Satellite telemetry reveals habitat selection decisions by black oystercatchers across seasonal, diel, and tidal cycles

by

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Abstract

Habitat use of indicator species is used to prioritize management activities, but habitat use can vary temporally in response to changes in predation risk and foraging rewards. I examined black oystercatcher habitat preferences at four sites in BC, Canada, during the breeding and non-breeding season, and across diel and tidal cycles. Oystercatchers generally preferred islets and shoreline with limited tree cover that provide a refuge from predators and shoreline associated with freshwater outflows and larger intertidal areas that provide greater foraging rewards. However, preferences varied temporally in response to differences in predation risk and foraging rewards. Across the year, Individuals made greater use of larger islets with few surrounding trees and freshwater outflows with gravel substrates. My study highlights the importance of examining habitat use throughout the annual cycle and suggests that managers should protect a mosaic of marine shoreline providing both refuge from predators and productive foraging opportunities.

Keywords: shorebird; Argos; indicator species; intertidal health; Recurse

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Table of Contents

List of Tables

List of Figures

Pius Sullivan

Chapter 1. General introduction

1.1. Overview

The coast of British Columbia (BC), Canada, supports strong ocean-based industries (Stocks and Vandeborne 2017) and is predicted to see a seven-fold increase in marine shipping by 2023 (Short 2015). However, the BC coast also supports a diverse assemblage of bird species throughout the year (Ethier et al. 2020). Baseline data on the habitat use and movements of marine birds are therefore essential to enable regulatory agencies to mitigate risk and to act effectively in the event of an oil spill. To facilitate effective responses to an emergency, Environment and Climate Change Canada has adopted a focal species approach using satellite tracking technology to monitor seven marine bird species long term. Year round spatial-temporal information for these representative species will provide detailed information about where and when coastal birdlife use offshore, nearshore, subtidal and intertidal habitats.

The black oystercatcher was selected as the representative species for marine intertidal habitats because they are the only bird restricted to these areas year-round. Individuals must find suitable habitat to breed successfully, rest safely, and forage efficiently within a very narrow strip of marine shoreline. Breeding pairs defend small rocky islets, rocky outcrops, or gravel beaches, where they lay eggs just above the high-tide line. Black oystercatchers forage exclusively on marine macroinvertebrates and use their long bill to pry open bivalves, or force epifauna off rock surfaces (Andres and Falxa 2020). Black oystercatchers' range along the Pacific coast from the Aleutian Islands in the north, to Baja California in the south. Populations in the southern range are considered non-migratory, while populations in the north are partially migratory, i.e., some individuals migrate while others are resident (Johnson et al. 2010). Although there is no evidence for a decline in numbers, the black oystercatcher is a 'species of high concern' in several shorebird conservation plans due to its small total population size and restricted range (Tessler et al. 2014; Bennett 2019).

Many conservation organizations monitor black oystercatcher populations during the breeding season (e.g., US Forest Service, US National Park Service, Parks Canada, Laskeek Bay Conservation Society, California State Parks, Portland Audubon Society, see Tessler et al. 2014). For this reason, we have a considerable understanding of the

shoreline characteristics which influence nest-site selection, pair occupancy and reproductive success (Vermeer et al. 1992; Andres 1998; Hazlitt and Butler 2001; McFarland 2010; Weinstein et al. 2014; Dalgarno et al. 2017). Habitat use is expected to change during the non-breeding season when parental care duties are complete, and movements are less constrained to a central location. Currently, year round habitat use by black oystercatchers is not well understood and limited to single-site foraging observations (Hartwick and Blaylock 1979; Frank 1982) and broad-scale winter range use (Johnson et al. 2010). Due to recent technological advances which have reduced the size of tracking devices and increased the effective battery life (Hussey et al. 2015; Kays et al. 2015), examining year-round habitat use by birds like the black oystercatcher is now possible.

1.2. Annual survival of black oystercatchers carrying satellite transmitters

Tracking devices provide valuable movement information but can have negative effects on the birds that carry them (Barron et al. 2010; Costantini and Møller 2013). Surgically implanted tracking devices can have significant negative effects (Johnson et al. 2010; Hooijmeijer et al. 2014) and externally mounted tracking devices can increase energetic expenditure and reduce the survival of smaller taxa (Pennycuick et al. 2012; Vandenabeele et al. 2012). Ethical guidelines generally advise using externally mounted tracking devices that are below 5% of the body weight of a bird to reduce negative effects (Cochran 1980). However, others argue that less than 3% is a more conservative guideline (Kenward 2000; Vandenabeele et al. 2012). In some cases, morphology, ecology, life history traits (e.g., migration distance), or study location can influence the success of a particular tracking method (Vandenabeele et al. 2012; Chan et al. 2016; Weiser et al. 2016) therefore population and species-specific studies are necessary to guide researchers towards the safest and most effective methods.

For studies examining movements of shorebirds, securing transmitters externally with a harness is preferred over the use of surgical implants (Weiser et al. 2016). The leg-loop harness, which is commonly used in North America, secures a tracking device on the back of a bird with loops fitted around each thigh (Mallory and Gilbert 2008). However, there has been variable success tracking large shorebirds with this method. Marbled godwits and whimbrels tolerated satellite transmitters without discernable

effects (Ruthrauff et al. 2019a; Ruthrauff et al. 2021) while bristle-thighed curlews experienced lowered adult survival (Ruthrauff et al. 2019b). Red knots (Chan et al. 2016) and Pacific golden plovers (Johnson et al. 2020) showed considerable premature tag failures which were attributed to mortality events. The leg-loop harness, which is typically made of Teflon ribbon (Bally Ribbon Mills, Bally, PA), can also be removed quickly with the long tool-like bills of oystercatcher species (Johnson et al. 2010; Loring et al. 2017; Shiloh Shulte pers. comm). Eurasian oystercatchers have been tracked successfully (Ens et al. 2008; Bakker et al. 2021) with the use a wing harness design (Thaxter et al. 2014) which is not generally encouraged for the use on shorebirds by permitting authorities in North America. Due to the potential negative effects on large shorebirds and significant cost-per-unit of tracking devices, more research is needed to determine the safest and most effective method for long term tracking of black oystercatchers.

For this thesis, I tracked black oystercatchers using solar-powered satellite transmitters (Microwave Technology, PTT-100) to investigate year-round movements and habitat use. Transmitter units (3.9 x 1.8 x 1.3 cm) and the harness had a combined mass of 10.5g representing, on average, 1.7% of the mass of an individual (range: 1.5-2.0%, body mass ± SD: 622g±44g). I externally mounted transmitters with a reinforced leg-loop harness design and threaded nylon string through the Teflon ribbon tube to reinforce the harness and therefore increase the retention time on the bird. I deployed 20 transmitters in 2019 at four sites in British Columbia (Sunshine Coast = 4, Pacific Rim National Park Reserve = 6, Masset Inlet = 4, Skidegate Inlet = 6) and assessed time-to-tag-failure and whether the birds were observed later without the harness (Table 1).

Microwave satellite transmitters had a low failure rate, and the reinforced harness had a retention time suitable for the goals of the study. One transmitter failed after six months, and the intact harness and device was found near the individual's breeding location under the perch of a bald eagle. Six individuals were tracked for approximately one year (10-12 months), and 13 individuals were tracked for greater than one year. Three black oystercatchers have been tracked for more than two years and their tags remain active as of September 2021. Tag failures appeared to be a result of the removal of the leg-loop harness. To date, 9 of 16 individuals with failed transmitters have been observed without the harness and tracking device. One transmitter with a broken harness was found at a popular location and is presumed to have been removed by the individual. The observed annual survival after tagging (95%) was comparable to survival

estimates for banded adult black oystercatchers (87%, Alaska 2003-2007, D. Tessler unpubl. data; 90±3%, BC 2008-2013, P.Clarkson & Y. Zharikov unpubl. data). I therefore recommend the reinforced leg-loop harness for future studies aiming to track non-migratory oystercatchers.

The primary objectives for this thesis are to provide baseline information on the year-round use of coastal habitat by black oystercatcher populations at each site. I also examine how the preferences for marine shoreline change from the breeding to the non-breeding season, from day to night, and from high to low tides (see Chapter 2). Further, I estimate individual home range size, and the associated length of shoreline within a home range, and examine whether home range size varies by sex, breeding status, or site. Within home ranges, I investigate which characteristics influence the repeated use of key habitat features by individuals over one year. In Chapter 3, I summarize my findings, suggest future directions, and discuss the management and conservation implications of my research.

Table 1.1. **Status of 20 black oystercatchers tracked with Microwave solar PTT-100 satellite transmitters (9.5g) externally mounted with a reinforced leg-loop harness. Last assessed September 21, 2021.**

Study Site	Individual	Date of Deployment	Date of last location	Active Period	Fate
Sunshine Coast	177756	2019-02-28	2020-06-08	> 1 year	Removed harness
	177757	2019-03-01	2020-07-17	> 1 year	Removed harness
	177758	2019-03-01	2020-11-14	> 1 year	Removed harness
	177759	2019-02-28		> 2 years	Ongoing
Pacific Rim National Park Reserve	177760	2019-03-09	2020-05-27	> 1 year	Unknown
	177906	2019-03-09	2020-09-16	> 1 year	Removed harness
	177907	2019-03-12	2020-01-16	~ 10 months	Removed harness
	177908	2019-03-11	2021-03-11	2 years	Unknown
	177909	2019-03-10		> 2 years	Ongoing
	177910	2019-03-10	2020-01-12	~ 10 months	Removed harness
Masset Inlet	177912	2019-03-21	2020-04-25	> 1 year	Removed harness
	177913	2019-03-22	2020-03-31	~ 1 year	Unknown
	177914	2019-03-22	2020-02-18	~ 11 months	Removed harness
	177915	2019-03-23	2020-01-29	~ 10 months	Unknown
Skidegate Inlet	177911	2019-03-28	2020-09-10	> 1 year	Removed harness
	177916	2019-03-25		> 2 years	Ongoing
	177917	2019-03-25	2019-08-12	~ 6 months	Depredated
	177918	2019-03-26	2020-06-02	> 1 year	Unknown
	177919	2019-03-26	2021-01-30	> 1 year	Unknown
	177920	2019-03-28	2020-03-18	~ 1 year	Removed harness

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Chapter 2. Selection of marine shoreline by black oystercatchers over one annual cycle

2.1. Introduction

Habitat selection decisions influence diet, energetic intake rates, survival, and reproductive success of individuals (Hutto 1985; Block and Brennan 1993). Resources, however, are unevenly distributed both in space and time requiring individuals to regularly update these decisions (Fretwell and Lucas 1969; Railsback and Harvey 2002). Individual habitat selection decisions and movement between sites can also be influenced by behavioural constraints, environmental stimuli and trade offs, and consequently reflect the risks and rewards to an individual (Block and Brennan 1993; Mayor et al. 2009). For example, during a breeding season, movement is likely constrained by the need to provide parental care, so individuals may prioritize reproduction and select habitat that reduces predation and increases offspring survival (Fontaine and Martin 2006). During the non-breeding season, individuals can move more widely and may instead prioritize the selection of habitat that enhances their own survival, energetic intake, and future reproductive success (Marra et al. 1998). Similarly, habitat selection decisions are likely to change across finer scales throughout the day when there are fluctuations in predation danger and foraging availability (Lima and Dill 1990). Many taxa, including zooplankton (Iwasa 1982), rodents, (Kotler et al. 1991), birds (Conklin et al. 2008), and ungulates (Tambling et al. 2012) move between safe refuges and foraging habitat during periods of the diel cycle, i.e., day or night (reviewed by Kohl et al. 2018).

Despite the spatio-temporal patterns of habitat use observed in many taxa, studies examining habitat selection decisions are frequently limited to one time-period or season (Schooley 1994; Lunardi et al. 2012; Marra et al. 2015; Specht et al. 2020). However, advances in tracking technology that allow smaller animals to be tracked for longer periods provide an opportunity to investigate individual movement and habitat selection decisions throughout the annual cycle (Cagnacci et al. 2010; Knight et al. 2021; Stanley et al. 2021). The quantity of high-quality spatial data which can be obtained provides valuable information and exciting opportunities for wildlife managers and conservationists (Kays et al. 2015; Fraser et al. 2017; Lamb et al. 2020). For

example, determining *when* and *how often* animals visit particular locations can be used to identify characteristics important for wildlife corridors (Bastille-Rousseau and Wittemyer 2021), foraging habitat (Watts 1998; Schloesing et al. 2020), roosts (Bracis et al. 2018) and breeding sites (McKeown et al. 2020; Picardi et al. 2020). However, increasing quantities of data can also pose analytical challenges (Lewis et al. 2018). Large datasets require new methods for data management, manipulation, and analysis to maintain data integrity and avoid redundancy (Hebblewhite and Haydon 2010; Urbano et al. 2010). More powerful tracking devices, and therefore more data, can also inflate existing biases (i.e., increased sampling during some behaviours or periods of abundant solar energy) which if unchecked can lead to erroneous conclusions (Fieberg et al. 2010; Frair et al. 2010; Silva et al. 2017). Fortunately, there has also been development of new and sophisticated analytical tools for describing, processing, visualizing, and analysing complex wildlife tracking datasets (Joo et al. 2020).

