentially with AW1 and AW2 buffers according to the manufacturer's instructions and eluted DNA in 60 µL of AE buffer and stored the extracted DNA at –20 °C. I measured the concentration of DNA using Qubit 4 Fluorometer (Thermo Fisher Scientific, USA) with the Qubit dsDNA High Sensitivity Assay Kit (Thermo Fisher Scientific, USA) because it provides highly sensitive and accurate quantification of double-stranded DNA, which is particularly important for the low-yield extractions obtained from eggshell membranes and feathers.

2.2.2 Sequencing

I used 3D-GBS, a modified version of Genotype by Sequencing (GBS), to sequence the DNA (De Ronne et al., 2023). The extracted DNA samples were digested using the restriction enzymes *MspI*, *NsiI* and *PstI* following De Ronne et al., (2023) to target specific genomic regions for SNP (Single Nucleotide Polymorphism) for genotyping. The library preparation for the samples was carried out at Laval University and sent to Génome Quebec for sequencing on Illumina NovaSeq 6000 S4 PE100 with paired end sequencing.

2.2.3 Data processing and filtering

After receiving the sequencing data from Génome Québec, I generated quality checks on the sequenced file using FastQC/0.11.5 to identify sequencing errors and remove low-quality sequencing reads with Phred score <30 (MacManes, 2014). To track individual samples, I demultiplexed the raw reads (individual DNA sequences) based on their unique barcodes (Cammen et al., 2016) using Sabre/1.00 with 'sabre pe' option. Following that I used Cutadapt 1.16 software to remove adapters and trimmed the sequences to same length of 80 bp and removed sequence with a Phred score < 30 to ensure high-quality reads for accurate alignment and downstream analyses (Bolger et al., 2014). I assembled all sequences with *de novo* alignment using the denovo_map.pl pipeline with minimum depth of coverage as 3 (m = 3), and minor allele frequency as 0.05 (maf = 0.05) threshold in Stacks/2.3e (Catchen et al., 2013). I then sorted and indexed the resulted binary alignment map (bam) files using the Samtools/0.1.2 (Li et al., 2009) and generated the output in variant call format (vcf). Finally, I filtered the vcf files to remove SNPs with more than 30% missing data and individuals with more than 70% missingness prior to downstream analyses, using VCFtools/0.1.16 (Danecek et al., 2011). This filtering retained 12,182 SNPs and 76 individuals for further analyses.

2.2.4 Neutral markers

Neutral markers are genetic loci that are not directly influenced by natural selection. They are widely used in population genetics to study genetic diversity, population structure, and historical

demography because they provide an unbiased view of genetic variation (Luna et al., 2023, Veale et al., 2024). An additional dataset was produced from original dataset using loci that were not under either directional or balancing or adaptive selection. To find putatively neutral loci, I used Bayescan v2.1 (Foll & Gaggiotti, 2008) to verify neutral loci from 12,182 SNPs and ran 100,000 iterations (-n 100,000) with a thinning interval of 10 (-thin 10) and 20 pilot runs (-nbp 20) at a length of 5000 (-pilot 5000) and a burn-in value of 50,000 (-burn 50,000) and prior to the neutral model (-pr_odds) set to 700. I determined 6512 putatively neutral loci based on loq q-value threshold of > 0.0001, while the other 5670 were under adaptive selection.

2.2.5 Population level analysis

To identify the population genetic structure, I performed Principal Coordinate Analysis (PCoA) with three datasets: all SNPs, putatively neutral loci and adaptive loci. Using the adegenet package in R studio (Jombart, 2008; Jombart et al., 2018), I calculated pairwise genetic distances among all individuals derived from the respective SNP genotype datasets. These distance matrices measure the overall genetic dissimilarity between individuals, where smaller distances indicate lower genetic differences and larger distances represent higher genetic differences. From the resulting genetic distance matrices, I generated and visualized the respective PCoA plot for each dataset in Excel using GenAlEx v6.5 (Peakall & Smouse, 2006).

2.2.6 Population differentiation and isolation by distance

I calculated pairwise F_{ST} values (Weir & Cockerham, 1984; Wright, 1965) and associated 95% confidence intervals using the R package dartR 2.9.9.5 (Gruber et al., 2019) to assess the magnitude of genetic divergence between sampling locations. I used only the sampling locations with at least four samples for F_{ST} calculations and excluded samples from non-breeding birds from the analyses. I generated confidence intervals and *P*-values by performing 999 bootstraps and calculated summary statistics including diversity values (observed heterozygosity, expected heterozygosity) with dartR in Rstudio (Gruber et al., 2019; Mijangos et al., 2022).

Isolation by distance (IBD) analyses help in understanding how spatial distances influence genetic structure in populations and help to address key objectives to understand population structure, gene flow, and barriers to genetic connectivity. I performed a Mantel test using genetic and geographic distances to quantify and assess isolation by distance (IBD; Wright, 1965). Pairwise F_{ST} estimates served as quantitative measures of genetic distances between sampling locations, while I generated pairwise least cost paths (shortest distance through more suitable habitats) between sampling locations in ArcGIS Pro (Esri, Redlands, CA, USA) using a cost surface raster (friction layer). Finally, I calculated the Spearman correlation between genetic and geographic distances using the *mantel* function in the vegan 2.6-10 package in R (Oksanen et al., 2007).

2.2.7 Seascape genetics

Both landscape and seascape genetics utilize concepts from landscape ecology to assess the influence of habitat configuration and environmental variables on genetic connectivity and differentiation (Riginos et al., 2016). The habitat-based resistance surfaces are utilized to understand patterns of gene flow and dispersal through least-cost path and corridor modelling (Adriaensen et al., 2003). By integrating seascape genetic methods, resistance surface modeling and species distribution models (SDMs), I identified how environmental variables, habitat suitability, and dispersal resistance influence patterns of genetic connectivity and differentiation (Wilcox et al., 2023). First, I generated a SDM (Appendix 1) by combining environmental variables from Bio-ORACLE v3.0, including bathymetry, chlorophyll, phosphate concentration, current velocity, salinity, pH, sea temperature, topographic ruggedness index, and slope (Assis et al., 2024, Appendix 2) and occurrence data of black oystercatcher from Global Biodiversity Information Facility (GBIF). I then filtered the occurrence data to remove records that were not reviewed or moderated and restricted it to the breeding season (May to June) to identify areas of suitable habitat and map the current distribution. To reduce spatial bias and help improve the predictability of SDM (Beck et al., 2014; Boria et al., 2014), I rarified the total 302,902 occurrence points using SDM toolbox (Brown et al., 2017) with 10-kilometer buffer, which resulted in total of 1031 rarified occurrence points. Following this, I calculated Pearson's correlation between environmental variables using SDM toolbox and removed variables with

correlation coefficient greater than 0.7 ($r > 0.7$) to reduce unstable predictions (Dormann et al., 2013). The variables retained after correlation mean bathymetry, chlorophyll, phosphate concentration, current velocity, mean salinity, mean pH, mean sea temperature, mean salinity (Appendix 3). After getting rarified occurrence points and non-correlated environmental variables, I developed a SDM of black oystercatcher using Maxent v3.4.1 software (Phillips et al., 2006; Phillips & Dudík, 2008) and evaluated the model's predictive performance by examining the area under the curve (AUC) value for the receiver operating characteristic (ROC) score. AUC value for the model was 0.987, indicating higher model performance.
By inverting the SDM, I created a resistance layer using the friction layer function in the SDM toolbox. Resistance surfaces are geographical data layers that offer a numerical assessment of how environmental conditions (e.g., oceanic variables) affect the movement of an organism through the landscape (Spear et al., 2015). I then used the least-cost corridors (LCC) and paths function with the default parameters in the SDM toolbox (Brown et al., 2017) to create a map depicting areas of high and low dispersal resistance.

2.2.8 Redundancy Analysis (RDA)

I performed partial (RDA) using neutral loci generated from Bayescan v 2.1 (Foll & Gaggiotti, 2008) to investigate how environmental variables and geographical variables affect the genetic variation across populations. Focusing on neutral markers helps to understand how genetic variation responds to the environmental selective pressures while accounting for underlying population structure. I first converted dataset into an allele frequency matrix using the adegenet package (Jombart, 2008; Jombart et al., 2018) in R (R Core Team 2021), which allowed me to summarize multi-locus genetic variation in a format suitable for multivariate analysis. Regarding the environmental variables, I chose topographic slope, terrain ruggedness index, sea surface temperature, mean bathymetry, mean current velocity, mean chlorophyll concentration and mean salinity because they represent key physical and oceanographic factors that are likely to influence the distribution, foraging behavior and survival of species (Andres, 2020; Meehan et al., 2018). Spatial coordinates (latitude and longitude) were also incorporated as spatial predictors to account for the geographical structure. Prior to running RDA, I calculated Pearson correlations among environmental variables and removed variables with correlation coefficient

greater than 0.7 (r > 0.7) (mean salinity and terrain ruggedness index). Finally, I ran RDA using rda() function in vegan package in R with scaled genotypes as the response matrix and environmental predictors as explanatory variables and visualized with ggplot2 and ggrepel packages in R (Wickham, 2011; Wickham et al., 2016). Furthermore, I calculated the total percent contribution of each variable in the model, with the vegan package (Appendix 4).

2.3 Results

2.3.1 Preprocessing of the data

After checking the mapping rate and filtering with VCFtools, I was able to retain 76 individuals from eight populations (Table 1) and 12,182 SNPs for all SNPs dataset with mean coverage of 25.3x (1.45x – 126.3x). Bayescan analysis for putatively neutral and adaptive loci retained a total of 6512 SNPs for the neutral dataset and 5670 SNPs for the adaptive or under balancing selection dataset.

2.3.2 Population genetic structure

The Principal Coordinates Analysis (PCoA) based on all SNPs (Figure 2) revealed no population structure across sampling sites. The first two axes explained low proportions of the total genetic variation (PCo1 = 5.93%, PCo2 = 5.39%) and individuals from all populations were broadly overlapping. Given the absence of structure while using all loci, I then generated a second PCoA using only neutral SNPs markers (Figure 3). The first two axes of this analysis explained 6.08% and 5.55% of the variation, respectively, indicating weak genetic structure. The individuals from northern populations (Aiktak, Chowiet, and St. Lazaria) clustered together whereas the southern populations (Lucy, VAN, TRI, ECVI and WCVI) formed a separate group. The Haida Gwaii individuals overlapped with individuals from northern and southern populations.
Based on neutral SNPs, F_{ST} estimates revealed low to moderate genetic differentiation (Figure 4). F_{ST} values ranged from 0.000 to 0.490. The highest differentiation was observed between Triangle Island (TRI) and the northern populations, namely TRI and Aiktak_Chowiet (F_{ST} =

0.490) and TRI and St. Lazaria (F_{ST} = 0.371), both statistically significant ($p < 0.001$). TRI and Haida Gwaii showed moderate level of differentiation (F_{ST} = 0.091, $p < 0.05$) while the comparisons among Haida Gwaii, ECVI and WCVI showed very low F_{ST} values (0.000-0.011). The observed heterozygosity (H_o) ranged from 0.064 to 0.190 while expected heterozygosity (H_e) ranged from 0.130 to 0.406. (Table 1).

2.3.3 Isolation by distance

Isolation by distance analysis revealed a moderately positive correlation between genetic differentiation and geographic distances (Mantel r = 0.483, p = 0.0417) (Figure 5), indicating evidence of isolation by distance (IBD) across the study area. As Haida Gwaii population showed overlap with all population. I performed an IBD analysis without Haida Gwaii population which resulted in r = 0.534, p = 0.117. This did not suggest that Haida Gwaii population was driving the pattern.

2.3.4 Seascape genetics

The least cost corridor model revealed possible dispersal routes and connectivity for the species throughout the coastal habitat in Alaska and British Columbia (Figure 6). The model showed a continuous corridor along the larger parts of North Pacific coastline suggesting the coastal habitat may facilitate the movement among sampling populations. High-dispersal corridors are concentrated along the southern Alaska Coast, the Alexander Archipelago, and the British Columbia coastline, extending down to Vancouver Island.

2.3.5 Redundancy analysis (RDA)

Redundancy analysis revealed weak associations between genetic differentiation and environmental variables across the sampling populations (Figures 7a and 7b). The first four axes of RDA explained 6.3% of the genetic variance (RDA1 = 1.8%, RDA2 = 1.7%, RDA3 = 1.4%, RDA4 = 1.4%).

In RDA1 vs. RDA2 (Figure 7a), most individuals exhibited a broad overlap, indicating weak environmental influence on genetic variation. Individuals from TRI, VAN, WCVI, ECVI, and most of Haida Gwaii cluster around the origin. A total variation of 3.5% was observed, and populations of Aiktak_Chowiet, WCVI, ECVI, and VAN in the negative region of RDA1 showed a correlation with mean chlorophyll concentration (chlorophyll_mean). In contrast, the population of St. Lazaria is in the positive region of RDA2, exhibiting a strong correlation with latitude.

The ordination of RDA3 and RDA4 (Figure 7b) explained an additional 2.8% of the variance. The populations of TRI and WCVI individuals appear in the positive region of RDA3, with a positive correlation with longitude and mean sea surface temperature (temperature_mean). Aiktak_Chowiet and St. Lazaria fall along the positive portion of RDA4, with a positive correlation with latitude. The spatial variable, latitude, points toward the positive region of RDA4, showing a weak north-south structuring. Overall, the RDA percentage of contribution (Appendix 4) for each variable in the RDA model revealed that latitude showed the highest contribution, showing a weak association between genetic variation among populations and environmental variables.

2.4 Discussion

This integrative study using genetic and spatial analyses revealed weak, geographically structured genetic differentiation among the black oystercatcher populations across the northeast Pacific Ocean. Analysis of the population differentiation using neutral loci (PCoA, pairwise F_{ST}, isolation by distance, least cost corridor modelling and redundancy analysis) showed subtle geographic structuring maintained by the species' philopatric behavior and connectivity.

2.4.1 Geographic patterns of genetic differentiation among black oystercatcher populations

Neutral genetic markers showed subtle genetic differentiation between northern (Aiktak_Chowiet and St. Lazaria) and southern populations (Triangle Island, Vancouver Island, and Vancouver) with moderate to low levels of genetic diversity and heterozygote deficit in black

oystercatcher along the North Pacific Coast. Strong breeding site philopatry and limited natal dispersal in black oystercatchers (Hazlitt & Butler, 2001) likely contribute to genetic differentiation among geographically distant populations due to restricted gene flow. In contrast, the species' partial migratory behavior facilitates some gene flow between nearby populations, mitigating genetic divergence among nearby populations (Johnson et al., 2010; Rankin, 2023). Similar patterns of weak and geographically structured genetic differentiation have been recorded in other oystercatcher species including the Eurasian oystercatcher (*Haematopus ostralegus*) and the American oystercatcher (*H. palliatus*), where spatial genetic patterns were characterized by connectivity across continuous habitats and regional genetic differentiation was driven by dispersal limitation and habitat discontinuities (Avila-Cárdenas et al., 2025; van de Pol et al., 2014; Van Treuren et al., 1999). Similarly, different seabirds including Tufted puffins (*Fratercula cirrhata*), Galapagos petrel (*Pterodroma phaeopugia*), Galapagos Nazca booby (*Sula granti*) and Xantus's murrelet (*Synthliboramphus hypoleucus*) exhibited fine-scale genetic structuring throughout their breeding ranges, where gene flow between colonies was limited by distance, philopatric behavior, and oceanographic barriers (Graham et al., 2023; Friesen et al., 2007; Levin & Parker, 2012). Structuring of northern and southern populations of black oystercatcher is further demonstrated by the F_{ST} differences between northern and southern populations, mainly with populations of Aiktak_Chowiet and St. Lazaria with Triangle Island and west coast of Vancouver Island. Higher genetic differentiation of Triangle Island compared to other populations can be linked with the behavior of the species and Hipfner et al., (2012) suggested that black oystercatchers breeding on Triangle Island stay on the island through the breeding and non-breeding season without migrating, which may restrict gene flow with other populations, resulting in higher genetic differentiation values.

Haida Gwaii black oystercatchers overlapped with both groups, indicating that it may facilitate gene flow. This pattern is similar to Rönkä et al., (2021) where central populations of southern dunlin (*Calidris alpina schinzii)* acted as a genetic bridge between northern and southern lineages. Furthermore, studies on Atlantic puffins (*Fratercula arctica*) (Kersten et al., 2021), and dolly varden trout *(Salvelinus malma)* (Redenbach & Taylor, 2002) have also shown similar patterns, suggesting that geographically central habitats help to maintain population connectivity. Such transition zones are characteristic of species whose dispersal is limited by geographical

features but sustained by habitat continuity (Friesen et al., 2007; Piersma, 2007; Ware et al., 2023).

2.4.2 Coastal connectivity and isolation along the North Pacific Coast

Least cost corridors analysis showed a connected habitat of black oystercatcher throughout the North Pacific Coast, however, the habitat permeability between northern populations is limited compared to connectivity among southern populations of black oystercatcher. The observed spatial pattern of habitat connectivity highlighted the strong influence of the species' habitat configuration on the dispersal potential. The predicted dispersal corridors closely followed nearshore environments, reflecting the species' dependence on the intertidal zones for nesting and foraging (Johnson et al., 2010; Roodenrijs et al., 2024). The preference for nearshore corridors, avoiding the wide oceanic expanses, is consistent with the movement ecology recorded in several seabirds and shore dependent species (Abecassis et al., 2013; Foley et al., 2025; Friesen et al., 2007; Warwick-Evans et al., 2016), including sea otters (*Enhydra lutris kenyoni*) and some terrestrial species with habitat-specific movements (McRae, 2006). These movement patterns highlighted the importance of habitat continuity in maintaining genetic exchange between populations. For instance, the continuous rocky coastlines facilitated dispersal in marine invertebrates and shorebirds, whereas large open-water gaps acted as barriers producing north-south genetic differentiation (Bustillo-de la Rosa et al., 2024; McRae & Beier, 2007). These findings reinforce the idea that gene flow is often mediated by landscape permeability rather than by simple geographic distance.

Despite the continuous habitat permeability, I detected genetic structure between northern and southern black oystercatcher populations corresponding geographical distance, limited dispersal ability and high breeding site fidelity (Andres, 2020; Johnson et al., 2010). An increase in genetic differentiation with geographical distance or isolation by distance is a commonly observed pattern among philopatric birds (Friesen et al., 2007; Milot et al., 2008). Similar patterns of genetic differentiation corresponding to restricted movements of species and isolation by distance were seen in other birds including northern fulmars (*Fulmarus glacialis*) (Burg et al., 2003) and Atlantic puffins *(Fratercula arctica*) (Kersten et al., 2021) and mammals including sea

lions (*Neophoca cinerea*) (Ahonen et al., 2016) and short-beaked common dolphins (*Delphinus delphis*) (Amaral et al., 2012).

2.4.4 Environmental and behavioral factors influencing gene flow

My study revealed weak associations between genetic differentiation and environmental gradients in black oystercatchers. This indicates that processes such as geographic isolation and limited dispersal show genetic differentiation, environmental variation contribute modestly to spatial genetic structure among black oystercatchers. Slope, bathymetry, temperature, chlorophyll concentration, and current velocity were associated with axes of RDA, suggesting local coastal topography and oceanographic conditions might subtly influence connectivity patterns.

These weak environmental effects align with the black oystercatchers' strong breeding site fidelity and limited dispersal (Andres, 2020; Tessler et al., 2014), which reduce gene flow and constrain local adaptation despite environmental heterogeneity. Similar patterns have been reported in other coastal birds with restricted dispersal, such as American oystercatcher (*Haematopus palliatus*), where isolation-by-distance explains most of the genetic variation across the Atlantic Coast (Avila-Cárdenas et al., 2025). Likewise, the common eider (*Somateria mollissima*) shows strong philopatry and genetic differentiation primarily driven by geographic distance rather than environmental gradients (Sonsthagen, 2006). Collectively, these results suggest that black oystercatcher population structure along the North Pacific Coast arises primarily from limited dispersal, geographic isolation and site fidelity, with weak effects of environmental variables.

2.5 Conclusions

The study provides a comprehensive assessment of population genetic structure and connectivity in black oystercatcher (*Haematopus bachmani*) across its range. The integration of genomic, spatial and environmental data revealed weak but geographically structured genetic differentiation. The population structure and differentiation analyses with PCoA and pairwise F_{ST}

indicated moderate to high connectivity among most sampled populations, yet subtle north-south structuring suggesting that dispersal and geographical distance are the main factors shaping regional differentiation. The moderate isolation by distance further supports this pattern, implying that gene flow decreases with increasing geographical distance. The least-cost corridor analyses provided complementary spatial context, by identifying pathways as corridors for dispersal and highlighting potential isolation among distant fragmented island populations. Furthermore, the redundancy analysis revealed weak associations with environmental factors and supports the pattern created by isolation by distance.

Together, these results depict the species maintaining genetic connectivity through a combination of habitat continuity, while fidelity to the breeding site fosters genetic structure. The presence of the Haida Gwaii region as an intermediate genetic and geographical node highlights its crucial role in maintaining gene flow between northern and southern populations. From a conservation perspective, the overall result underscores the importance of preserving continuous and undisturbed coastal habitats that sustain dispersal and gene flow. Given the species' high-site fidelity and sensitivity to human disturbance, maintaining connectivity between breeding and non-breeding regions will be critical for long-term stability.

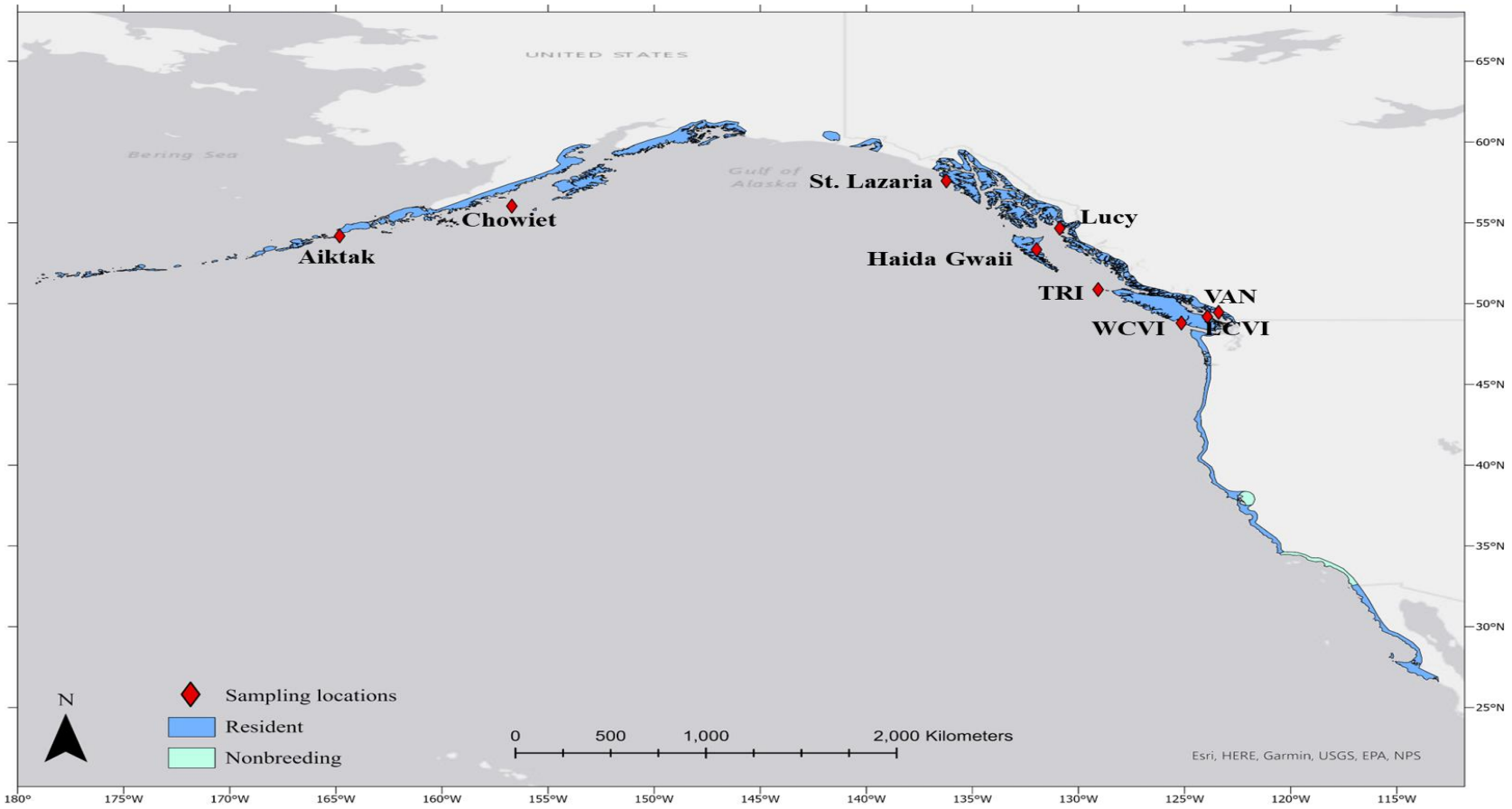


Figure 1: Range map of black oystercatcher with sampling locations (red diamond), the blue color indicates the breeding range of the species and the green color indicates the nonbreeding range of the species at the southern end of its range. For the abbreviations of sampling locations refer to Table 1.