The black oystercatcher (*Haematopus bachmani*) is a shorebird restricted marine shoreline habitat on the Pacific coast of North America, where they forage exclusively in the intertidal zone for macro-invertebrate prey (Tessler et al. 2014). Suitable territories for nesting are limited because a site must provide protection from nest predators as well as nearby foraging resources (Dalgarno et al. 2017). Adult breeding pairs aggressively defend their territories (Andres and Falxa 2020), which may constrain their movements during the spring and summer. Previous habitat research on the black oystercatcher has focussed on selection decisions during the breeding season, determined where individuals choose to nest, and measured how habitat characteristics influence breeding success. Studies found that nest-site selection is greatly influenced by habitat characteristics which reduce predation risk such as isolation or distance from vegetation (McFarland 2010; Weinstein et al. 2014; Dalgarno et al. 2017). Slope of the intertidal of the intertidal, which influences foraging availability, has been shown to affect breeding pair density (Andres 1998) and reproductive success (Hazlitt 2001). Although habitat use is expected to change as reproductive duties have concluded, habitat studies outside the breeding season are limited (Hartwick and Blaylock 1979).

Here, I use satellite tracking data to describe the year-round space use and habitat selection decisions by black oystercatchers at four study sites in British Columbia, Canada. I examine habitat selection at the level of the population and the individual (Johnson 1980). First, I compare the coastal marine habitat used by black

oystercatchers with the available habitat at each site. I examine whether these population level habitat preferences vary across seasons, diel, and tidal cycles. I predicted that black oystercatchers would prioritize the use of safe areas during the breeding season, during the night, and during high daytime tides. I predicted black oystercatchers would use more productive shoreline during the non-breeding season, when individuals are less constrained by reproductive behaviour, and during low daytime tides, when access to marine prey was greatest. Having identified two key features of the marine shoreline used by oystercatcher populations (rocky islets and shoreline associated with freshwater outflows), I evaluate the function and ecological value of these features by examining how their location and physical attributes affect their use by the tracked individuals.

2.2. Methods

2.2.1. Study species

The black oystercatcher (*Haematopus bachmani*) is a large shorebird (500-700g) found on rocky Pacific shores of North America from the Aleutian Islands, Alaska, to Baja California, Mexico (Andres and Falxa 2020). Black oystercatchers are one of the continent's least abundant shorebird species with an estimated global population of 12,500-17,500 (Tessler et al. 2014; Weinstein et al. 2014; Bennett 2019). The black oystercatcher is considered a species of concern by coastal agencies and breeding pairs are often monitored as indicators of rocky shoreline health (Tessler et al. 2014). In BC, egg laying occurs between late April (Kenyon 1949; Hatler et al. 1978) and early June (Vermeer et al. 1992; Hipfner et al. 2012) and are incubated for 26-28 days. Semi-precocial young depend on provisioning adults for 5-6 weeks (Nysewander 1977). Adults and chicks feed exclusively on intertidal macro-invertebrates, particularly mussels, limpets, and chitons (Hartwick 1973; Hazlitt et al. 2002).

2.2.2. Study area

The province of British Columbia (BC) hosts over 25,000 kilometres of coastline characterized by rocky shores and temperate forest (Gilkeson et al. 2006). The coast of BC has mild temperatures year-round (average winter: 2C, average summer: 26C) and high rainfall, ranging from 140-330cm annually, and occurring primarily between October

and March (Environment Canada 2020). I studied black oystercatchers at four coastal areas of BC (Figure 1): Sunshine Coast on the southern mainland, Pacific Rim National Park Reserve on the west coast of Vancouver Island, Skidegate and Masset Inlets on the archipelago of Haida Gwaii. The Sunshine Coast is located within the Salish Sea, a relatively protected body of water with considerable freshwater and sediment discharge from several major rivers (Gilkeson et al. 2006). Pacific Rim National Park Reserve is situated on exposed coastline with nutrient rich nearshore waters (Parks Canada Agency 2021). The Haida Gwaii archipelago, located on the northern BC coast, is rugged and experiences harsh weather, however the two study sites are relatively sheltered from the elements.

2.2.3. Field methods

I captured black oystercatchers between February 28 and March 28, 2019, using noose-mats, decoys (Mad River Decoys), and an audio lure (Foxpro Inferno). I targeted pairs and flocks and used both passive and active capture techniques. I banded all black oystercatchers with a USGS stainless steel band on the right tarsus and a pair of green alpha-numeric plastic bands for unique identification (Haggie Engraving, Millington, MD). Plastic bands were fitted on the tibia as they are known to become worn and incomprehensible within 3 years when worn on the tarsus (Hazlitt 2001). I measured the exposed culmen (± 0.1mm) and tarsus (± 0.1mm) with plastic calipers (SPI Polymid Dial 150mm) and mass (± 5g) using a hanging scale (Pesola Medio 1000g). I assigned individuals a probable sex by eyefleck category (Guzzetti et al. 2008), where females show a moderate to distinct eyefleck (category 3) and males show little to no eyefleck (category 1). Black oystercatchers with an intermediate eyefleck (category 2) cannot be confidently assigned a sex outside the breeding season and were not assigned a probable sex (Guzzetti et al. 2008).

I deployed solar-powered Argos satellite transmitters (9.5g, PTT-100, Microwave Technology, Columbia, MD) on 20 adult black oystercatchers. Transmitters, glued to a 3mm neoprene patch to prevent abrasion, were mounted on the synsacrum of the birds using leg-loop harness (Mallory and Gilbert 2008) made from Teflon ribbon tubing (Bally Ribbon Mills, Bally, PA). I reinforced harnesses with nylon trammel-line because oystercatchers can rapidly remove harnesses made with Teflon ribbon alone (Johnson et al. 2010; Loring et al. 2017, Shiloh Shulte pers. comm.). Transmitter units (3.9 x 1.8 x

1.3 cm) and harness had a combined mass of 10.5g representing, on average, 1.7% (range: 1.5-2.0%) of the bird's mass (body mass ± SD: 622g±44g).). Satellite transmitters were programmed to transmit 10 hours ON and 48 hours OFF when they had suitable solar charge. Transmitters switched off when they did not have suitable charge but resumed the duty cycle when the batteries re-charged.

Where possible, I attempted to relocate birds in the field between April and July 2019, to determine whether tagged birds were defending breeding territories. I classified birds as "breeding" if they were observed in territorial pairs in suitable nesting habitat, or with an active nest or chicks. Birds were classified as "non-breeding" if they were not territorial and/or observed in unsuitable nesting habitat during the breeding season.

2.2.4. Processing satellite tracking data

The Argos system (CLS America, Lanham, MD) uses seven satellites to detect radio transmissions from the tracking device and estimates its location on the earth's surface with a radius of error. Accuracy of coordinates are improved when the transmitter/tracked animal is motionless, or when multiple satellites triangulate the source of transmission. Estimated locations are assigned a quality class of 3, 2, 1 or 0, or locations with no estimates are assigned a class A, B or Z. For this study, I retained location classes 3 (<250m), 2 (250-500m), and 1 (500-1500m). The reduced dataset included 17,954 Argos locations for 19 individuals over a 12-month period (562-1256 per individual). One transmitter failed after six months due to a mortality event and data from this individual were excluded from analyses.

I determined whether each location occurred during day or night hours, during high or low tides, and breeding or non-breeding seasons. I defined 'daytime' as the hours between sunrise and sunset, and 'nighttime' as the hours between sunset and sunrise. I determined twilight times using the R package 'suncalc' for each date and location as sunrise and sunset times change over the year and by location (Thieurmel and Elmarhraoui 2019). I classified 'high' and 'low' tides as the highest and lowest 50% of tide height predictions, by tide-station and week of the year. I obtained hourly tide height predictions from 15 tide-stations from the website 'http://tbone.biol.sc.edu/tide' and assigned stations to each oystercatcher location based on proximity and logical geography of the coastline (e.g., inlets). I defined the 'breeding season' as the months of

April to July (4 months) when individuals are most likely defending a territory, incubating eggs, or caring for young (Andres and Falxa 2020). I defined the 'non-breeding season' as August to March (8 months) when individuals are less likely to be restricted to a central location by breeding behaviour.

Some individuals and periods of time contributed more Argos location data than others. To reduce bias associated with unequal sampling, I retained 4 locations per week per individual. I selected a ratio of 3 daytime to 1 nighttime location to retain the original proportion of day to night locations in the dataset and favoured higher quality Argos location classes (e.g., selecting class 3 locations over class 2, and class 2 locations over class 1 locations). The filtered dataset included 2681 locations, with 19 individuals contributing an average of 138 data points (117-161). There were time gaps in the sample due to limited solar power during winter months, however the data were evenly split between the breeding and non-breeding periods and high and low tides. The final dataset was composed of 86% class 3 locations, 10% class 2, and 4% class 1.

2.2.5. Description of individual home range

Methods for estimating home range of animals constrained to linear features (e.g., canyons, rivers, coastlines) are prone to overestimation of actual space-use (Slaght et al. 2013; Tarjan and Tinker 2016). I therefore described the geographic extent of the home range, calculated the total length of shoreline within this area, and estimated the length of shoreline used by black oystercatchers. I first generated 95% minimum convex polygons (MCP) to estimate the area within which individuals spent the year using the R package 'adehabitathr' (Calenge 2006). The MCP method is simple and remains commonly used allowing comparison with other studies and species (Yetter et al. 2018; Knüsel et al. 2019; Weithman et al. 2020; Jourdan et al. 2021). I calculated the total length of shoreline within each annual home range area by overlaying the MCPs on top of the ShoreZone polyline dataset (Howes et al. 1994). Next, I used the Argos location data to estimate the total length of shoreline (km) used by individuals by generating a 250m buffer around locations and calculating the length of shoreline intersecting the buffer. Finally, I calculated the proportion of shoreline used by individuals within each MCP.

2.2.6. Habitat selection across seasonal, diel, and tidal cycles

Habitat units and potential drivers of habitat use

To determine what drives population-level habitat use by black oystercatchers, I described the marine shoreline at a resolution matching the satellite tracking data (approximately 250m). Within four site-specific 95% MCP areas (Figure 2), I generated representative points, hereafter 'shore-points', every 500m along the shoreline with ArcGIS Pro (version 3.2.0) and the 'Generate Points Along Lines' tool. The straight-line distance between these shore-points averaged 290m (range: 65-2110m) depending on coastline geography. I manually generated additional shore-points on islets/islands, or groups of islets/islands separated by <250m, that were not captured by the automated tool (i.e., the length of shoreline associated with the island was less than 500m). This resulted in a total of 2125 shore-points (Sunshine Coast = 834, Pacific Rim National Park Reserve = 776, Skidegate Inlet = 362, Masset Inlet = 153).

I described the characteristics of each shore-point using 10 variables associated with either prey availability, safety, or human disturbance (Table 1). The availability and abundance of marine invertebrates in the intertidal zone can be influenced by several physical characteristics of the shoreline, such as substrate, slope, aspect, and nutrient supply (Kaiser et al. 2011). Substrate size is important to invertebrate species composition. I categorised shoreline substrate information into 6 classes ('bedrock', 'mixed-rock', 'gravel', 'sand', 'mudflat,' 'man-made') by reclassifying 34 ShoreZone coastal classes (Howes et al. 1994). ShoreZone classes containing multiple substrate types were assigned to the category of the larger substrate type (Substrate). For example, 'sand and gravel beach' (class 25) would be reclassified into a new category 'gravel' rather than 'sand'. I also extracted wave exposure information from the ShoreZone dataset in the form of 6 ordinal values (Exposure): 'very protected', 'protected', 'semi-protected', 'semi-exposed', 'exposed', 'very exposed'. Shoreline associated with freshwater outflows, like estuaries, support high numbers of invertebrates, fish, and birds (Ravenscroft and Beardall 2003; Kaiser et al. 2011). I categorised shore-points as being associated with a freshwater outflow (Outflow: yes/no) if they were within 500m of a permanent freshwater stream. I used second-order streams and above (stream orders 2-5), because first-order streams do not flow year-round and therefore do not provide a consistent nutrient supply. I chose 500m because a

freshwater source influences the marine environment several hundred metres from a rivers mouth and varies by stream size and season (Tallis 2009). In the northern hemisphere, south facing slopes receive more solar energy than north facing areas, which influences rates of primary productivity (Kaiser et al. 2011). I first obtained a 100x100m Digital Elevation Model (DEM) for each study area from the website 'https://maps.canada.ca/' and converted the cell values to represent a direction value in degrees (0-360), which was then extracted by intersecting shore-points. Because aspect is a circular value (e.g., 0 and 360 both indicate north) and is therefore problematic for linear regression analysis, I converted these values to represent how southward facing the shoreline was (Southness: 0-180). For example, 0 is north facing shoreline, 90 is east or west, and 180 is south. Finally, I estimated the amount of intertidal habitat available to oystercatchers at low tides. Slope of the shoreline plays a role in structuring intertidal communities (Ricciardi and Bourget 1999; Bloch and Klingbeil 2016) and impacts accessibility for terrestrial predators. A lower sloping shoreline has larger intertidal areas and longer exposure times between tidal cycles in which predators like the black oystercatcher can search for and consume marine invertebrate prey (Hazlitt 2001). I created a spatial layer representing the intertidal area exposed during Lowest Normal Tide at the four study sites. I downloaded the Canadian Hydrographic Service 'high water mark' and 'low water mark' vector polylines from the DataBC website (https://data.gov.bc.ca/) and used the 'Feature To Polygon' tool to convert the independent line features to a single polygon layer. I used the 'Within' tool to calculate the percent of intertidal area within a 250m radius of shore-points (Intertidal$_{250}$).