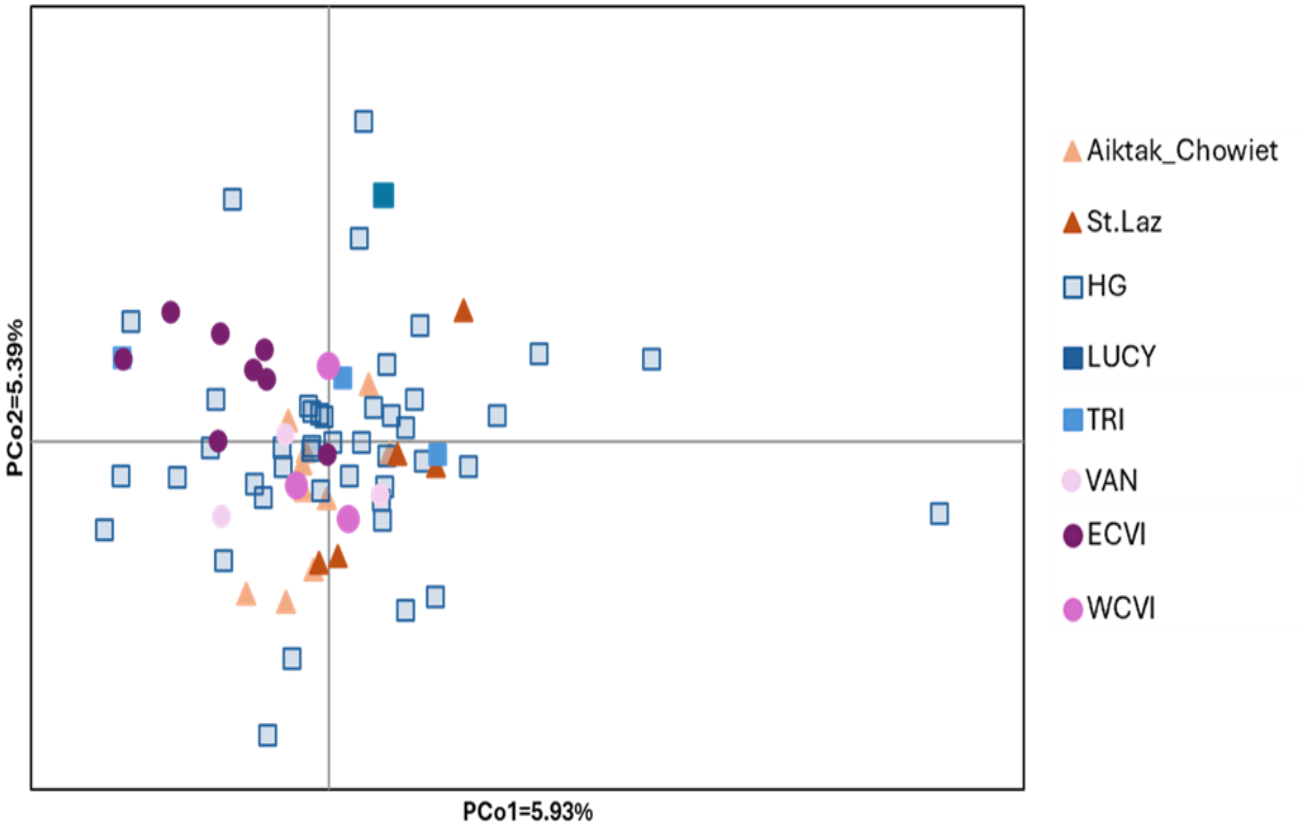


Figure 2: Principal coordinate analysis of all 12,182 SNPs with 76 individuals. For abbreviations of sampling locations refer to Table 1.

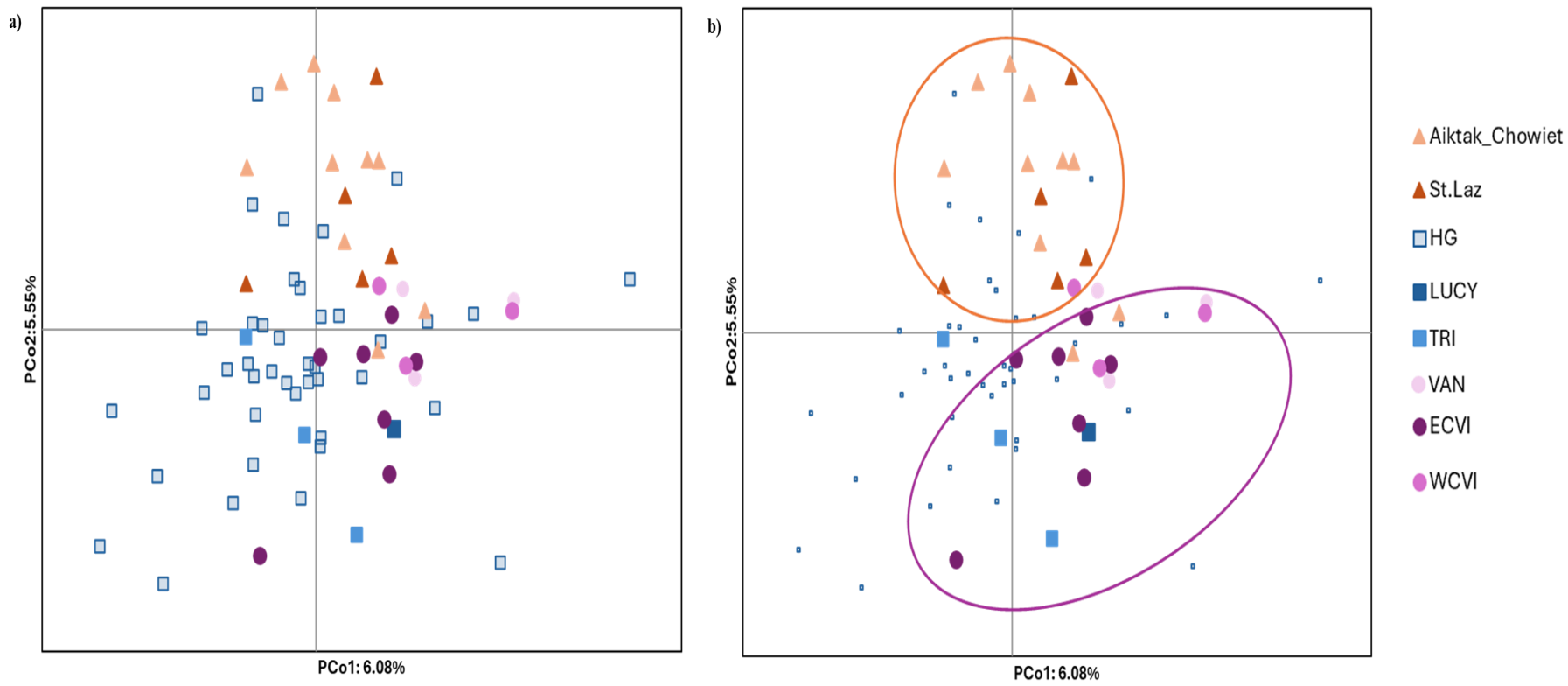


Figure 3: a) Principal coordinate analysis of 6512 putatively neutral loci, b) is the same figure with the points for HG individuals reduced, the large orange circle groups individuals from northern population, and pink circle groups individuals from the southern populations. Abbreviations for sampling locations are in Table 1.

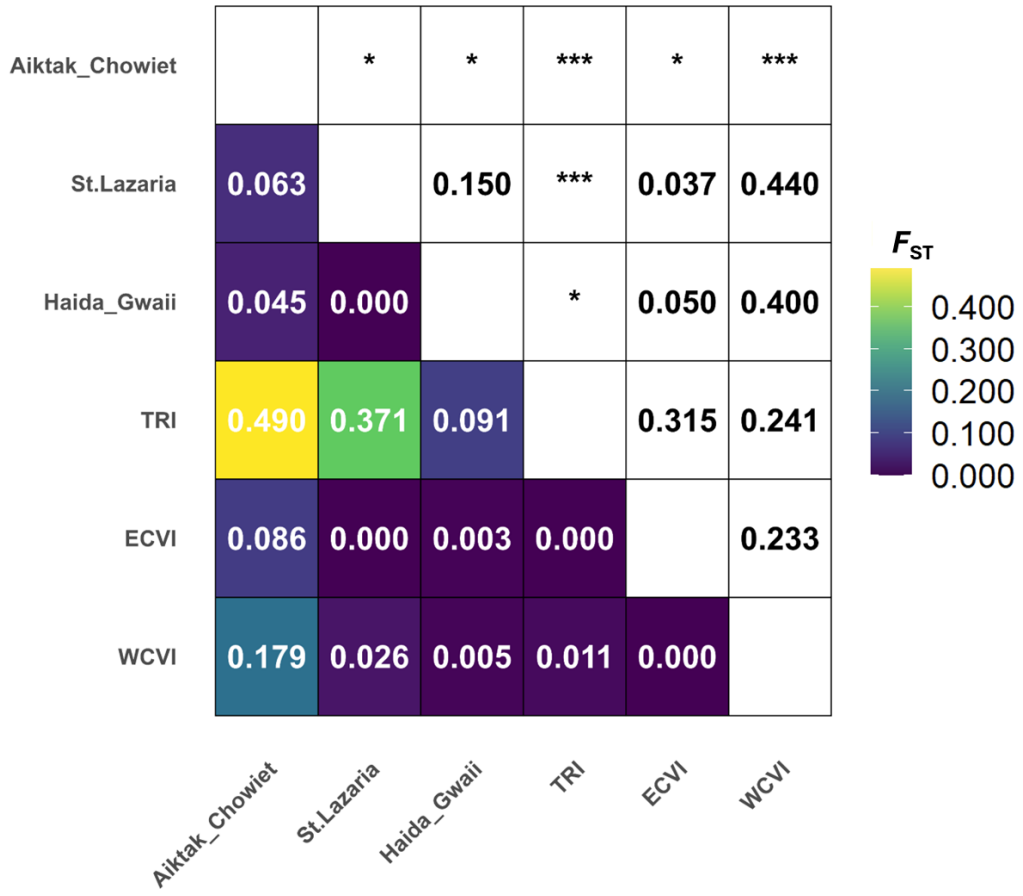


Figure 4: Heatmaps of pairwise F_{ST} values among the sampling locations for black oystercatchers. Regions with fewer than four individuals were excluded from the F_{ST} calculations. In the heatmaps, the lower left triangle displays the F_{ST} values, and the upper right triangle shows the significance levels * $p < 0.05$, *** $p < 0.001$.