Shorebirds will adjust habitat selection decisions based on the perceived risk of predation (Pomeroy et al. 2008; Sprague et al. 2008; Johnston-González and Abril 2019; Hope et al. 2020). Black Oystercatchers prefer rocky islets as nest-site locations (Hazlitt and Gaston 2002; Weinstein et al. 2014; Dalgarno et al. 2017) which are difficult for mammalian predators to access and often lack trees used as hunting perches by birds of prey (e.g., bald eagle). Trees and other vegetation also act as visual barriers that reduce the ability of shorebirds to detect oncoming predators (Pomeroy 2006). I defined shore-points as islets (Islet: yes/no) if a shore-point was located on a small island with an area less than 1.5 hectares. I chose the threshold of 1.5 hectares because larger islands typically supported trees. I created a polygon layer that represented the forested areas along the shore by manually digitizing polygons over 1:5000 satellite imagery (ESRI

Basemap Imagery) then estimated the percent area that was treed within a 250m radius of shore-point locations ($Tree_{250}$). Bushes and shrubs were not included in the tree layer.

Shorebirds are sensitive to human disturbance (Burger 1986; Goss-Custard and Verboven 1993; Peters and Otis 2006; Yasué 2006) and oystercatcher pairs tend to be especially vulnerable to disturbance during the breeding season (Leseberg et al. 2000; Borneman et al. 2016; Andres and Falxa 2020). I used distance from roads (RoadDist) and the proportion of urban development within a 250m radius of each shore-point ($Human_{250}$) as indices of human disturbance. I measured RoadDist as the Euclidean distance (km) of a shore-point to the nearest road, including all road types from the BC Road Atlas. To calculate $Human_{250}$, I used the 'Urban' class from the BC Baseline Thematic Mapping Land Use layer (https://data.gov.bc.ca/).

Use of shoreline by black oystercatchers at four sites

For each site, I defined shore-points as being used by black oystercatchers during the breeding and non-breeding season, day and night, and high and low tide if a satellite transmitter location from one or more individuals was within 250m of a shore-point. To do this, I overlaid the filtered Argos data from individuals with overlapping home ranges (n=18) on the shore-points layer within four site-level MCPs (Figure 2). I split the tracking data into the three categories (day/night, daytime high/low tides, breeding/non-breeding seasons) and for each set coded shore-points within 250m of locations as '1' (present) and other shore-points as '0' (available).

Statistical analysis

I used generalized linear mixed-models (GLMM) to compare the habitat used by black oystercatchers with habitat available at each site and evaluate how habitat characteristics associated with foraging opportunity, safety, and disturbance influenced use. The set of six GLMMs representing the seasons, diel and tidal periods, included site as a random effect and were fitted using a binomial distribution and logit link with the R package 'glmmTMB' (Brooks et al. 2017). I chose to combine the locations from multiple individuals because habitat used overlapped considerably (see Figures A.2-A.5), individuals contributed a relatively small number of locations, and the number of locations and shore-points used per individual declined as the dataset was split by seasons, day/night and high/low tides. Combining the tracking data allowed for a more

representative set of used and available shoreline at the population level, a more clear examination of changes across the temporal cycles, and reduction of spatial autocorrelation in the models. To further reduce spatial autocorrelation in the models, I compared the characteristics of shore-points that were used by oystercatchers with a randomly selected subset (50%) of shore-points available. The dataset therefore included 388 shore-points that were used by black oystercatchers during any of the six time periods and 1063 shore-points that were available.

Prior to building the models, I examined the suitability of each variable for this analysis. I found little variation in Exposure, with most shore-points within a site categorized as the same ordinal value. $Urban_{250}$, which was only greater than zero in a small proportion of shore-points (Sunshine Coast = 20%, Pacific Rim National Park Reserve = 5%, Masset Inlet = 3%, Skidegate Inlet = 7%), was unsuitable for this analysis. Substrate information was missing for some shore-points (3%) and was excluded from this analysis because all islets were bedrock; however, Substrate was evaluated as a predictor for the high use of key habitat features (see subsequent section). RoadDist was removed because roads were generally absent from three of the sites and therefore could not affect within-site movements. I also assessed the relationship between the two binary variables (Islet and Outflow) and the other descriptive variables. Islets were associated with low proportions of trees, and outflows tended to be associated with larger intertidal areas (Appendix A, Figure 1), however variation inflation factors remained low (VIF < 3) suggesting that the inclusion of all 4 variables was not problematic (Zuur et al. 2010). The final models included two binary variables, Outflow (15.3% of shore-points) and Islet (14.7% of shore-points) as well as two numerical variables, $Intertidal_{250}$ (range: 0.3-88.6%, mean: 14.0 ± 13.2) and $Tree_{250}$ (range: 0.0-85.9%, mean: 36.4 ± 19.9).

Spatial dependence (autocorrelation) is a common issue in ecological analyses and can cause erroneous inferences when data points that are closer together in space are not independent (Fletcher and Fortin 2018). I evaluated spatial autocorrelation (SAC) by calculating the Morans I value for model residuals and inspecting the correlogram plot. Model residuals within 500m showed evidence of spatial autocorrelation (Morans I > 2.0). I therefore generated and included a spatial auto-covariate term in each model which reduced SAC in the model residuals to negligible levels (Fortin et al. 2002). All

statistical analyses were conducted using R Studio 3.6.1 (R Development Core Team 2015).

2.2.7. Use of key shoreline features by individuals

Habitat features and characteristics

Preliminary results showed that black oystercatchers made repeated use of islets and shoreline associated with freshwater outflows within their home ranges. I identified 131 islets (Sunshine Coast = 14, Pacific Rim National Park Reserve = 75, Skidegate Inlet = 25, Masset Inlet = 17) and 39 outflows (Sunshine Coast = 13, Pacific Rim National Park Reserve = 6, Skidegate Inlet = 15, Masset Inlet = 5) visited by a tracked oystercatcher at least once during the annual cycle. I described islets and outflows using characteristics known to be associated with foraging opportunity, safety, and disturbance (Table 1). Metrics assessing the proportion of intertidal, trees, or urban development used a 1000m buffer, rather than 250m, because islets and outflows were generally spatially segregated, and I aimed to describe the surrounding area of the habitat feature rather than the segment of shoreline. For each islet and outflow feature I additionally calculated the distance (kilometres) to the centre of an individual's core home range (50% MCP).

Islets were described by five characteristics. Intertidal area, wave exposure, and distance to a freshwater outflow were expected to influence foraging opportunities in the area surrounding the islet. Intertidal area ($Intertidal_{1000}$) and Exposure were calculated as described in the previous section and OutflowDist was calculated as the Euclidian distance in kilometres from a freshwater outflow (stream order > 1). The area of an islet and the trees in the surrounding area are expected to influence the perceived safety. While smaller islets are less likely to host trees, and they may be more susceptible to wave inundation. To determine whether larger or smaller islets are revisited more often, I calculated the area of each islet above the mean high tide line (hectares). The percent area of trees within 1000m ($Tree_{1000}$) was calculated as described in the previous section.

Outflows were described by nine characteristics: Intertidal area, substrate type, aspect, exposure, and stream size were expected to influence foraging opportunity for the black oystercatcher. $Intertidal_{1000}$, Substrate, Southness and Exposure were

calculated as described in the previous section. The amount of freshwater entering the marine environment has major influence on the production, diversity, and distribution of invertebrates in the surrounding system (Kaiser et al. 2011). I determined the stream order (StreamOrder) and stream magnitude (StreamMag) of the stream segment intersecting the intertidal zone. Stream order is a commonly used ordinal metric to group stream segments by similar hydraulic properties, and stream magnitude quantifies the number of tributaries flowing into a given segment. Stream locations and attributes were obtained from the BC Freshwater Atlas obtained from the DataBC website (https://catalogue.data.gov.bc.ca/).

I used the 'recurse' package in R (Bracis et al. 2018) to assess the repeated use of islets and outflows by individual black oystercatchers. Using the filtered Argos locations, I calculated the number of visits individuals made to unique islets and outflows. I used a central coordinate for each islet/outflow and considered a visit as an individual's location within 500m of the habitat feature.

Statistical analysis

I developed two sets of candidate models to examine the factors driving the repeated use of islets and shoreline associated with freshwater outflows, within the home ranges of individual oystercatchers. Preliminary examination of human disturbance, hypothesized to influence the use of shoreline, found that almost all islets and outflows had no urban cover and were located long distances from roads, so Urban$_{1000}$ and RoadDist were excluded from these analyses. I also excluded the variable Exposure because it did not demonstrate enough variation within individual home ranges to influence repeated use. I therefore examined the role of Intertidal$_{1000}$, OutflowDist, IslandArea and Tree$_{1000}$ on the relative revisitation to islets. For outflows, I examined the role of Intertidal$_{1000}$, Substrate, StreamOrder, and Tree$_{1000}$ and Southness.

The candidate set examining the repeated use of islets included univariate and multivariate models with all combinations of the four habitat variables (n = 16). All models in this set included a variable CentroidDist, which controlled for the distance of an islet to the centre of an individual's home range as well as a spatial autocovariate term. CentroidDist was estimated as the Euclidean distance in kilometres from the central coordinate of the 50% MCP to each islet. The autocovariate term corrected the spatial autocorrelation within 500m (Morans I > 2.0) in the model residuals.

The candidate set examining the repeated use of outflows included univariate and multivariate models with combinations of two and three variables. Models with four variables failed to converge. I did not include the variable CentroidDist in the candidate set because preliminary analyses indicated that visits by black oystercatchers were not influenced by the outflow's proximity to their core area. Models in this set also did not include an autocovariate term because there was no evidence for spatial autocorrelation in the model residuals (Morans I < 2.0).

All GLMMs included individual as a random term and were fitted using a negative binomial distribution for over-dispersed count data (Brooks et al. 2017). I ranked models in each candidate set by Akaike's information criterion (AICc) and Akaike weights (w_i) (Burnham and Anderson 2004) and models with the lowest AIC values were identified as the most parsimonious. I calculated ΔAIC as the difference in AIC between each model and the top model and report % model deviance, marginal and conditional R^2. I used the R package 'glmmTMB' to run the models (Brooks et al 2017) and the package 'performance' to estimate marginal and conditional R^2 (Nakagawa and Schielzeth 2013). Last, I validated the models by inspecting the observed model residuals against the expected with the package 'DHARMa' (Hartig 2020). All statistical analyses were conducted using R Studio 3.6.1 (R Development Core Team 2015).

2.3. Results

All 20 black oystercatchers that carried transmitters were non-migratory and remained within the region they were captured. Nineteen individuals were tracked for approximately one year and eight continued to transmit into the subsequent year. One transmitter failed after six months and was recovered near its nest site under the perch of a bald eagle. Nine individuals with failed tags were later observed alive without transmitters and harnesses.

2.3.1. Description of individual home range

I estimated the annual space use and associated linear shoreline use of 19 black oystercatchers from four sites in BC (Sunshine Coast = 4, Pacific Rim National Park Reserve = 6, Skidegate Inlet = 5, Masset Inlet = 4). Black oystercatcher movements over the course of a year encompassed an area of, on average, 153 km², but there was

enormous variation among individuals (95% MCP range: 5-1193 km^2). Individuals in the Sunshine Coast study area moved over a larger area than those residing at the other three sites (mean 95% MCP ± SD: Sunshine Coast = 501±483, Pacific Rim = 92±91, Skidegate Inlet = 44±61, Masset Inlet = 25±13; controlling for breeding status and sex, $F_{3,11}$ = 6.5, p < 0.01). Black oystercatchers that were later confirmed as breeding (n = 7) also tended to have smaller MCPs than those that were later confirmed not breeding (n = 5), or whose breeding status was unknown (breeding = 56±77, non-breeding = 282+510, unknown status = 159±160, $F_{2,11}$ = 2.4, p = 0.14; breeding-nonbreeding contrast: t = -2.6, p = 0.02). However, the sex of an individual had no detectable effect on the size of their 95% MCP (female = 298±502, n = 5; male = 112±128, n = 5; unknown sex = 97±142, n = 9; $F_{2,11}$ = 4.0, p = 0.05; female-male contrast: t = 0.58, p = 0.57). Black oystercatcher MCPs contained, on average, 46 km of shoreline (range: 12-156km) with larger MCPs containing more linear shoreline habitat (r_p = 0.92, p < 0.01). Black oystercatchers used, on average, 10.4 km or 33% of the shoreline within their MCP. All birds used a similar amount of shoreline (range: 6.7-13.9 km) as individuals with a larger MCP used a smaller proportion of the shoreline available than those with a small MCP (r_p = -0.60, p < 0.01).

2.3.2. Habitat selection across seasonal, diel, and tidal cycles

Black oystercatcher populations used 11-39% of the habitat units (shore-points) that described the marine shoreline available at each study site (Sunshine Coast = 11%, Pacific Rim National Park Reserve = 15%, Skidegate Inlet = 32%, Masset Inlet = 39%). Black oystercatchers made extensive use of islets and selected shoreline near freshwater outflows, with larger intertidal areas and fewer trees. These shoreline characteristics are associated with variation in predation risk and foraging opportunities and therefore vary seasonally and across diel and tidal cycles.

Black oystercatchers used islets more than expected based on their availability, during the non-breeding season (z = 3.7, p < 0.001) but this pattern was not observed in the breeding season, when the movement of some individuals was likely constrained due to territoriality and parental care (z = 0.9, p = 0.36). Islets were also used more than expected during daylight hours (z = 3.3, p < 0.001), the night (z = 2.1, p < 0.05), and during periods of high tides (z = 2.8, p < 0.05), when access to the intertidal zone was restricted. Black oystercatchers used freshwater outflows more than expected during the

non-breeding season (z = 2.5, p < 0.05) but not during the breeding season (z = 0.3, p = 0.7). Freshwater outflows were also used more than expected during daylight hours (z = 2.3, p < 0.05) but not during the night (z = 1.4, p = 0.2), when black oystercatchers likely prioritize safety away from vegetation and mainland shores. Interestingly, freshwater outflows were used more than expected during daytime high tides (z = 3.0, p < 0.05) and not during low tides (z = -0.4, p = 0.7).

Black oystercatcher preferences for shoreline with more foraging habitat were not apparent when assessed at a seasonal scale; populations did not use shorelines with more intertidal habitat during either the non-breeding or breeding season (non-breeding: z = 1.8, p = 0.07; breeding: z = 1.0, p = 0.34). Intuitively, shoreline with larger intertidal areas was used more than expected during daylight hours (day: z = 1.9, p = 0.05; night: z = 1.0, p = 0.31) and during daytime low tides (low tide: z = 3.0, p < 0.05; high tide: z = 0.8, p = 0.42).

Black oystercatchers avoided shoreline with more tree cover, expected to increase the risk of predation by birds of prey, during all time periods. Avoidance of shoreline with greater tree cover was stronger during the breeding season relative to the non-breeding season, stronger at night relative to the daytime, and stronger during high tides relative to low tides (Figures 3-6). The GLMMs that evaluated the importance of habitat characteristics on shoreline use by black oystercatchers explained 43-58% of the variation in the data (marginal R^2 = 0.43-0.58, percent deviance = 3-24%).

2.3.3. Use of key shoreline features by individuals

Black oystercatchers made extensive use of islet and outflow features over the course of one year. Individuals visited, on average, 11 islets (range: 3-29, n = 19) but returned to some islets up to 29 different times while using other islets only once. Individuals visited an average of four freshwater outflows (range: 1-8, n = 16) in one year, from one to 10 times. Islets were visited more often if they were closer to the centre of an individual's core area (ΔAICc: Null model = 42, CentroidDist = 19, CentroidDist+CentroidDist^2 = 15) but this did not influence intensity of outflow use (ΔAICc: Null model = 20, CentroidDist = 21 , CentroidDist+CentroidDist^2 = 24).

Islets

After controlling for the location of islets relative to the centre of an individual's core area, black oystercatchers returned more times to islets if there was less tree cover within a 1000m radius, if the islet was larger, and if the islet was closer to a freshwater outflow. Five of the 16 models in the candidate set, examining variation in the use of islets, received substantial support (ΔAICc < 2.0, Table 2). The top-ranked model included three terms: percent tree cover within a 1000m radius ($Tree_{1000}$), islet area (IsletArea), and distance to freshwater outflow (OutflowDist). This model received substantially more support than the null model and twice as much support as a more parsimonious model that only included the tree cover variable. $Tree_{1000}$ was included in all well supported models (Σw_i = 1.0). The top model predictions estimate that the number of times an individual visited an islet decreased 6-fold as the proportion of tree cover increased from 0% to 50% (β = -0.02, 95% CI = -0.04 to -0.01, Figure 6A).

The size of an islet term (IsletArea) was included in three of the five well-supported models and received moderate support (Σw_i = 0.50), although the model averaged parameter estimate had confidence that bounded zero (β = 0.27, 95% CI = -0.05 to 0.60). The top model predictions estimated that the number of times an individual visited an islet increased by 50% as the islet area increased from 0.01 to 1.5ha (Figure 6B). The distance to a freshwater outflow term (OutflowDist) was included in two of the five well-supported models and received moderate support (Σw_i = 0.41), although the model averaged parameter estimate, again, had confidence that bounded zero (β = -0.07, 95% CI = -0.15 to 0.01). The top model estimated that the number of times an individual visited an islet decreased by 40% as the distance from the islet to a freshwater outflow increased from 1km to 10km (Figure 6C). The remaining term, the amount of intertidal habitat within 1000m radius of the islet ($Intertidal_{1000}$), was included in one well-supported model. However, this model received half of the support as the top model and the model averaged parameter estimate suggested that intertidal habitat had little impact on islet use by individuals (β = 0.0, 95% CI = -0.03 to 0.03).

Freshwater outflows

Over the course of one year, black oystercatchers returned to outflows more often if they were associated with larger intertidal areas, gravel dominated substrates, and large streams. Three out of 21 candidate models received strong support (Table 3).

The top ranked model (w_i = 0.43) included three terms: intertidal area within a 1000m radius (Intertidal$_{1000}$), dominant substrate type (Substrate), and stream order (StreamOrder). This model received substantially more support than the null and twice as much support as the next best. The terms Intertidal$_{1000}$ and Substrate were included in all well-supported models (Σw_i = 1.0). The top model predictions estimated that the number of times an individual visited an outflow increased 3-fold as the area of intertidal habitat within a 1000m increased from 10% to 20% (β = 0.05, 95% CI = 0.02 to 0.08, Figure 7A). Individuals returned most to outflows with gravel dominated substrates, followed by sand, mudflat, and mixed rock (Figure 7B). Black oystercatchers did not use outflows of bedrock or man-made substrate types. The top model estimated that the number of times an individual visited an outflow increased by 67% (Figure 7C) as the stream order increased from second to fifth order (β = 0.16, 95% CI = 0.01 to 0.31). The remaining terms, tree cover within a 1000m radius (Tree$_{1000}$) and Southness, received less support and model averaged parameter estimates for both terms bounded zero, suggesting that tree cover and solar energy had little influence on outflow use by black oystercatchers.

2.4. Discussion

Animals can select habitat to maximise their foraging intake, increase reproductive success or minimize mortality (MacArthur and Pianka 1966; Hutto 1985; Lima and Dill 1990; Block and Brennan 1993). Here, I show that black oystercatchers in four populations are highly selective in their use of marine habitat throughout the year. Populations preferred islets and shoreline associated with freshwater outflows, limited tree cover, and larger intertidal areas, which were used more than expected based on availability within a site. Islets and shoreline with less tree cover are likely considered safe places to roost or reproduce, while freshwater outflows and large intertidal areas are likely productive foraging sites. Individuals within each population made extensive use of islets and freshwater outflows within their home-ranges. Islets were used more when they were close to the centre of an individual's home range, more isolated (i.e., less surrounding tree cover within 1000m radius), larger, or closer to a freshwater outflow. Freshwater outflows were used more when they were associated with higher stream orders, larger intertidal areas, and medium sized or gravel substrates.

Home range estimates for adult black oystercatchers, resident on the coast of BC, were extremely variable, ranging from 5 to 1195 km^2. Traditional home range analyses can overestimate space-use by animals constrained to linear features like shoreline (Slaght et al. 2013) so consideration of the area used, and the length of the linear feature, may aid in understanding the home range of animals like the black oystercatcher (Fieberg and Börger 2012). I found that non-breeding adults tended to have larger home ranges, containing more shoreline, than individuals that attempted to breed. Site differences explained most of the variation in home range size; individuals residing on the Sunshine Coast had much larger home ranges, with more shoreline, than individuals inhabiting Pacific Rim National Park Reserve, Skidegate Inlet, and Masset Inlet. Differences in home range size by species restricted to shoreline could be due to the tortuosity of the coastline, the distribution of suitable habitat (Rolando 1998), or both. Here, the area of an individual's home range was strongly correlated with the length of shoreline within the area, indicating that the geometry of the coastline did not explain the variation in space use. The length of coastline within an individual's home range was not correlated with the length of shoreline used, and all individuals used a similar amount of shoreline (7-14 km), suggesting the distribution of suitable habitat explained site differences in home range size (Rolando 1998; Tarjan and Tinker 2016).

Habitat selection decisions are expected to vary over time as the behavioural states of individuals, and availability of resources change from season to season, and individuals prioritize either maximizing the rewards or minimizing the risks. However, studies are often restricted to a single season (Marra et al. 2015) and therefore limit our understanding of how habitat is used across the annual cycle. I predicted habitat use by adult black oystercatchers during the breeding season would be constrained and that individuals would be more likely to use shoreline with features that enhance reproductive success. Consistent with these expectations, I found that habitat use during the breeding season was best predicted by a single characteristic: less tree cover within 250m of the shore. Other studies have argued that isolation and 'less vegetation' are the strongest drivers for nest-site occupancy because they reduce access by terrestrial mammals and ambush by avian predators (Vermeer, Morgan, et al. 1992; McFarland 2010; Dalgarno et al. 2017). In contrast, I found that during the non-breeding season black oystercatchers were more likely to use shoreline associated with freshwater outflows. Selection for areas associated with freshwater outflows was somewhat surprising because these

areas are generally characterized by soft sediments deposited by streams, and black oystercatchers are considered a rocky intertidal specialist. However, freshwater streams carry particulate organic matter used by filter feeders in the intertidal zone which can increase invertebrate productivity when released in marine environments (Tallis 2009; Kaiser et al. 2011). The apparent seasonal difference in the use of freshwater outflow habitats could be explained by the constraints related to reproductive duties of the breeding season, freshwater outflows provide greater foraging rewards during the non-breeding season, or outflows are safer in the non-breeding season due to aggregation (i.e., safety in numbers). The extent to which habitat selection decisions of black oystercatchers change over the course of the seasons, days, and tides, highlight the importance of including the question of *when* as well as the question of *where* in habitat studies (McGarigal et al. 2016).

Individuals which are sensitive to the risk of predation will use habitat that is more dangerous if that habitat provides greater foraging benefits (Lima and Dill 1990). In the four study areas, large intertidal areas and freshwater outflows typically occurred on mainland shores with greater tree cover (Figure A.1). The changes in habitat use by black oystercatchers from day to night, and from high to low tides, suggests they are sensitive to predation risk associated with increased tree cover. I found that during daytime low tides, when marine invertebrate prey were accessible, black oystercatchers used shoreline with large intertidal areas. During the night, black oystercatchers used safer areas with less tree cover, like offshore islets, when compared to shoreline used during the daytime. Counter-intuitively, black oystercatchers were more likely to use shoreline associated with freshwater outflows during daytime high tides; suggesting these areas provide foraging resources in the upper intertidal zones.

The function and ecological value of highly used areas within individual home ranges can be determined by examining the associated habitat characteristics (Bracis et al. 2018; Wittemyer et al. 2019). Black oystercatchers made extensive use of rocky islets within their home ranges, favouring those that were larger, had less surrounding tree cover, and those that were closer to the centre of their core home range area. Black oystercatchers in BC typically nest on rocky islets where territorial pairs are expected to spend significant time during the breeding season (Tessler et al. 2014). Offshore islets have characteristics which reduce attacks by predators and are popular high tide and night roosts for shorebirds (Piersma et al. 2006; Sprague et al. 2008; Watts et al. 2021).