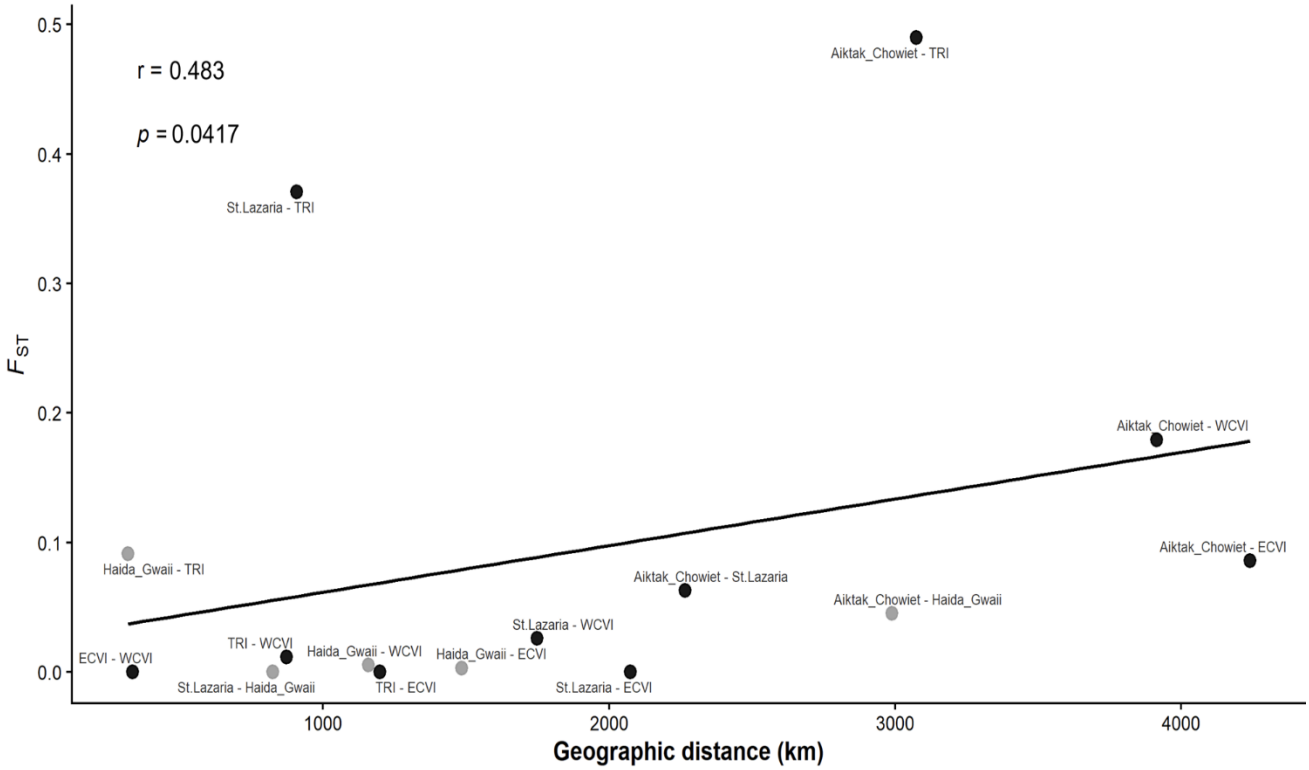


Figure 5: IBD plot shows the relationship between pairwise F_{ST} values and geographic distance (km) with r = 0.483, p = 0.0417. Comparison including Haida Gwaii are in grey, IBD excluding the Haida Gwaii has r = 0.534, p = 0.117.

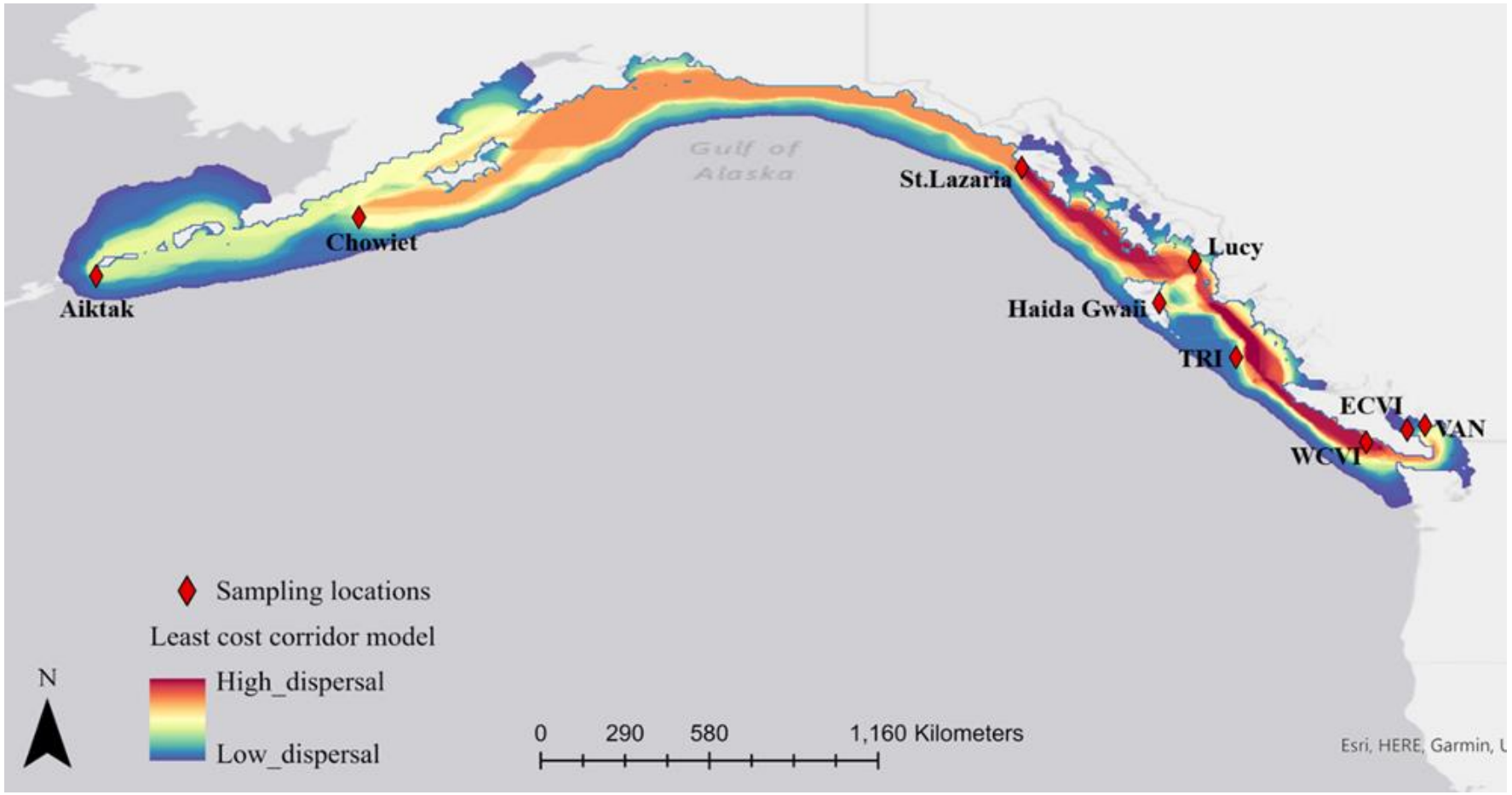


Figure 6: Least-cost corridor analysis showing area of high dispersal (red) and low dispersal (blue) and sampling sites in red diamond used for genetic analyses.

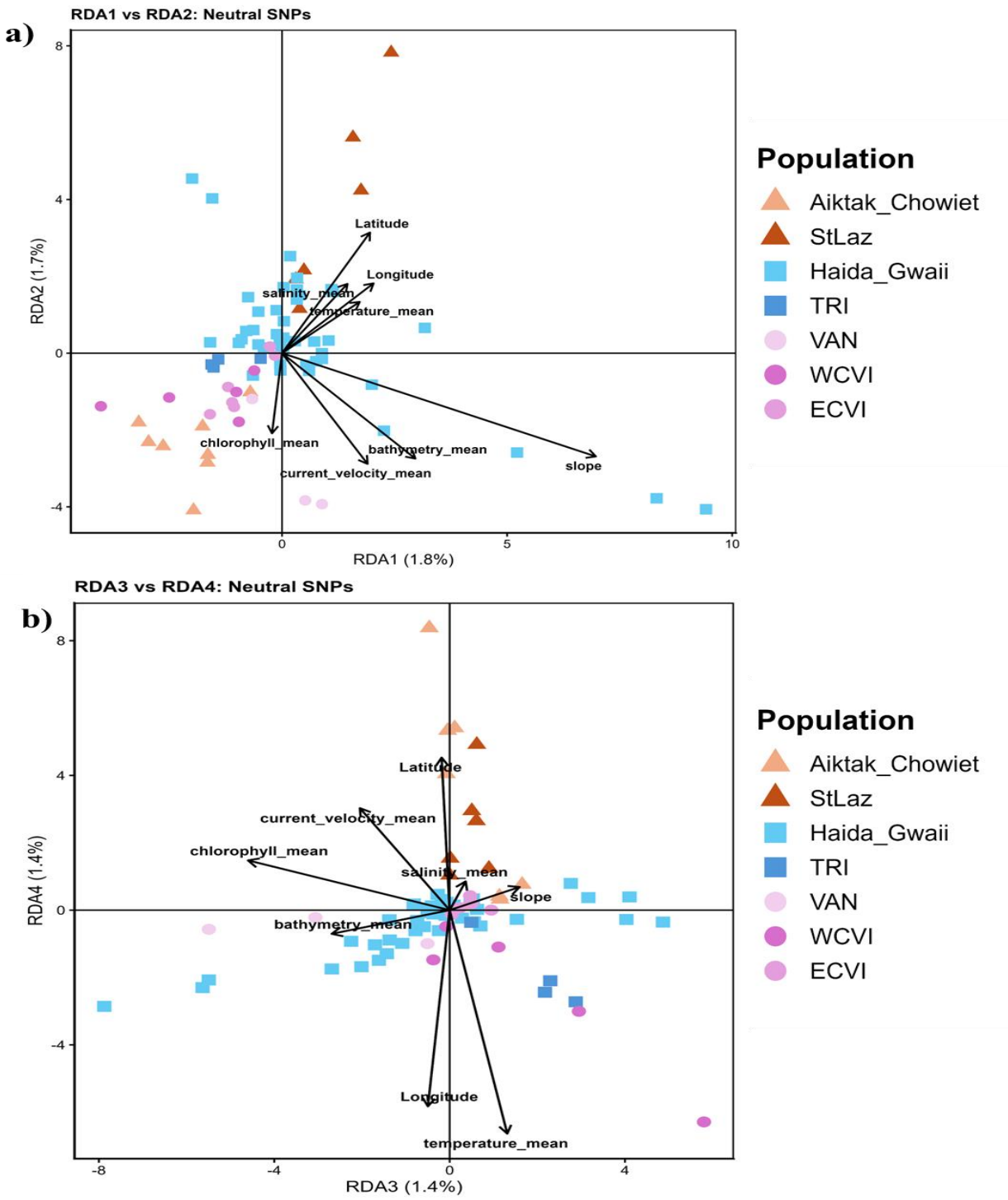


Figure 7: Redundancy analysis (RDA) plot showing the relationship between putatively neutral loci and environmental variables where a) shows RDA1 vs RDA2 and b) shows RDA3 vs RDA4. Arrows represent environmental variables. Abbreviations of the sampling sites are in Table 1.

Table 1: Location, code, sample size (n) observed (H_o) and expected (H_e) heterozygosity for 76 black oystercatchers.

Population	**Code**	**n**	**Ho**	**He**
Aiktak_Chowiet	Aiktak_Chowiet	10	0.186	0.406
St. Lazaria	StLaz	5	0.099	0.331
Haida Gwaii	Haida_Gwaii	43	0.132	0.256
LUCY	LUCY	1	0.064	0.231
Vancouver	VAN	3	0.156	0.132
Triangle Island	TRI	5	0.190	0.130
East Coast Vancouver Island	ECVI	5	0.169	0.173
West Coast Vancouver Island	WCVI	4	0.190	0.295

2.6 References

Abecassis, M., Senina, I., Lehodey, P., Gaspar, P., Parker, D., Balazs, G., & Polovina, J. (2013). A model of loggerhead sea turtle (*Caretta caretta*) habitat and movement in the oceanic North Pacific. *PloS One*, *8*(9), e73274.

Adriaensen, F., Chardon, J., 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.

Ahonen, H., Lowther, A. D., Harcourt, R. G., Goldsworthy, S. D., Charrier, I., & Stow, A. J. (2016). The limits of dispersal: fine scale spatial genetic structure in Australian sea lions. *Frontiers in Marine Science*, *3*, 65.

Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Boutov, D., Freitas, L., Robertson, K. M., Sequeira, M., Stockin, K. A., Coelho, M. M., & Möller, L. M. (2012). Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (genus *Delphinus*). *PloS One*, *7*(2), e31482.

Andres, B. A. F., G.A. (2020). *Black Oystercatcher (Haematopus bachmani), version 1.0.*

Assis, J., Fernández Bejarano, S. J., Salazar, V. W., Schepers, L., Gouvêa, L., Fragkopoulou, E., Leclercq, F., Vanhoorne, B., Tyberghein, L., & Serrão, E. A. (2024). Bio-ORACLE v3. 0. Pushing marine data layers to the CMIP6 Earth System Models of climate change research. *Global Ecology and Biogeography*, *33*(4), e13813.