Roost site availability may even constrain access to foraging sites and therefore the distribution of some shorebird populations (Dias et al. 2006; Rogers et al. 2006). Extensive use of islets closer to an individual's core home range indicates islet location may be key to shaping the year-round space use for this species (McKeown et al. 2020).

Individual black oystercatchers made repeated use of shoreline associated with large stream orders, large intertidal areas, and gravel substrates. Larger streams have higher discharge rates, carrying more organic matter through the intertidal where it can be consumed by filter feeding invertebrates. Larger intertidal areas provide longer exposure times for terrestrial predators to search for and consume marine prey. The preference for outflows with gravel substrates was unanticipated because black oystercatchers are thought to primarily forage on epifauna, such as limpets and mussels, which typically attach to large and unmoving substrates like boulders/bedrock (Hartwick 1973; Tessler et al. 2014; Andres and Falxa 2020). Several clam species are known to proliferate along gravel beaches on the north Pacific coast (Quayle and Bourne 1972), indicating clams may be more important to the diet of this shorebird species than previously known. Gravel provides greater sediment stability and increases interstitial spaces (Cigarría and Fernandez 2000) resulting in higher growth rates and juvenile survival and therefore greater clam densities and biomass (Thompson 1995; Gillespie et al. 2001). Furthermore, the introduced varnish clam (*Nuttallia obscurata*) prefers freshwater runoff in the upper intertidal zone (Dudas et al. 2007) which may explain why black oystercatchers were more likely to use freshwater outflows during high tides (Hollenberg and Demers 2017).

Black oystercatchers that are restricted to the Pacific northwest coast are considered an indicator of the health of rocky intertidal ecosystems. Tracking their movements throughout the year illustrates their reliance on shoreline that provides both a refuge from predators, and access to invertebrate prey. I found that islets and shoreline associated with freshwater outflows are important features which provide black oystercatchers with refuge from predators and preferred foraging sites and may drive the high variation in home range size observed. Rocky islets provide safe areas for roosting and raising young and may be key to shaping the home range of a black oystercatcher. Low-sloping gravel shoreline associated with freshwater outflows is considered high quality clam habitat in BC. Historically, local Indigenous peoples created 'clam gardens' by reducing the slope of natural beaches and mixing in gravel, shells, and fine

sediments; cultivating a highly productive environment for several species of clams (Groesbeck et al. 2014; Lepofsky et al. 2021). My study provides evidence that clams may be a seasonally important part of the diet of black oystercatchers. I show how habitat use can be dynamic, for specialists restricted to one ecosystem type, and for resident individuals with permanent home ranges. Critical shoreline habitat for black oystercatchers is likely indicative of important habitat for other coastal wildlife species dependent on safe and productive marine shoreline for breeding, overwintering, or migratory stopover in BC.

2.5. Tables

Table 2.1.   Variables hypothesized to influence black oystercatcher use of marine shoreline habitat.

Function	Name	Description	Data Type	Source	Retained
Population-level shoreline selection					
Foraging opportunity	$Intertidal_{250}$	Percent intertidal area within a 250m radius	Continuous	Canadian Hydrological Survey 2020	Yes
	Substrate	ShoreZone coastal class (reclassified)	Categorical	Howes et al 1994	No
	Exposure	ShoreZone wave exposure estimate	Ordinal	Howes et al 1994	No
	Outflow	Occurrence of a freshwater outflow within 500m	Binary	BC Freshwater Atlas 2020	Yes
Safety	$Tree_{250}$	Percent tree cover within a 250m radius	Continuous	Ware 2020	Yes
	Islet	Small island (area <1.5ha)	Binary	Ware 2020	Yes
Anthropogenic disturbance	$Urban_{250}$	Percent area developed within 250m radius	Continuous	BC Landcover 2020	No
	RoadDist	Distance from nearest road (km)	Continuous	BC Digital Roads Atlas 2020	No
Individual use of key islet features					
Foraging opportunity	$Intertidal_{1000}$	Percent intertidal area within a 1000m radius	Continuous	Canadian Hydrological Survey 2020	Yes
	Exposure	ShoreZone wave exposure estimate	Ordinal	Howes et al 1994	No
	OutflowDist	Distance to nearest freshwater outflow (km)	Continuous	BC Freshwater Atlas 2020	Yes
Safety	$Tree_{1000}$	Percent tree cover within 1000m radius	Continuous	Ware 2020	Yes
	IsletArea	Area of islet (hectares)	Continuous	Ware 2020	Yes
Anthropogenic disturbance	$Urban_{1000}$	Percent area developed within a 1000m radius	Continuous	BC Landcover 2020	No
	RoadDist	Distance from nearest road (km)	Continuous	BC Digital Roads Atlas 2020	No
Individual use of key outflow features					
Foraging opportunity	$Intertidal_{1000}$	Percent intertidal area within a 1000m radius	Continuous	Canadian Hydrological Survey 2020	Yes
	Substrate	ShoreZone coastal class (reclassified)	Categorical	Howes et al 1994	Yes
	Southness	Degree the shoreline is facing south (0-180)	Continuous	Ware 2020	Yes
	Exposure	ShoreZone wave exposure estimate	Ordinal	Howes et al 1994	No
	StreamOrder	Order of stream outflow (2-5)	Ordinal	BC Freshwater Atlas 2020	Yes
Safety	$Tree_{1000}$	Percent tree cover within a 1000m radius	Continuous	Ware 2020	Yes
Anthropogenic disturbance	$Urban_{1000}$	Percent area developed within a 1000m radius	Continuous	BC Landcover 2020	No
	RoadDist	Distance from nearest road (km)	Continuous	BC Digital Roads Atlas 2020	No

Table 2.2. **Candidate models evaluating the repeated use of islets by individual oystercatchers (n=19) over one year using satellite telemetry information. All models include an autocovariate term to correct for spatial dependence and the term 'CentroidDist+CentroidDist^2' to correct for an individual's preference towards their core home range area. K is the number of parameters in the model, AICc is the Akaike's Information Criterion, ΔAICc is the differences between the model and the lowest AICc score, wt is the likelihood of each model in relation to all other models in the candidate set, marginal R^2 is the variance explained by fixed terms, and conditional R^2 is the variance explained by both the fixed and random factors.**

| Parameters	K	AICc	ΔAICc	Wt	Marginal R^2	Conditional R^2
Islet Features						
$Tree_{1000}$ + IsletArea + OutflowDist	9	1120.6	0.0	0.22	0.45	0.59
$Tree_{1000}$ + $Intertidal_{1000}$	8	1120.7	0.1	0.21	0.44	0.59
$Tree_{1000}$ + IsletArea	8	1120.8	0.2	0.20	0.44	0.58
$Tree_{1000}$	7	1121.9	1.2	0.12	0.44	0.58
$Tree_{1000}$ + IsletArea + $Intertidal_{1000}$ + OutflowDist	10	1122.6	2.0	0.08	0.45	0.59
$Tree_{1000}$ + $Intertidal_{1000}$ + OutflowDist	9	1122.8	2.2	0.07	0.45	0.58
$Tree_{1000}$ + IsletArea + $Intertidal_{1000}$	9	1122.9	2.3	0.07	0.44	0.59
$Tree_{1000}$ + OutflowDist	8	1124.0	3.4	0.04	0.45	0.58
IsletArea + $Intertidal_{1000}$	8	1131.5	10.9	0.00	0.40	0.55
IsletArea	7	1132.5	11.8	0.00	0.38	0.55
IsletArea + $Intertidal_{1000}$ + OutflowDist	9	1133.3	12.7	0.00	0.40	0.55
IsletArea + OutflowDist	8	1134.6	13.9	0.00	0.38	0.55
Null (CentroidDist + CentroidDist^2)	6	1136.1	15.4	0.00	0.37	0.53
$Intertidal_{1000}$	7	1136.1	15.4	0.00	0.22	0.31
$Intertidal_{1000}$ + OutflowDist	8	1137.4	16.8	0.00	0.39	0.53
OutflowDist	7	1138.0	17.3	0.00	0.37	0.52

Table 2.3. Candidate models evaluating the repeated use of freshwater outflows by individual oystercatchers (n=16) over one year using satellite telemetry information. K is the number of parameters in the model, AICc is the Akaike's Information Criterion, ΔAICc is the differences between the model and the lowest AICc score, wt is the likelihood of each model in relation to all other models in the candidate set, marginal R^2 is the variance explained by fixed terms, and conditional R^2 is the variance explained by both the fixed and random factors.

Parameters	K	AICc	ΔAICc	Wt	Marginal R^2	Conditional R^2
Outflow Features						
$Intertidal_{1000}$ + Substrate + StreamOrder	8	255.4	0.0	0.43	0.49	0.61
$Intertidal_{1000}$ + Substrate + $Tree_{1000}$	8	256.4	1.0	0.26	0.49	0.61
$Intertidal_{1000}$ + Substrate	7	256.7	1.3	0.23	0.45	0.58
$Intertidal_{1000}$ + Substrate + Southness	8	259.1	3.7	0.07	0.45	0.57
$Intertidal_{1000}$ + StreamOrder	5	265.3	9.8	0.00	0.24	0.37
$Tree_{1000}$ + Substrate	7	265.4	10.0	0.00	0.38	0.41
$Intertidal_{1000}$ + $Tree_{1000}$	5	265.5	10.0	0.00	0.26	0.33
$Intertidal_{1000}$ + $Tree_{1000}$ + StreamOrder	6	266.1	10.6	0.00	0.27	0.37
$Intertidal_{1000}$ + $Tree_{1000}$ + Southness	6	267.6	12.2	0.00	0.26	0.34
$Intertidal_{1000}$ + StreamOrder + Southness	6	267.6	12.2	0.00	0.24	0.37
$Tree_{1000}$ + StreamOrder + Substrate	8	267.8	12.3	0.00	0.34	0.42
$Tree_{1000}$ + Substrate + Southness	8	267.9	12.5	0.00	0.38	0.41
Substrate + StreamOrder	7	268.3	12.9	0.00	0.33	0.42
$Tree_{1000}$	4	269.0	13.5	0.00	0.18	0.19
Substrate	6	269.0	13.6	0.00	0.31	0.33
$Intertidal_{1000}$	4	269.3	13.9	0.00	0.15	0.25
Substrate + Southness	7	270.0	14.6	0.00	0.32	0.34
StreamOrder + Substrate + Southness	8	270.1	14.7	0.00	0.34	0.42
$Tree_{1000}$ + StreamOrder	5	270.5	15.0	0.00	0.18	0.22
$Tree_{1000}$ + Southness	5	271.1	15.7	0.00	0.18	0.20
$Intertidal_{1000}$ + Southness	5	271.5	16.1	0.00	0.16	0.25
StreamOrder	4	272.1	16.7	0.00	0.10	0.19
$Tree_{1000}$ + StreamOrder + Southness	6	272.8	17.4	0.00	0.18	0.22
Southness + StreamOrder	5	274.2	18.8	0.00	0.11	0.20
Null	3	275.9	20.5	0.00	0.00	NA
Southness	4	277.8	22.4	0.00	0.01	NA