Avila-Cárdenas, J. E., Llera-Herrera, R., Castillo-Guerrero, J. A., Palacios, E., & Fernández, G. (2025). Population genetic structure of the American oystercatcher in Northwestern Mexico. *Conservation Genetics*, *26*, 1127–1139.

Barr, K., Bossu, C. M., Bay, R. A., Anderson, E. C., Belthoff, J., Trulio, L. A., Chromczak, D., Wisinski, C. L., Smith, T. B., & Ruegg, K. C. (2023). Genetic and environmental drivers of migratory behavior in western burrowing owls and implications for conservation and management. *Evolutionary Applications*, *16*(12), 1889-1900.

Bay, R. A., Harrigan, R. J., Underwood, V. L., Gibbs, H. L., Smith, T. B., & Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science*, *359*(6371), 83-86.

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.

Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, *30*(15), 2114-2120.

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.

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.

Burg, T., Lomax, J., Almond, R., Brooke, M. d. L., & Amos, W. (2003). Unravelling dispersal patterns in an expanding population of a highly mobile seabird, the northern fulmar *Fulmarus glacialis*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1518), 979-984.

Burke, L. H. R. a. J. M. (2001). The biological reality of species: gene flow, selection, and collective evolution. *Taxon*, *50*(1), 47-67. https://doi.org/https://onlinelibrary.wiley.com/doi/pdf/10.2307/1224511

Bustillo-de la Rosa, D., Barrero, A., Traba, J., García, J. T., Morales, M. B., & Vázquez-Domínguez, E. (2024). Landscape features influencing gene flow and connectivity of an endangered passerine. *Ecology and Evolution*, *14*(5), e11078.

Cammen, K. M., Andrews, K. R., Carroll, E. L., Foote, A. D., Humble, E., Khudyakov, J. I., Louis, M., McGowen, M. R., Olsen, M. T., & Van Cise, A. M. (2016). Genomic methods take the plunge: recent advances in high-throughput sequencing of marine mammals. *Journal of Heredity*, *107*(6), 481-495.

Carlson-Bremer, D., Norton, T. M., Gilardi, K. V., Dierenfeld, E. S., Winn, B., Sanders, F. J., Cray, C., Oliva, M., Chen, T. C., & Gibbs, S. E. (2010). Health assessment of American oystercatchers (*Haematopus palliatus palliatus*) in Georgia and South Carolina. *Journal of Wildlife Diseases*, *46*(3), 772-780.

Conklin, J. R., Senner, N. R., Battley, P. F., & Piersma, T. (2017). Extreme migration and the individual quality spectrum. *Journal of Avian Biology*, *48*(1), 19-36.

Conklin, J. R., Verkuil, Y. I., Battley, P. F., Hassell, C. J., Ten Horn, J., Johnson, J. A., Tomkovich, P. S., Baker, A. J., Piersma, T., & Fontaine, M. C. (2022). Global flyway evolution in red knots *Calidris canutus* and genetic evidence for a Nearctic refugium. *Molecular Ecology*, *31*(7), 2124-2139.

Conklin, J. R., Verkuil, Y. I., Lefebvre, M. J., Battley, P. F., Bom, R. A., Gill Jr, R. E., Hassell, C. J., Ten Horn, J., Ruthrauff, D. R., & Tibbitts, T. L. (2024). High dispersal ability versus migratory traditions: Fine-scale population structure and post-glacial colonisation in bar-tailed godwits. *Molecular Ecology*, *33*(15), e17452.

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., & Sherry, S. T. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*(15), 2156-2158.

De Ronne, M., Légaré, G., Belzile, F., Boyle, B., & Torkamaneh, D. (2023). 3D-GBS: A universal genotyping-by-sequencing approach for genomic selection and other high-throughput low-cost applications in species with small to medium-sized genomes. *Plant Methods*, *19*(1), 13.

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

Epps, C. W., & Keyghobadi, N. (2015). Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. *Molecular Ecology*, *24*(24), 6021-6040.

Feder, J. L., Egan, S. P., & Nosil, P. (2012). The genomics of speciation-with-gene-flow. *Trends in Genetics*, *28*(7), 342-350.

Foley, M., Lato, K. A., Fuirst, M., Veit, R. R., Cerrato, R. M., & Thorne, L. H. (2025). Spatial and temporal predictability drive foraging movements of coastal birds. *Movement Ecology*, *13*(1), 5.

Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics*, *180*(2), 977-993.

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

Graham, B. A., Hipfner, J. M., Rojek, N. A., Stephensen, S. W., & Burg, T. M. (2023). Tufted Puffins exhibit low levels of genetic differentiation among breeding colonies in North America. *Ornithological Applications*, *125*(3), 1-8.

Gruber, B., Unmack, P., Berry, O., & Georges, A. (2019). *Introduction to dartR* (Vol. 51).

Hazlitt, S. L., & Butler, R. W. (2001). Site fidelity and reproductive success of black oystercatchers in British Columbia. *The International Journal of Waterbird Biology*, *24*(2), 203-207.

Hipfner, J. M., Morrison, K. W., & Kouwenberg, A.-L. (2012). Biology of Black Oystercatchers Breeding on Triangle Island, British Columbia, 2003–2011. *Northwestern Naturalist*, *93*(2), 145-153.

Holderegger, R., & Wagner, H. H. (2008). Landscape genetics. *Bioscience*, *58*(3), 199-207.

Johnson, M., Clarkson, P., Goldstein, M. I., Haig, S. M., Lanctot, R. B., Tessler, D. F., & Zwiefelhofer, D. (2010). Seasonal movements, winter range use, and migratory connectivity of the black oystercatcher. *The Condor*, *112*(4), 731-743.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*(11), 1403-1405.

Jombart, T., Kamvar, Z. N., Collins, C., Lustrik, R., Beugin, M.-P., Knaus, B. J., & Jombart, M. T. (2018). Package 'adegenet'. *Github Repository*.

Kersten, O., Star, B., Leigh, D. M., Anker-Nilssen, T., Strøm, H., Danielsen, J., Descamps, S., Erikstad, K. E., Fitzsimmons, M. G., & Fort, J. (2021). Complex population structure of the Atlantic puffin revealed by whole genome analyses. *Communications Biology*, *4*(1).

Klinga, P., Mikoláš, M., Smolko, P., Tejkal, M., Höglund, J., & Paule, L. (2019). Considering landscape connectivity and gene flow in the Anthropocene using complementary landscape genetics and habitat modelling approaches. *Landscape Ecology*, *34*(3), 521-536.

Kobayashi, K. M., Bond, R. M., Reid, K., Garza, J. C., Kiernan, J. D., & Palkovacs, E. P. (2024). Genetic divergence and one-way gene flow influence contemporary evolution and ecology of a partially migratory fish. *Evolutionary Applications*, *17*(6), e13712.

Levin, I. I., & Parker, P. G. (2012). Philopatry drives genetic differentiation in an island archipelago: comparative population genetics of Galapagos Nazca boobies (*Sula granti*) and great frigatebirds (*Fregata minor*). *Ecology and Evolution*, *2*(11), 2775-2787.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., & Subgroup, G. P. D. P. (2009). The sequence alignment/map format and SAMtools. *Bioinformatics*, *25*(16), 2078-2079.

Lopes, F., Oliveira, L. R., Kessler, A., Beux, Y., Crespo, E., Cárdenas-Alayza, S., Majluf, P., Sepúlveda, M., Brownell Jr, R. L., & Franco-Trecu, V. (2021). Phylogenomic discordance in the eared seals is best explained by incomplete lineage sorting following explosive radiation in the southern hemisphere. *Systematic Biology*, *70*(4), 786-802.

López-Goldar, X., & Agrawal, A. A. (2021). Ecological interactions, environmental gradients, and gene flow in local adaptation. *Trends in Plant Science*, *26*(8), 796-809.

Luna, L. W., Williams, L. M., Duren, K., Tyl, R., Toews, D. P., & Avery, J. D. (2023). Whole genome assessment of a declining game bird reveals cryptic genetic structure and insights for population management. *Molecular Ecology*, *32*(20), 5498-5513.

MacManes, M. D. (2014). On the optimal trimming of high-throughput mRNA sequence data. *Frontiers in Genetics*, *5*, 13.

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

McRae, B. H. (2006). Isolation by resistance. *Evolution*, *60*(8), 1551-1561.

McRae, B. H., & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences*, *104*(50), 19885-19890.

Meehan, T. D., Harvey, A. L., Michel, N. L., Langham, G. M., & Weinstein, A. (2018). A population model exploring factors influencing black oystercatcher (*Haematopus bachmani*) population dynamics. *Waterbirds*, *41*(2), 115-221.

Mijangos, J. L., Gruber, B., Berry, O., Pacioni, C., & Georges, A. (2022). dartR v2: An accessible genetic analysis platform for conservation, ecology and agriculture. *Methods in Ecology and Evolution*, *13*(10), 2150-2158.

Milot, E., Weimerskirch, H., & Bernatchez, L. (2008). The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. *Molecular Ecology*, *17*(7), 1658-1673.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). *The vegan package*. In *Community ecology package*.

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.

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.

Piersma, T. (1988). Hop, skip, or jump? Constraints on migration of Arctic waders by feeding, fattening, and flight speed. *Wader Study Group Bulletin*, *53*(1), 6.

Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*, *148*(Suppl 1), 45-59.

Piersma, T., & Lindström, Å. (2004). Migrating shorebirds as integrative sentinels of global environmental change. *Ibis*, *146*, 61-69.

Rankin, C. (2023). Migration strategies of black oystercatchers (*Haematopus bachmani*) breeding in the Gulf of Alaska. Simon Fraser University. Retrieved from https://summit.sfu.ca/item/36665.

Ravinet, M., Faria, R., Butlin, R., Galindo, J., Bierne, N., Rafajlović, M., Noor, M., Mehlig, B., & Westram, A. (2017). Interpreting the genomic landscape of speciation: a road map for finding barriers to gene flow. *Journal of Evolutionary Biology*, *30*(8), 1450-1477.

Redenbach, Z., & Taylor, E. B. (2002). Evidence for historical introgression along a contact zone between two species of char (Pisces: *Salmonidae*) in northwestern North America. *Evolution*, *56*(5), 1021-1035.

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., & Treml, E. A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. *Current Zoology*, *62*(6), 581-601.

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

Rönkä, N., Pakanen, V.-M., Pauliny, A., Thomson, R. L., Nuotio, K., Pehlak, H., Thorup, O., Lehikoinen, P., Rönkä, A., & Blomqvist, D. (2021). Genetic differentiation in an endangered and strongly philopatric, migrant shorebird. *BMC Ecology and Evolution*, *21*(1), 125.

Roodenrijs, H., Ware, L., Rankin, C., Maftei, M., Hipfner, J. M., Robinson, B. H., Esler, D., Coletti, H., & Green, D. J. (2024). Latitudinal gradients and sex differences in morphology of the black oystercatcher (*Haematopus bachmani*). *Ecology and Evolution*, *14*(9), e70115.

Row, J. R., Oyler-McCance, S. J., Fike, J. A., O'Donnell, M. S., Doherty, K. E., Aldridge, C. L., Bowen, Z. H., & Fedy, B. C. (2015). Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: A holistic modeling approach. *Ecology and Evolution*, *5*(10), 1955-1969.

Silva, C. N., & Gardner, J. P. (2016). Identifying environmental factors associated with the genetic structure of the New Zealand scallop: linking seascape genetics and ecophysiological tolerance. *ICES Journal of Marine Science*, *73*(7), 1925-1934.

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

Sonsthagen, S. A. (2006). Population genetic structure and phylogeography of common eiders (*Somateria mollissima*) https://scholarworks.alaska.edu/handle/11122/4920.

Spear, S. F., Cushman, S. A., & McRae, B. H. (2015). Resistance surface modeling in landscape genetics. *Landscape Genetics*, 129-148.

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.

Tessler, D. F., Johnson, J. A., Andres, B. A., Thomas, S., & Lanctot, R. B. (2014). A global assessment of the conservation status of the black oystercatcher *Haematopus bachmani*. *International Wader Studies*, *20*, 83-96.

Tigano, A., & Friesen, V. L. (2016). Genomics of local adaptation with gene flow. *Molecular Ecology*, *25*(10), 2144-2164.

van de Pol, M., Atkinson, P., Blew, J., Crowe, O., Delany, S., Duriez, O., Ens, B. J., Halterlein, B., Hotker, H., & Laursen, K. (2014). A global assessment of the conservation status of

the nominate subspecies of Eurasian oystercatcher *Haematopus ostralegus ostralegus*. *International Wader Studies*, *20*, 47-61.