2.6. Figures

Figure 2.1. **Four areas in BC where black oystercatchers were studied. The inset map shows the location of coastal BC on the west coast of North America. Coordinate System: NAD 1983. Projection: BC Environment Albers.**
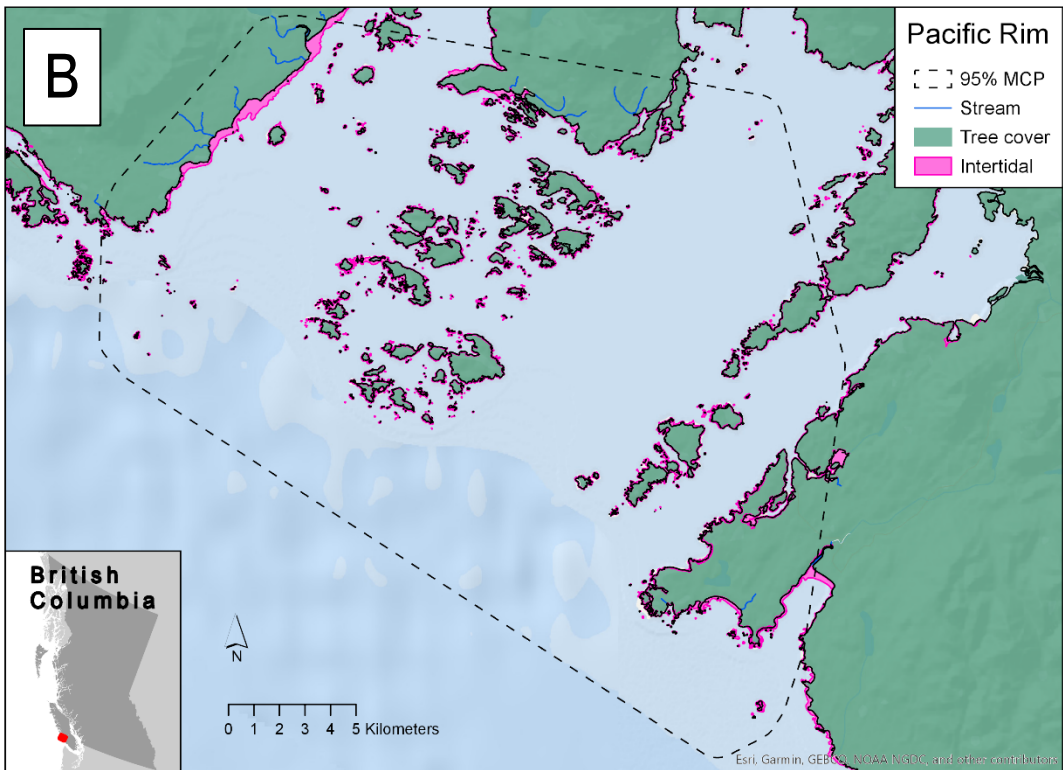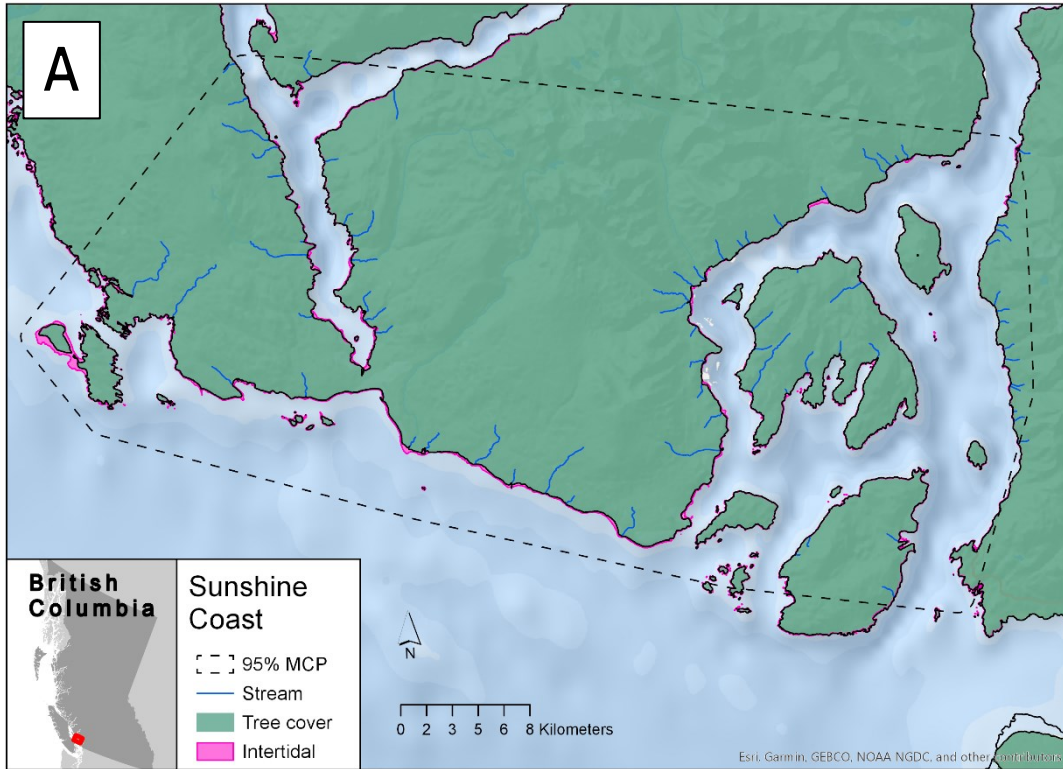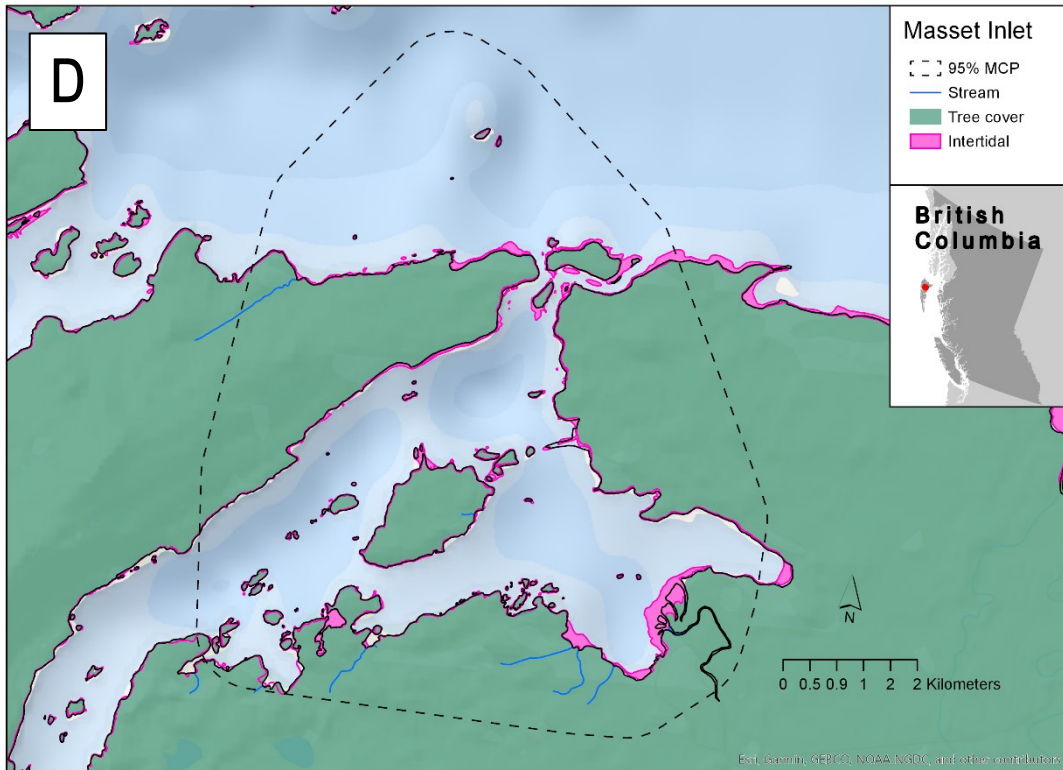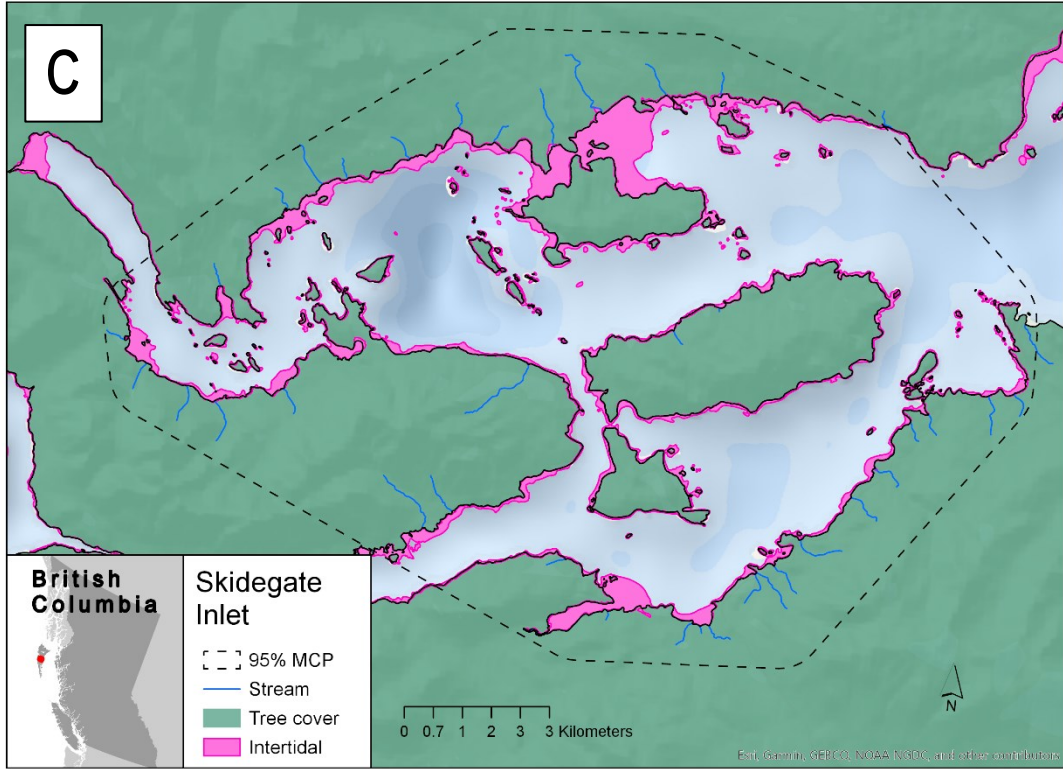
Figure 2.2. Four study sites where tracked black oystercatchers spent the year: (A) Sunshine Coast (n=4), (B) Pacific Rim National Park Reserve (n=5), (C) Skidegate Inlet (n=5), (D) Masset Inlet (n=4). Dashed lines are population level 95% MCP of pooled individuals with overlapping home ranges. Blue lines are streams (order >1). Green polygons represent tree cover digitized from 1:5000 satellite imagery. Pink polygons represent the intertidal area between high water mark and mean low tide lines. The inset map shows the study site location in British Columbia, Canada. Note that the scale is different on each map layout.
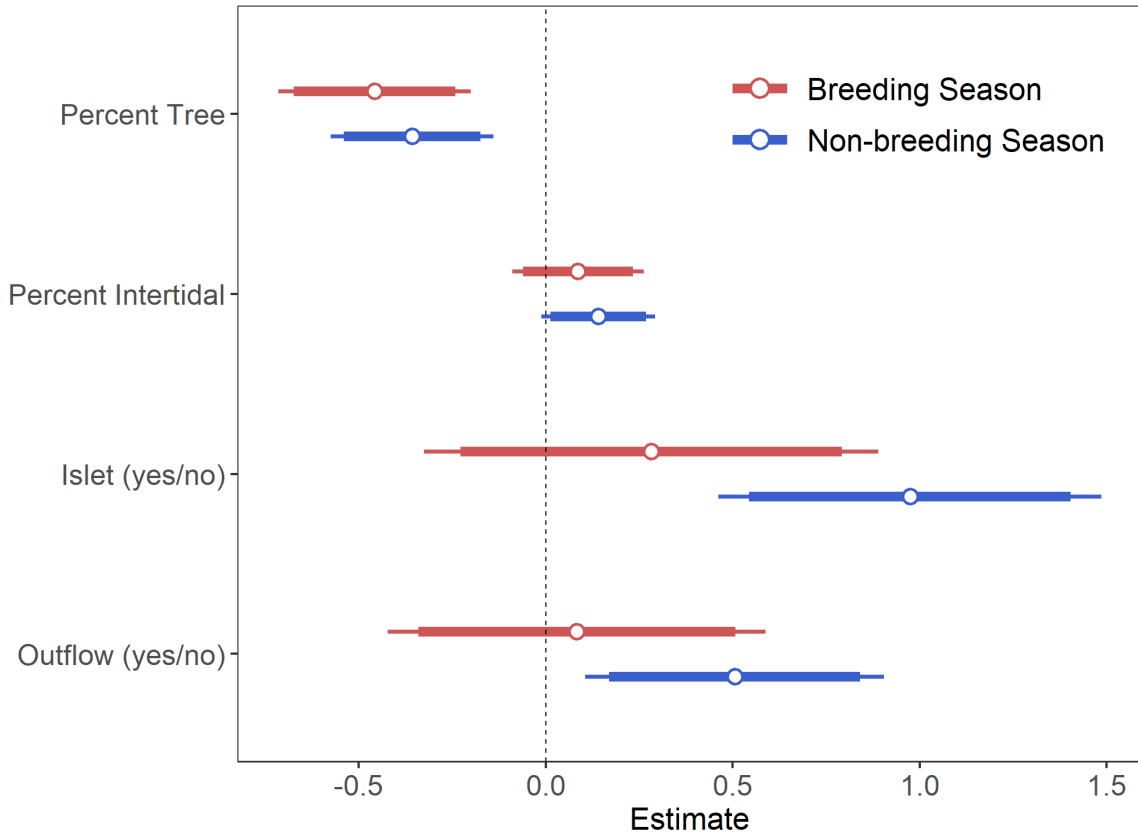
Figure 2.3. Standardized effects plot showing the influence of four variables on shoreline use by black oystercatchers during the breeding season (red) and non-breeding season (blue). The breeding season was defined as April-July (4 months) when movements by adult oystercatchers are most likely to be constrained. The non-breeding season was defined as August-March (8 months) when reproductive duties were expected to be complete. A shore-point was considered 'used' by and oystercatcher if a satellite location was within 250m during the focal time period. 'Used' shore-points were compared with a subset of 'available' shore-points using generalized linear mixed models with study site as a random term. Thin lines represent associated 95% confidence intervals and thick lines are 90% confidence intervals. 95% confidence intervals that do not overlap 0 are considered significant. An autocovariate term is included in each model (to correct for spatial dependence) but it is not shown in this figure.
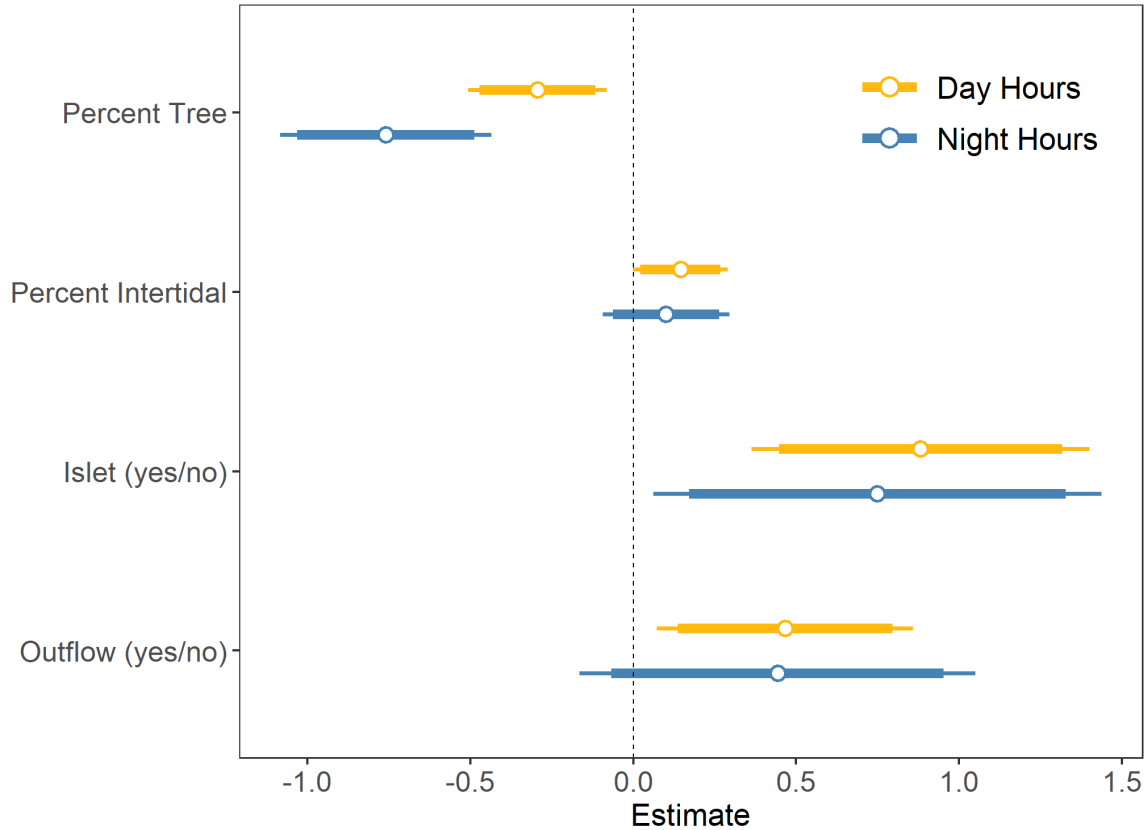