Van Treuren, R., Bijlsma, R., Tinbergen, J., Heg, D., & Van de Zande, L. (1999). Genetic analysis of the population structure of socially organized oystercatchers (*Haematopus ostralegus)* using microsatellites. *Molecular Ecology*, *8*(2), 181-187.

Veale, A., Reudink, M. W., & Burg, T. M. (2024). Neutral markers reveal complex population structure across the range of a widespread songbird. *Ecology and Evolution*, *14*(7), e11638.

Warwick-Evans, V. C., Atkinson, P. W., Robinson, L. A., & Green, J. A. (2016). Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season. *PloS One*, *11*(3), e0150592.

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution 38*(6), 1358-1370.

Wickham, H. (2011). ggplot2. *Wiley interdisciplinary reviews: computational statistics*, *3*(2), 180-185.

Wickham, H., Chang, W., & Wickham, M. H. (2016). *Package 'ggplot2'*. In *Create elegant data visualisations using the grammar of graphics. Version*

Wilcox, M. A., Jeffery, N. W., DiBacco, C., Bradbury, I. R., Lowen, B., Wang, Z., Beiko, R. G., & Stanley, R. R. (2023). Integrating seascape resistances and gene flow to produce area-based metrics of functional connectivity for marine conservation planning. *Landscape Ecology*, *38*(9), 2189-2205.

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

Chapter 3: General Discussion

3.1 General discussion

Population structure can be challenging to elucidate, especially in highly mobile species with large ranges (Lah et al., 2016; Nance et al., 2011; Stenzler et al., 2009; Younger et al., 2017). This study of the contemporary population genetic structure in black oystercatchers (*Haematopus bachmani*) revealed moderate genetic structure between northern and southern populations. The black oystercatcher has an expansive distribution range; however, it has limited dispersal (Tessler et al., 2014) and exhibits philopatric behavior (Andres, 2020; Tessler et al., 2014) and partial migration (Rankin, 2023), which might facilitate gene flow among them (Andres, 2020; Rankin, 2023; Roodenrijs et al., 2024; Sexton et al., 2014; Tessler et al., 2014). In addition, overlapping populations of Haida Gwaii acted as a genetic bridge between the northern and southern populations, as seen in southern dunlin (Rönkä et al. 2021) and dolly varden trout (Redenbach & Taylor, 2002). This trade-off between philopatry and limited dispersal with ongoing partial movements reflects the weak genetic differentiation in the black oystercatcher. Philopatry reinforces genetic structure and regional differentiation in many seabirds by reducing the gene flow between distant colonies (Friesen et al., 2007; Levin & Parker, 2012). However, partial migration and occasional dispersal events can prevent complete isolation, resulting in weak genetic structure (Cobben & van Noordwijk, 2016). The European shag (*Phalacrocorax aristotelis*) (Barlow et al., 2011) and the grey kangaroo (*Macropus fuliginosus*) (Neaves et al., 2009), which exhibit weak genetic structure across wide geographic ranges, showed a comparable pattern to my study. Among marine mammals, bottlenose dolphins (*Tursiops truncatus*) (Lowther-Thieleking et al., 2015) and harbor seals (*Phoca vitulina*) also show weak differentiation despite geographic separation, highlighting that dispersal or habitat connectivity facilitates gene flow. In birds with mixed migratory strategies, such as the Kentish plover (*Charadrius alexandrinus*) (Küpper, 2008; Küpper et al., 2009), a weak but detectable structure has been observed, reflecting limited dispersal coupled with site fidelity.

Black oystercatcher, despite having an extensive geographical range, their populations are confined in patches with small individual size (Hipfner et al., 2012; Roodenrijs et al., 2024; Tessler et al., 2014), which provides enough room for inbreeding and genetic drift (Rönkä et al., 2021; Velando et al., 2015). The difference between observed (H_o) and expected heterozygosity

(H_e) between black oystercatcher populations indicated a deficit of heterozygotes likely caused by inbreeding or population sub structuring (Wahlund effect). The philopatric behavior of the species, combined with limited dispersal, reduces the likelihood of random mating and increases the probability of mating among related individuals, which can lead to elevated local inbreeding and genetic drift, resulting in lower heterozygosity (Velando et al., 2015). The study of Mallee emu-wren (*Stipiturus mallee*) by Brown et al., (2013) showed a similar pattern with restricted movement.

The continuous habitat corridors of black oystercatchers from southern Alaska to Vancouver Island, extending through the Alexander Archipelago and the British Columbia coastline, likely represent historical and contemporary pathways of the species, especially during their non-breeding periods when they travel over larger coastal extents (Abecassis et al., 2013). Although having connected habitats along the North Pacific Coast, their behavioral strategies, including breeding site philopatry and limited dispersal ability, could explain their moderate genetic differentiation between northern and southern populations. Cory's shearwater (*Calonectris diomedea*) (Genovart et al., 2013) exhibits low genetic structure despite having connectivity due to its philopatric behavior. The increase in genetic differentiation with geographical distance is an observed pattern among philopatric birds (Friesen et al., 2007; Milot et al., 2008; Genovart et al., 2013). The black lip pearl oyster (*Pinctada margaritifera*) (Lal et al., 2017) and the European shag (*Phalacrocorax aristotelis*) (Thanou et al., 2017) exhibited similar landscape-mediated connectivity, yet an isolation by distance pattern. Weak association between environmental variables and genetic variations is common in species where geographical distance determines genetic patterns (Avila-Cárdenas et al., 2025; Sonsthagen, 2006). Comparable patterns of weak but spatially structured genetic structure in thick-billed murres (*Uria lomvia*) (Tigano et al., 2017), eastern great bustard (*Otis tarda dybowskii*) (Liu et al., 2022), and Florida scrub-jay (*Aphelocoma coerulescens*) (Stenzler & Fitzpatrick, 2002) found that genetic differentiation is the effect of geographic distance rather than strong environmental selection.

The overall genetic pattern observed in my study showed that the black oystercatcher is neither fully panmictic nor firmly structured. Larger distribution range and higher habitat continuity maintain genetic connectivity yet breeding site fidelity and geographic isolation promote localized differentiation (Rönkä et al., 2021). This dynamic balance between gene flow and isolation may allow populations to remain resilient to environmental changes while retaining the

potential for local adaptation (Klinga et al., 2019; López-Goldar et al., 2021). On the other hand, historical factors, including post-glacial recolonization following the Last Glacial Maximum, might have contributed to the observed genetic structure by shaping the current distribution of habitats and breeding populations (Shafer et al., 2010). The overlap of northern and southern genetic clusters around Haida Gwaii could represent a historical contact zone between recolonization fronts expanding from glacial refugia in the south and recolonized northern habitats which is a pattern observed in many birds, mammals, fishes and intertidal invertebrates (Cook et al., 2001; Orchard & Szpak, 2015; Pruett et al., 2013; Sawyer et al., 2019).

From a conservation perspective, these results indicate that, although populations of black oystercatchers are connected, restricted gene flow may exist in some regional populations, particularly between northern and southern populations. Designing successful conservation and management plans that preserve genetic connectivity while maintaining adapted lineages thus requires an understanding of regional population structure. The species has an extensive geographical range, characterized by strong philopatry and a small population size, which may put the small breeding population at a vulnerable stage. Protecting key breeding sites, minimizing disturbance during the nesting season, and monitoring population trends at regional scales will be essential for preserving both demographic stability and genetic diversity. Together, these results suggest the importance of habitat-focused, coordinated management to ensure the long-term survival of black oystercatchers.

3.2 Future directions

Although this study represents a crucial step in understanding the genetic structure of the black oystercatcher, further research is necessary to expand on these findings. Additional research with an understanding of their genetic structure and connectivity is essential, particularly with the expansion of genomic sampling, improvements in sequencing strategies, and the incorporation of satellite tracking, to better understand their population dynamics. In particular, increasing sample coverage across the breeding range, especially in Washington, Oregon, and California, will be crucial for gaining better knowledge of genetic structure throughout the geographical range. These southern populations are currently underrepresented in my study, and additional sampling could clarify if they form a distinct lineage. More comprehensive sampling may also reveal hidden population substructure, barriers to gene flow, or signs of local adaptation to different coastal environments and prey communities. Overall, this broader coverage would improve our understanding of range-wide population structure, refine management units, and strengthen demographic models.

Utilizing satellite telemetry in this genomic framework would be valuable for understanding partial migration. Tracking individuals from both northern and southern breeding grounds could reveal where partial migratory birds spend the non-breeding season, whether they move between breeding regions across years, and whether migrants play a key role in connecting populations genetically. Overlaying GPS tracks with environmental data, such as sea-surface temperature, current velocity, chlorophyll concentration, and coastal disturbance, could help identify what drives migratory decisions and highlights important corridors or wintering hotspots. By linking movement data with genomics, we could test whether migrants help maintain gene flow, preserve genetic diversity, or buffer small populations against inbreeding.

To enhance genomic resolution, the next step is to adopt high-resolution markers such as whole-genome sequencing (WGS) or low-coverage WGS (lcWGS). By using high-coverage resolution, lcWGS can increase the power to detect the subtle population structure, recent gene flow, and fine-scale relatedness, which is an essential consideration for a species with limited dispersal. Combining high-coverage WGS for a representative subset of individuals with lcWGS across populations would provide the most robust framework for studying both neutral and adaptive processes shaping BLOY populations.

This integrated approach is crucial because partial migration and regional differentiation can have a significant impact on long-term population resilience. Understanding cryptic population structure, migratory routes, and the habitats used by migrants will directly inform conservation planning, guide habitat protection along the Pacific Coast, and help define meaningful management units. Ultimately, combining expanded U.S. sampling, lcWGS approaches, and satellite tracking will provide the most comprehensive picture of how environmental variation, movement behavior, and evolutionary processes interact to shape the future of the black oystercatcher population.

3.3 References

Abecassis, M., Senina, I., Lehodey, P., Gaspar, P., Parker, D., Balazs, G., & Polovina, J. (2013). A model of loggerhead sea turtle (*Caretta caretta*) habitat and movement in the oceanic North Pacific. *PloS One*, *8*(9), e73274.

Andres, B. A. F., G.A. (2020). *Black Oystercatcher (Haematopus bachmani), version 1.0.*

Avila-Cárdenas, J. E., Llera-Herrera, R., Castillo-Guerrero, J. A., Palacios, E., & Fernández, G. (2025). Population genetic structure of the American oystercatcher in Northwestern Mexico. *Conservation Genetics*, *26*, 1127–1139.

Balza, U., Lois, N. A., Harrington, K. J., León, F., Pütz, K., Raya-Rey, A., & Ceballos, S. G. (2025). Glacial history and ecological restrictions shape island-scale genetic structure and demography in the southernmost bird of prey. *Journal of Biogeography*, *52*(4), e15083.

Barlow, E. J., Daunt, F., Wanless, S., Alvarez, D., Reid, J. M., & Cavers, S. (2011). Weak large-scale population genetic structure in a philopatric seabird, the European shag *Phalacrocorax aristotelis*. *Ibis*, *153*(4), 768-778.

Brown, S. M., Harrisson, K. A., Clarke, R. H., Bennett, A. F., & Sunnucks, P. (2013). Limited population structure, genetic drift and bottlenecks characterise an endangered bird species in a dynamic, fire-prone ecosystem. *PloS One*, *8*(4), e59732.

Cobben, M. M., & van Noordwijk, A. J. (2016). Stable partial migration under a genetic threshold model of migratory behaviour. *Ecography*, *39*(12), 1210-1215.

Cook, J., Bidlack, A., Conroy, C. J., Demboski, J., Fleming, M., Runck, A., Stone, K., & MacDonald, S. (2001). A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska. *Biological Conservation*, *97*(2), 215-227.

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

Genovart, M., Thibault, J. C., Igual, J. M., Bauzà-Ribot, M. D. M., Rabouam, C., & Bretagnolle, V. (2013). Population structure and dispersal patterns within and between Atlantic and Mediterranean populations of a large-range pelagic seabird. *PLoS One*, *8*(8), e70711.

Klinga, P., Mikoláš, M., Smolko, P., Tejkal, M., Höglund, J., & Paule, L. (2019). Considering landscape connectivity and gene flow in the Anthropocene using complementary landscape genetics and habitat modelling approaches. *Landscape Ecology*, *34*(3), 521-536.

Küpper, C. (2008). Molecular ecology of the Kentish plover *Charadrius alexandrinus* University of Bath].

Küpper, C., Augustin, J., Kosztolányi, A., Burke, T., Flguerola, J., & Székely, T. (2009). Kentish versus snowy plover: phenotypic and genetic analyses of *Charadrius alexandrinus* reveal divergence of Eurasian and American subspecies. *The Auk*, *126*(4), 839-852.

Lah, L., Trense, D., Benke, H., Berggren, P., Gunnlaugsson, Þ., Lockyer, C., Öztürk, A., Öztürk, B., Pawliczka, I., & Roos, A. (2016). Spatially explicit analysis of genome-wide SNPs detects subtle population structure in a mobile marine mammal, the harbor porpoise. *PloS One*, *11*(10), e0162792.

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.

Levin, I. I., & Parker, P. G. (2012). Philopatry drives genetic differentiation in an island archipelago: comparative population genetics of Galapagos Nazca boobies (*Sula granti*) and great frigatebirds (*Fregata minor*). *Ecology and Evolution*, *2*(11), 2775-2787.

Liu, G., Li, C., Kessler, M., Flatz, R., Meng, D., Wei, M., & Gong, M. (2022). Geographic distance, landscape heterogeneity and migratory connectivity influence population genetic structure of farmland-dependent wintering birds and their conservation. *Biological Conservation*, *272*, 109649.

López-Goldar, X., & Agrawal, A. A. (2021). Ecological interactions, environmental gradients, and gene flow in local adaptation. *Trends in Plant Science*, *26*(8), 796-809.

Lowther-Thieleking, J. L., Archer, F. I., Lang, A. R., & Weller, D. W. (2015). Genetic differentiation among coastal and offshore common bottlenose dolphins, *Tursiops truncatus*, in the eastern North Pacific Ocean. *Marine Mammal Science*, *31*(1), 1-20.

Nance, H. A., Klimley, P., Galván-Magaña, F., Martínez-Ortíz, J., & Marko, P. B. (2011). Demographic processes underlying subtle patterns of population structure in the scalloped hammerhead shark, Sphyrna lewini. *PloS One*, *6*(7), e21459.

Neaves, L. E., Zenger, K. R., Prince, R. I., Eldridge, M. D., & Cooper, D. W. (2009). Landscape discontinuities influence gene flow and genetic structure in a large, vagile Australian mammal, *Macropus fuliginosus*. *Molecular Ecology*, *18*(16), 3363-3378.

Orchard, T. J., & Szpak, P. (2015). Zooarchaeological and isotopic insights into locally variable economic patterns: a case study from late holocene southern Haida Gwaii, British Columbia. *BC Studies: The British Columbian Quarterly (187*), 85-125.

Pruett, C. L., Topp, C. M., Maley, J. M., McCracken, K. G., Rohwer, S., Birks, S., Sealy, S. G., & Winker, K. (2013). Evidence from the genetics of landbirds for a forested Pleistocene glacial refugium in the Haida Gwaii area. *The Condor*, *115*(4), 725-737.

Rankin, C. (2023). Migration strategies of black oystercatchers (*Haematopus bachmani*) breeding in the Gulf of Alaska. MSc Thesis, Simon Fraser University. Retrieved from https://summit.sfu.ca/item/36665.

Rönkä, N., Pakanen, V.-M., Pauliny, A., Thomson, R. L., Nuotio, K., Pehlak, H., Thorup, O., Lehikoinen, P., Rönkä, A., & Blomqvist, D. (2021). Genetic differentiation in an endangered and strongly philopatric, migrant shorebird. *BMC Ecology and Evolution*, *21*(1), 125.

Roodenrijs, H., Ware, L., Rankin, C., Maftei, M., Hipfner, J. M., Robinson, B. H., Esler, D., Coletti, H., & Green, D. J. (2024). Latitudinal gradients and sex differences in morphology of the black oystercatcher (*Haematopus bachmani*). *Ecology and Evolution*, *14*(9), e70115.

Sawyer, Y. E., MacDonald, S. O., Lessa, E. P., & Cook, J. A. (2019). Living on the edge: Exploring the role of coastal refugia in the Alexander Archipelago of Alaska. *Ecology and Evolution*, *9*(4), 1777-1797.

Sexton, J. P., Hangartner, S. B., & Hoffmann, A. A. (2014). Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution*, *68*(1), 1-15.

Shafer, A. B., Cullingham, C. I., Côté, S. D., & Coltman, D. W. (2010). Of glaciers and refugia: a decade of study sheds new light on the phylogeography of northwestern North America. *Molecular Ecology*, *19*(21), 4589-4621.

Sonsthagen, S. A. (2006). Population genetic structure and phylogeography of common eiders *(Somateria mollissima)* https://scholarworks.alaska.edu/handle/11122/4920.

Stenzler, L., & Fitzpatrick, J. (2002). Isolation of microsatellite loci in the Florida scrub-jay *Aphelocoma coerulescens*. *Molecular Ecology Notes*, *2*(4), 547-550.

Stenzler, L. M., Makarewich, C. A., Coulon, A., Ardia, D. R., Lovette, I. J., & Winkler, D. W. (2009). Subtle edge-of-range genetic structuring in transcontinentally distributed North American tree swallows. *The Condor*, *111*(3), 470-478.

Tessler, D. F., Johnson, J. A., Andres, B. A., Thomas, S., & Lanctot, R. B. (2014). A global assessment of the conservation status of the black oystercatcher *Haematopus bachmani*. *International Wader Studies*, *20*, 83-96.

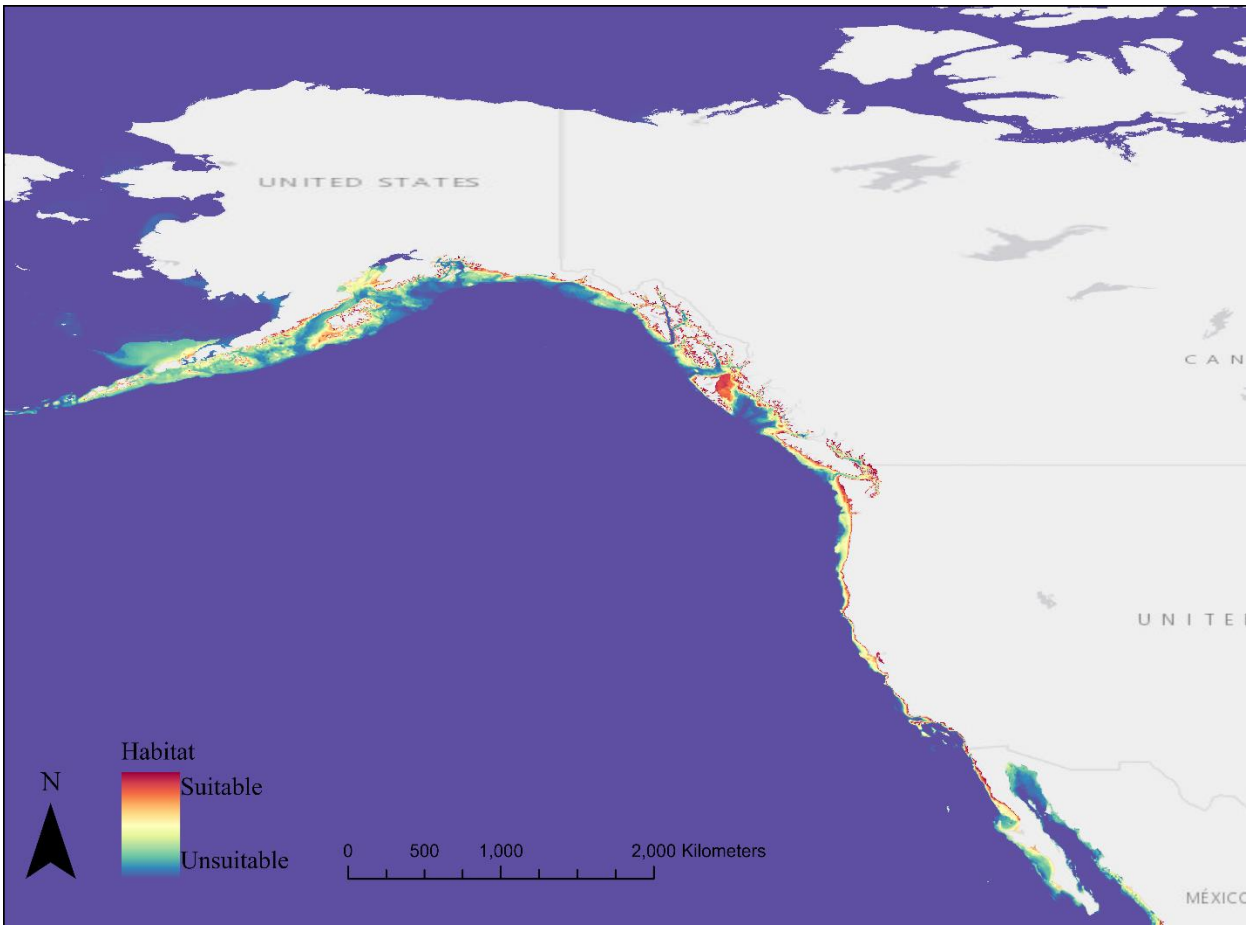
Thanou, E., Sponza, S., Nelson, E. J., Perry, A., Wanless, S., Daunt, F., & Cavers, S. (2017). Genetic structure in the European endemic seabird, *Phalacrocorax aristotelis*, shaped by a complex interaction of historical and contemporary, physical and nonphysical drivers. *Molecular Ecology*, *26*(10), 2796-2811.

Tigano, A., Shultz, A. J., Edwards, S. V., Robertson, G. J., & Friesen, V. L. (2017). Outlier analyses to test for local adaptation to breeding grounds in a migratory Arctic seabird. *Ecology and Evolution*, *7*(7), 2370-2381.

Velando, A., Barros, Á., & Moran, P. (2015). Heterozygosity–fitness correlations in a declining seabird population. *Molecular Ecology*, *24*(5), 1007-1018.

Younger, J. L., Clucas, G. V., Kao, D., Rogers, A. D., Gharbi, K., Hart, T., & Miller, K. J. (2017). The challenges of detecting subtle population structure and its importance for the conservation of emperor penguins. *Molecular Ecology*, *26*(15), 3883-3897.

Appendix 1: Species distribution model of black oystercatcher the pink-purple area shows suitable habitat, the red area shows area of unsuitable habitat.



Appendix 2: Environmental GIS rasters obtained from Bio-ORACLE (max, min, mean & range) datasets. Pearson's correlation coefficient was used to check all variables for correlation. Variables $r > 0.7$ were highly correlated and removed from further analysis. In total 11 variables.

Available environmental layers	**Description**	**Retained variable(s)**
Bathymetry: mean	depth to sea floor	mean
Chlorophyll: max, min,mean, range	chlorophyll concentration in water	mean
Phosphate concentration: max, min, mean, range	phosphate concentration in water	mean
Current velocity: mean	average speed of ocean currents	mean
Salinity: max,min,mean and range	dissolved salts in water	mean
pH concentration: mean	pH level in water	mean
Nitrate: max, min, mean range	nitrate concentration in water	mean
sea surface temperature: max, min, mean and range	temperature in sea surface	mean
topographic rudgness index: mean	seafloor elevation	removed
Slope: mean	topographic steepness of the seafloor	removed

Appendix 3: Environmental layers used to develop SDM for black oystercatchers. Contribution to the model values is 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 percentage value.

Variables	**Description**	**Percent contribution**	**Permutation importance**
Bathymetry	depth to sea floor	39.6	71.8
Chlorophyll	chlorophyll concentration in water	35.6	2.8
Sea surface temperature	temperature in sea surface	9.3	8.5
pH	pH level in water	8	0.2
Phosphate	phosphate concentration in water	6.8	15.3
Nitrate	nitrate concentration in water	0.3	0.6
Salinity	dissolved salts in water	0.2	0.6
Current velocity	average speed of ocean currents	0.1	0.2

Appendix 4: Percentage contribution of environmental variables to the redundancy analysis (RDA) explaining genetic variation in black oystercatchers. The latitude and longitude contributed the most to the explained variance, followed by bathymetry, slope, current velocity, salinity, temperature and chlorophyll concentration.

Variables	**Description**	**Percent contribution**
Latitude	Latitude	25.61
Longitude	Longitude	15.68
bathymetry_mean	depth to sea floor	13.50
Slope	topographic steepness of the seafloor	12.53
current_velocity_mean	average speed of ocean currents	10.21
salinity_mean	dissolved salt concentration	8.24
temperature_mean	temperature in sea surface	8.11
chlorophyll_mean	chlorophyll concentration in water	6.12

Appendix 5: Individual sample detail for the black oystercatcher (BLOY) included in this study.