Figure 2.4. Standardized effects plot showing the influence of four variables on shoreline use by black oystercatchers during the day (yellow) and the night (blue). Day was defined as hours occurring between civil sunrise and sunset for each location and date. Night occurred between civil sunset and sunrise. A shore-point was considered 'used' by and oystercatcher if a satellite location was within 250m during the focal time period. 'Used' shore-points were compared with a subset of 'available' shore-points using generalized linear mixed models with study site as a random term. Thin lines represent associated 95% confidence intervals and thick lines are 90% confidence intervals. 95% confidence intervals that do not overlap 0 are considered significant. An autocovariate term is included in each model (to correct for spatial dependence) but it is not shown in this figure.
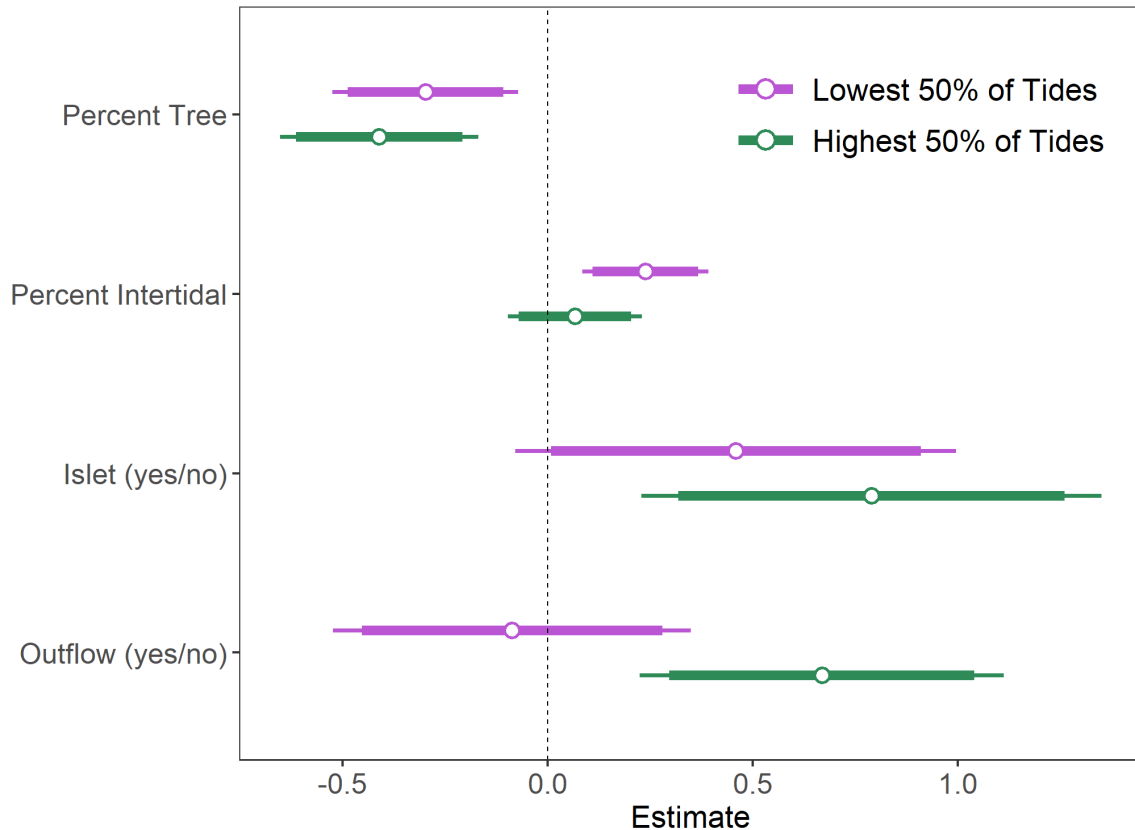
Figure 2.5. Standardized effects plot showing the influence of four variables on shoreline use black oystercatchers during low tides (pink) and high tides (green). Low tides are considered 50% of the lowest tide height predictions for each week and location. High tides are 50% of the highest tide height predictions for each week and location. Oystercatcher locations were assigned a tide-station by proximity and geography of the coastline. A shore-point was considered 'used' by and oystercatcher if a satellite location was within 250m during the focal time period. 'Used' shore-points were compared with a subset of 'available' shore-points using generalized linear mixed models with study site as a random term. Thin lines represent associated 95% confidence intervals and thick lines are 90% confidence intervals. 95% confidence intervals that do not overlap 0 are considered significant. An autocovariate term is included in each model (to correct for spatial dependence) but it is not shown in this figure.
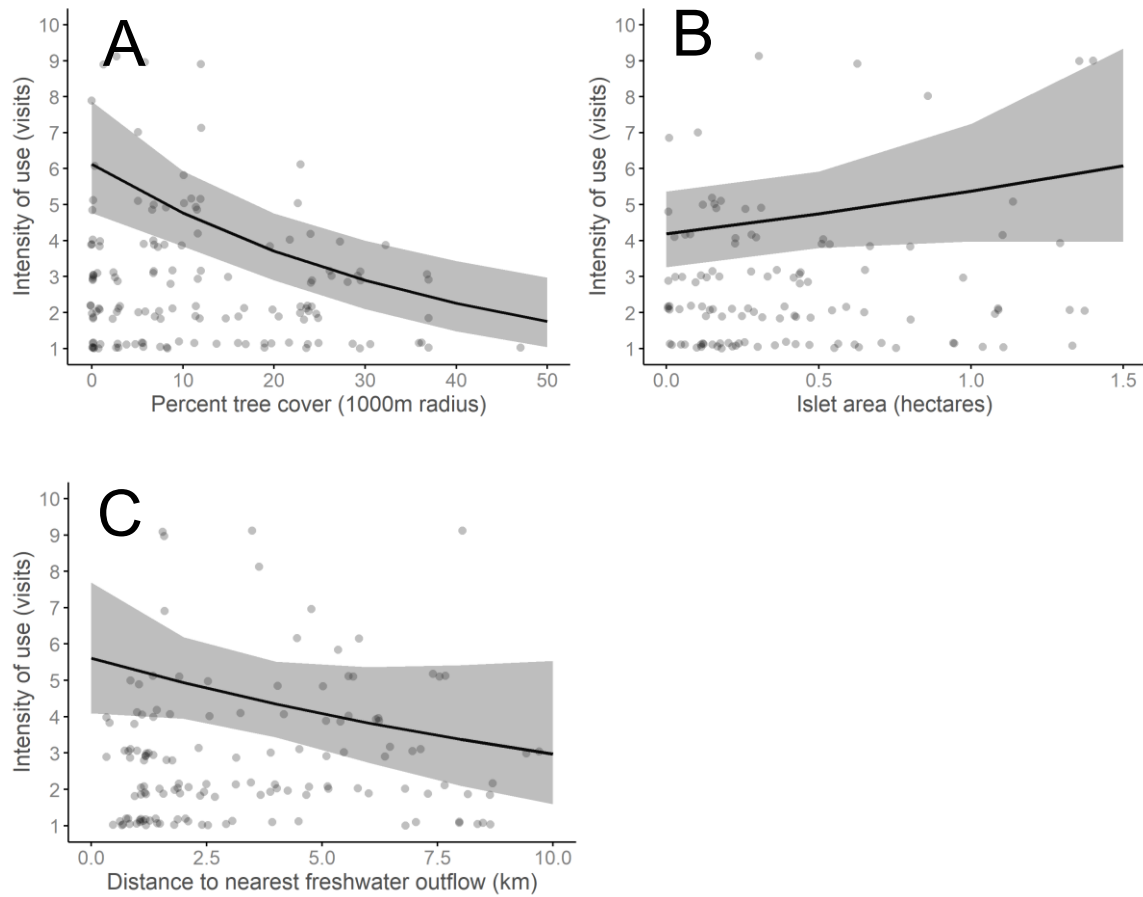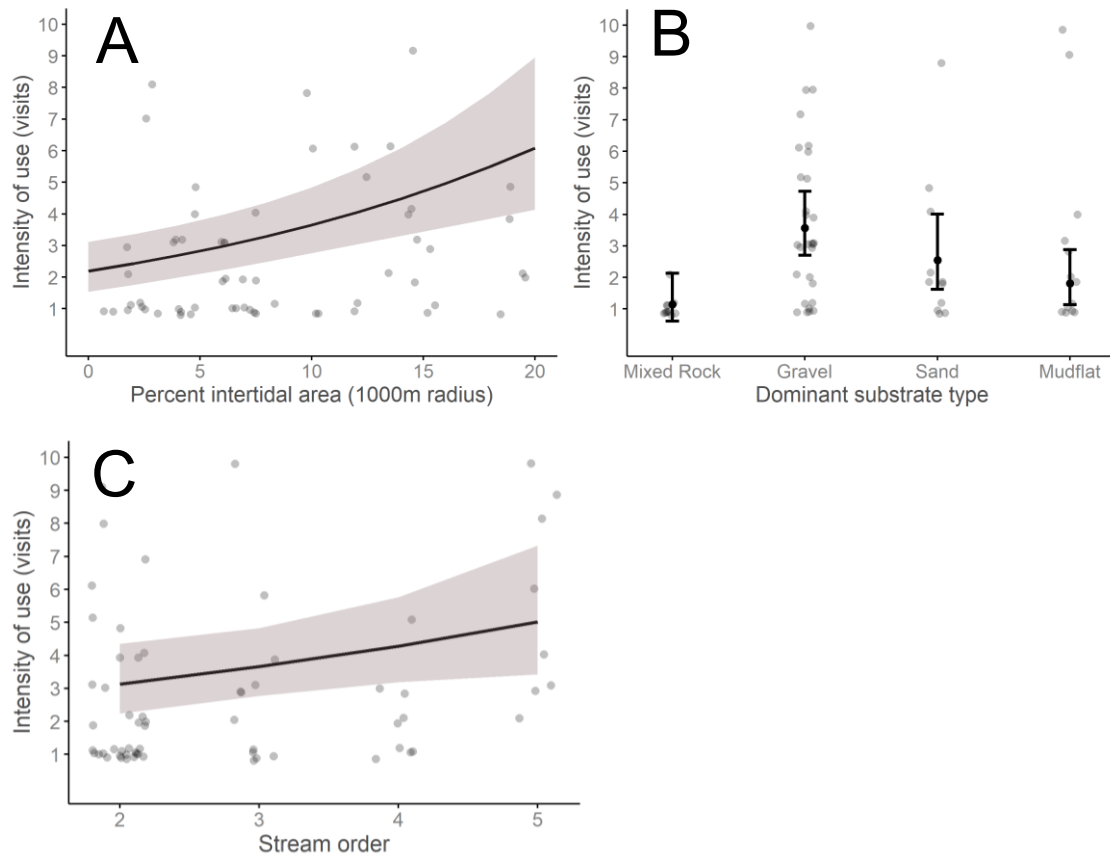
Figure 2.6. Conditional relationships between (A) percent tree cover, (B) islet size, (C) distance to the nearest freshwater outflow, and the predicted number of visits to an islet by an individual black oystercatcher using the model with the most support (ΔAIC = 0.0, wt = 0.22). Data points represent islets within the home range of oystercatchers that were visited at least once, and up to 29 times. The number of visits is relative to actual visits i.e., visits that were captured by four locations per week per bird (mean number of locations per individual: 138, range: 117-161).