Locations	Sample ID	Population	Latitude	Longitude
Aiktak, AK	BLOY_AIKT001	Aiktak_Chowiet	54.18378	-164.84817
Aiktak, AK	BLOY_AIKT002A	Aiktak_Chowiet	54.18553	-164.84600
Aiktak, AK	BLOY_AIKT002B	Aiktak_Chowiet	54.18553	-164.84600
Aiktak, AK	BLOY_AIKT003	Aiktak_Chowiet	54.18706	-164.84123
Chowiet, AK	BLOY_CHOW001	Aiktak_Chowiet	56.02180	-156.71393
Chowiet, AK	BLOY_CHOW002	Aiktak_Chowiet	56.02189	-156.71405
Chowiet, AK	BLOY_CHOW003	Aiktak_Chowiet	56.04152	-156.74682
Chowiet, AK	BLOY_CHOW004	Aiktak_Chowiet	56.02284	-156.71470
Chowiet, AK	BLOY_CHOW005	Aiktak_Chowiet	56.02214	-156.71497
Chowiet, AK	BLOY_CHOW006	Aiktak_Chowiet	56.03863	-156.74185
St Lazaria, AK	BLOY_STLA001	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA002	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA003	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA004	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA005	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA006	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA007	St. Lazaria or StLaz	56.98888	-135.71292
St Lazaria, AK	BLOY_STLA008	St. Lazaria or StLaz	56.98888	-135.71292
Dyer Point (Lina Island), Skidegate Inlet, BC	BLOY_HG_SKI006	Haida_Gwaii or HG	53.22770	-132.16050

Weed Rock, Skidegate Inlet, BC	BLOY_HG_SKI007	Haida_Gwaii or HG	53.23170	-132.16310
Hallet Island, Skidegate Inlet, BC	BLOY_HG_SKI008	Haida_Gwaii or HG	53.21530	-132.23997
Hallet Island, Skidegate Inlet, BC	BLOY_HG_SKI009	Haida_Gwaii or HG	53.21530	-132.23997
Hallet Island, Skidegate Inlet, BC	BLOY_HG_SKI010	Haida_Gwaii or HG	53.21511	-132.24028
Transit Island, Skidegate Inlet, BC	BLOY_HG_SKI011	Haida_Gwaii or HG	53.19921	-132.01037
Alder Island, Gwaii Haanas, BC	BLOY_HG_ALD001	Haida_Gwaii or HG	52.45261	-131.32573
Alder Island, Gwaii Haanas, BC	BLOY_HG_ALD002	Haida_Gwaii or HG	52.44321	131.31445
Arichika Island, Gwaii Haanas, BC	BLOY_HG_ARIC001	Haida_Gwaii or HG	52.46751	-131.33984
Bischof Islands, Gwaii Haanas, BC	BLOY_HG_BISC001	Haida_Gwaii or HG	52.58020	-131.55589
Cumshewa Island, Haida Gwaii, BC	BLOY_HG_CUIS012	Haida_Gwaii or HG	53.02996	131.60167
Kawas Islets, Gwaii Haanas, BC	BLOY_HG_KAW001	Haida_Gwaii or HG	52.64526	-131.40765
Kawas Islets, Gwaii Haanas, BC	BLOY_HG_KAW002	Haida_Gwaii or HG	52.64516	-131.40770
Kawas Islets, Gwaii Haanas, BC	BLOY_HG_KAW003	Haida_Gwaii or HG	52.64309	-131.41403
Kingsway Rock, Haida Gwaii, BC	BLOY_HG_KING001	Haida_Gwaii or HG	52.86225	-131.67249
Kingsway Rock, Haida Gwaii, BC	BLOY_HG_KING002	Haida_Gwaii or HG	52.86257	-131.67255
Kingsway Rock, Haida Gwaii, BC	BLOY_HG_KING003	Haida_Gwaii or HG	52.86276	-131.67270
Kingsway Rock, Haida Gwaii, BC	BLOY_HG_KING004	Haida_Gwaii or HG	52.86289	-131.67253
Kingsway Rock, Haida Gwaii, BC	BLOY_HG_KING005	Haida_Gwaii or HG	52.86271	-131.67262
Kingsway Rock, Haida Gwaii, BC	BLOY_HG_KING006	Haida_Gwaii or HG	52.86239	-131.67278
Kul Rock, Gwaii Haanas, BC	BLOY_HG_KUL001	Haida_Gwaii or HG	52.73570	-131.60493
Kul Rock, Gwaii Haanas, BC	BLOY_HG_KUL002	Haida_Gwaii or HG	52.73564	-131.60385
Kul Rock, Gwaii Haanas, BC	BLOY_HG_KUL003	Haida_Gwaii or HG	52.73581	-131.60497

Kul Rock, Gwaii Haanas, BC	BLOY_HG_KUL004	Haida_Gwaii or HG	52.73544	-131.60406
Lost Islands, Haida Gwaii, BC	BLOY_HG_LOST001	Haida_Gwaii or HG	52.80388	131.48982
Lost Islands, Haida Gwaii, BC	BLOY_HG_LOST002	Haida_Gwaii or HG	52.80308	131.48488
Lost Islands, Laskeek Bay, BC	BLOY_HG_LOST003	Haida_Gwaii or HG	52.80296	-131.48503
Lost Islands, Laskeek Bay, BC	BLOY_HG_LOST004	Haida_Gwaii or HG	52.80167	-131.48566
Lost Islands, Laskeek Bay, BC	BLOY_HG_LOST005	Haida_Gwaii or HG	52.80141	-131.48599
SE Murchison Rocks, Gwaii Haanas, BC	BLOY_HG_MURC001	Haida_Gwaii or HG	52.59607	-131.42555
SE Murchison Rocks, Gwaii Haanas, BC	BLOY_HG_MURC002	Haida_Gwaii or HG	52.59715	-131.42465
Murchison Island, Gwaii Haanas, BC	BLOY_HG_MURC003	Haida_Gwaii or HG	52.59975	-131.45663
Ramsay Island, Gwaii Haanas, BC	BLOY_HG_RAM001	Haida_Gwaii or HG	52.57454	-131.39870
Ramsay Island, Gwaii Haanas, BC	BLOY_HG_RAM002	Haida_Gwaii or HG	52.54696	-131.36137
Ramsay Island, Gwaii Haanas, BC	BLOY_HG_RAM003	Haida_Gwaii or HG	52.54072	-131.39316
Ramsay Island, Gwaii Haanas, BC	BLOY_HG_RAM004	Haida_Gwaii or HG	52.54895	-131.40109
Ramsay Islets, Gwaii Haanas, BC	BLOY_HG_RAM005	Haida_Gwaii or HG	52.57454	-131.39870
Ramsay Islets, Gwaii Haanas, BC	BLOY_HG_RAM006	Haida_Gwaii or HG	52.57518	-131.39952
Ramsay Islets, Gwaii Haanas, BC	BLOY_HG_RAM007	Haida_Gwaii or HG	52.57521	-131.39865
Ramsay Islets, Gwaii Haanas, BC	BLOY_HG_RAM008	Haida_Gwaii or HG	52.57444	-131.39664
Reef Island, Haida Gwaii, BC	BLOY_HG_REI001	Haida_Gwaii or HG	52.87412	-131.49268
Reef Island, Haida Gwaii, BC	BLOY_HG_REI002	Haida_Gwaii or HG	52.86353	-131.51385
Skedans Islands, Haida Gwaii, BC	BLOY_HG_SKE001	Haida_Gwaii or HG	52.95356	-131.55309
Balch Islands (Bird Rock), Skidegate Inlet, BC	BLOY_HG_SKI001	Haida_Gwaii or HG	53.22430	-132.08700
Bush Island, Skidegate Inlet, BC	BLOY_HG_SKI002	Haida_Gwaii or HG	53.21480	-132.00650

Bush Island, Skidegate Inlet, BC	BLOY_HG_SKI003	Haida_Gwaii or HG	53.21480	-132.00650
Tree Islet, Skidegate Inlet, BC	BLOY_HG_SKI004	Haida_Gwaii or HG	53.20250	-132.13750
South Low Island, Haida Gwaii, BC	BLOY_HG_SL001	Haida_Gwaii or HG	52.89206	-131.57010
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR001	Haida_Gwaii or HG	52.66116	-131.42218
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR002	Haida_Gwaii or HG	52.66201	-131.42094
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR003	Haida_Gwaii or HG	52.66230	-131.43451
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR004	Haida_Gwaii or HG	52.66692	-131.41467
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR005	Haida_Gwaii or HG	52.66641	-131.41501
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR006	Haida_Gwaii or HG	52.66685	-131.41876
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR007	Haida_Gwaii or HG	52.67467	-131.41444
Tar Islets, Gwaii Haanas, BC	BLOY_HG_TAR008	Haida_Gwaii or HG	52.67434	-131.41527
Tatsung Rock, Gwaii Haanas, BC	BLOY_HG_TATS001	Haida_Gwaii or HG	52.54522	-131.34837
Lucy Island, South-West, BC	BLOY_LUCY001	LUCY	54.29270	-130.62120
Triangle Island, BC	BLOY_TRI001	TRI	50.86509	-129.08129
Triangle Island, BC	BLOY_VI_TRI002	TRI	50.86509	-129.08129
Triangle Island, BC	BLOY_VI_TRI003	TRI	50.86509	-129.08129
Triangle Island, BC	BLOY_VI_TRI004	TRI	50.86509	-129.08129
Triangle Island, BC	BLOY_VI_TRI005	TRI	50.86509	-129.08129
Christie Islet, NW of Vancouver, BC	BLOY_VAN_CHIS001	VAN	49.49972	-123.30185
Christie Islet, NW of Vancouver, BC	BLOY_VAN_CHIS002	VAN	49.49972	-123.30185
Christie Islet, NW of Vancouver, BC	BLOY_VAN_CHIS003	VAN	49.49972	-123.30185
Grebe Islets, NW of Vancouver, BC	BLOY_VAN_GRE001	VAN	49.34209	-123.27301

Castle Is, BC	BLOY_VI_CAS001	ECVI	49.17654	-123.92863
Cleland Island, BC	BLOY_VI_CLEL001	WCVI	48.84316	-123.92863
Cleland Island, BC	BLOY_VI_CLEL002	WCVI	48.84316	-123.92863
Cleland Island, BC	BLOY_VI_CLEL003	WCVI	48.84316	-123.92863
Cleland Island, BC	BLOY_VI_CLEL004	WCVI	48.84316	-123.92863
Cleland Island, BC	BLOY_VI_CLEL005	WCVI	48.84316	-123.92863
Faber Isl, BC	BLOY_VI_FABE001A	ECVI	48.46683	-123.26458
Dock Islet, Gulf Islands, BC	BLOY_VI_GULF001	ECVI	49.17654	-123.92863
Arbutus Island, Gulf Islands, BC	BLOY_VI_GULF002	ECVI	48.89607	-123.47092
Dock Islet, Gulf Islands, BC	BLOY_VI_GULF003	ECVI	49.17654	-123.92863
Dock Islet, Gulf Islands, BC	BLOY_VI_GULF004	ECVI	49.17654	-123.92863
Snake Island, Nanaimo, BC	BLOY_VI_NAN001	ECVI	49.21820	-123.89164
Snake Island, Nanaimo, BC	BLOY_VI_NAN002	ECVI	49.21820	-123.89164
Five Finger Island, Nanaimo, BC	BLOY_VI_NAN003	ECVI	49.23122	-123.91594
Brandon Island, Nanaimo, BC	BLOY_VI_NAN004	ECVI	49.20712	-123.95838
Hudson Rocks, Nanaimo, BC	BLOY_VI_NAN005	ECVI	49.22596	-123.92666
Pinder Rock, BC	BLOY_VI_PIND001	ECVI	48.89233	-123.49804
Village Reef, BC	BLOY_VI_VIRE001	ECVI	48.87237	-123.47493
Wizard Is, BC	BLOY_VI_WIZ001	WCVI	48.89339	-125.14564
Wizard Is, BC	BLOY_VI_WIZ002	WCVI	48.89339	-125.14564
Wizard Is, BC	BLOY_VI_WIZ003	WCVI	48.89339	-125.14564
Wizard Island, BC	BLOY_VI_WIZ004	WCVI	48.89339	-125.14564