Figure 2.7. Conditional relationships between (A) percent intertidal area, (B) substrate type, (C) stream order and the predicted number of visits to shoreline associated with freshwater outflows by individual black oystercatchers using the model with the greatest support (ΔAIC = 0.0, wt = 0.43). Data points represent outflows within the home range of individuals that were visited at least once and up to 8 times. The number of visits is relative to actual visits i.e., these are visits that were captured by four locations per week per bird (mean number of locations per individual: 138, range: 117-161).

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Chapter 3.   General conclusion

3.1. Summary of findings

This thesis demonstrates that black oystercatchers are selective in their use of marine shoreline with populations and individuals using a small proportion of the shoreline within their region or home range (populations: 11-39%, individuals: 8-68%). Black oystercatchers made habitat selection decisions that reflected trade-offs between predation and foraging rewards. Black oystercatchers appeared to prioritize safety during the breeding season and the night by using safe locations like islets or shoreline with fewer trees. Black oystercatchers also used more dangerous shoreline during low daytime tides when intertidal flats were exposed, indicating there are likely foraging benefits associated with using these areas. Black oystercatchers used more dangerous shoreline near freshwater outflows during the non-breeding season and high daytime tides, suggesting that the resources that occur there are seasonally available and/or in the upper intertidal zone. The preference for freshwater outflows by black oystercatchers was somewhat unexpected. However, other rocky intertidal shorebirds like the black turnstone (*Arenaria melanocephala*) and rock sandpiper (*Calidris ptilocnemis*) can be found overwintering at tidal distributaries (Handel and Gill 2020) and gravel flats at the mouths of small streams (Gill et al. 2020), respectively. Surfbirds (*Calidris virgata*) are also associated with rocky intertidal habitats but have not been linked to freshwater outflows (Handel and Gill 2020).

3.2. Conservation and management implications

Black oystercatchers are considered a 'species of high concern' and are monitored as indicators of rocky intertidal health along the Pacific coast of north America (Tessler et al. 2014). Most long-term monitoring of black oystercatchers consists of breeding pair surveys and there is limited understanding of habitat use during the non-breeding season. Identifying and monitoring foraging sites during the non-breeding season, however, might provide additional information about changes in the rocky intertidal ecosystem. For example, Eurasian oystercatchers consistently forage on areas of the intertidal with higher invertebrate prey abundance and biomass (Schwemmer et al. 2016). Furthermore, the foraging sites used by Eurasian oystercatchers were strongly

dependent on abiotic factors, so valuable foraging sites could be identified without the need for time-consuming collection of prey-based data (Schwemmer et al. 2016). I found that the presence of black oystercatchers was strongly related to physical characteristics (i.e., abiotic factors) of the shoreline including intertidal area, freshwater outflows and gravel substrates. The presence of black oystercatchers during the non-breeding season and low daytime tides could therefore indicate productive foraging areas suitable for long term monitoring.

Under Canada's Oceans Protections Plan, Environment Canada initiated telemetry studies on focal species to incorporate marine wildlife distributions into emergency response planning (e.g., in the event of an oil spill). The black oystercatcher was one of 7 selected priority bird species because they are the only bird species in BC who entirely depend on marine shoreline habitats for the entire year. BC's coasts are important to an abundance of bird species who depend on a variety of habitats for breeding, migration and/or overwintering (Ethier et al. 2020). My research highlights that rocky islets are important for black oystercatchers year-round. Rocky islets, which used for nesting by black oystercatchers are also safe nesting sites for other coastal marine birds such as glaucous-winged gulls (Vermeer et al. 1992). I found that black oystercatchers preferred shoreline with large intertidal areas only during low daytime tides, and preferred shoreline associated with freshwater outflows during high tides and the non-breeding season. Mainland shores with large intertidal areas and freshwater outflows were associated with increased tree cover, and therefore were more dangerous, suggesting the benefits gained from using these areas outweighed the costs.

The benefits black oystercatchers gain by using large intertidal areas and freshwater outflows are likely related to foraging resources. Selection of large intertidal areas during low daytime tides suggests that the preferred invertebrate prey in these areas occur in the low-mid intertidal zones. Selection of freshwater outflows during high tides suggests that invertebrate prey occur in the upper intertidal zones. Protection of foraging habitat for black oystercatchers are likely to benefit other coastal wildlife since many birds (shorebirds, gulls, seaducks, corvids) also forage on intertidal invertebrates, particularly during the winter or non-breeding season. In conclusion, the productive and safe areas of the shoreline used by black oystercatchers are likely important to a suite of coastal species who have similar habitat requirements. In the event of an oil spill in BC,

shoreline cleanup should target rocky islets and large intertidal areas year-round, and shoreline at freshwater stream outflows between August and March.

3.3. Future directions

In this thesis, I did not examine the effects of anthropogenic disturbance on habitat use by black oystercatchers because there was, in general, little human development across sites. Interestingly, I did find that individuals residing on the Sunshine Coast had significantly larger home range sizes than individuals from the other three sites, even though the amount of shoreline used was similar. These results suggests that the suitable shoreline habitat was more dispersed on the Sunshine Coast than at the other three sites or suitable habitat cannot be used due to increased human activity. The Sunshine Coast is part of the complex water body known as the Salish Sea, that has greater human impacts compared to other coastal areas of BC (Sobocinski 2021). Specifically, nearly 9 million people live within the region surrounding the Salish Sea which has driven urbanization, development and associated ecological stressors (Sobocinski 2021). For example, nutrient pollution from rivers, wastewater inputs, and invasive species have been recognized as primary threats to the ecological health of the Salish Sea (Khangaonkar et al. 2019). Additional pressures include shipping, fishing, recreation, and shoreline development, all of which are likely to affect the Salish Sea to a greater extent than the outer coastal waters of the Pacific Ocean (e.g., Stocks and Vandeborne 2017). Human activities may therefore explain that over 20 years, wintering waterbird species experienced significant declines in the Salish Sea compared to populations on the outer Pacific coast of BC (Ethier et al. 2020). Black oystercatchers who spend the year in the Salish Sea likely experience different human-induced pressures than individuals from other coastal areas, and therefore future studies should investigate how anthropogenic stressors differentially impact the use of rocky intertidal habitats by marine shorebirds in BC.

I used satellite tracking data from resident black oystercatchers to understand year-round habitat use in British Columbia. Tessler et al. (2014) suggests that 1) black oystercatcher populations are regulated by the availability of high-quality nesting and foraging habitat; and 2) that high-quality habitat is saturated. My research supports this first idea by showing that suitable habitat makes up a small proportion of available habitat, and that neighboring individuals use the same key habitat features (i.e., have

overlapping home ranges). The second idea that habitat is saturated, remains contentious because the BC population of black oystercatchers is thought to double in the winter when 75% of individuals that breed in the Gulf of Alaska migrate south (Johnson et al. 2010; Tessler et al. 2014; Bennett 2019). If suitable habitat is saturated, how do migrant and resident black oystercatchers share the limited high-quality areas? Significantly increasing the number of black oystercatchers at limited foraging sites could put pressures on both resident and migrant overwintering populations. Alternatively, migrant and resident black oystercatchers may partition habitat to reduce effects of intraspecific competition (De La Hera et al. 2018). More research is needed to understand non-breeding habitat use by migratory black oystercatchers in BC and how their arrival may alter selection decisions by residents.

3.4. References

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Appendix.

Supplemental information
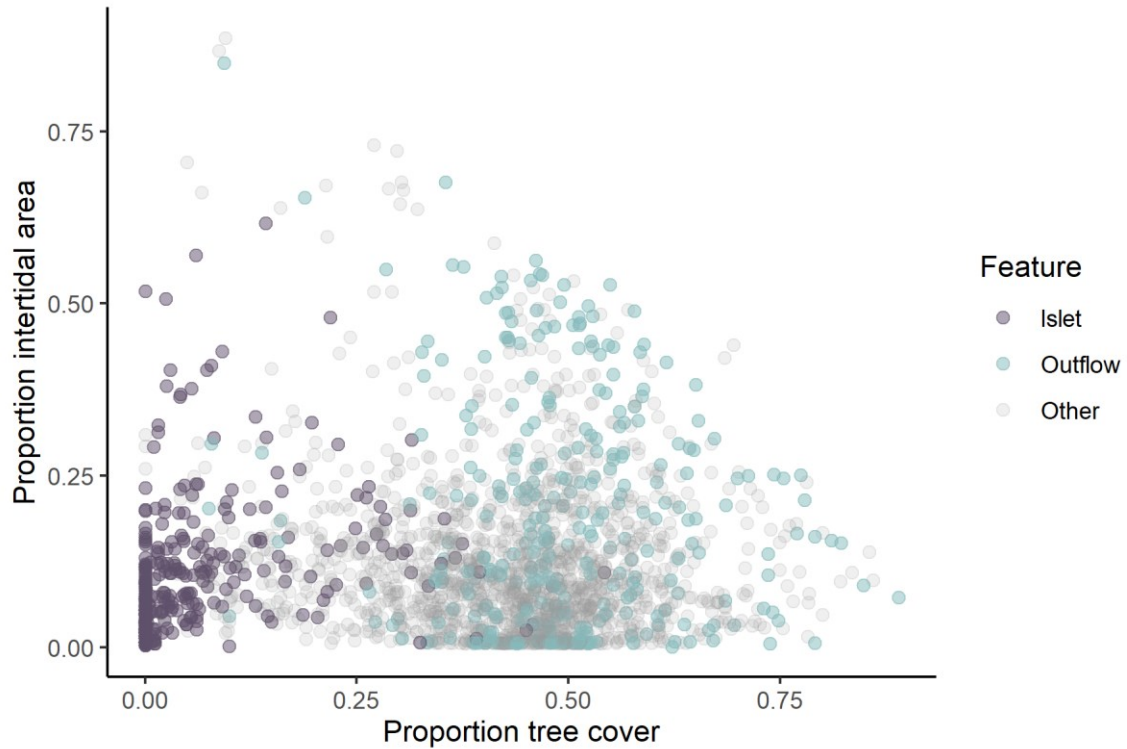
Figure A.1. Each data point represents a shore-point included in the analysis evaluating habitat use by black oystercatchers over seasonal, diel and tidal cycles (n = 1063). Shore-points are locations generated every 500m along the shoreline that represent habitat units and average 290m apart depending on the ruggedness of the coastline (range: 65-2110m). Percent intertidal within a 250m radius of shore-points (range: 0.3-88.6%, mean: 14.0 ± 13.2) is plotted against percent tree cover within the same radius (range: 0.0-85.9%, mean: 36.4 ± 19.9). Shore-points on islets are shown in purple (14.7% of shore-points) and shore-points within 500m of a freshwater outflow are shown in blue (15.3% of shore-points). All other shore-points are shown in grey.
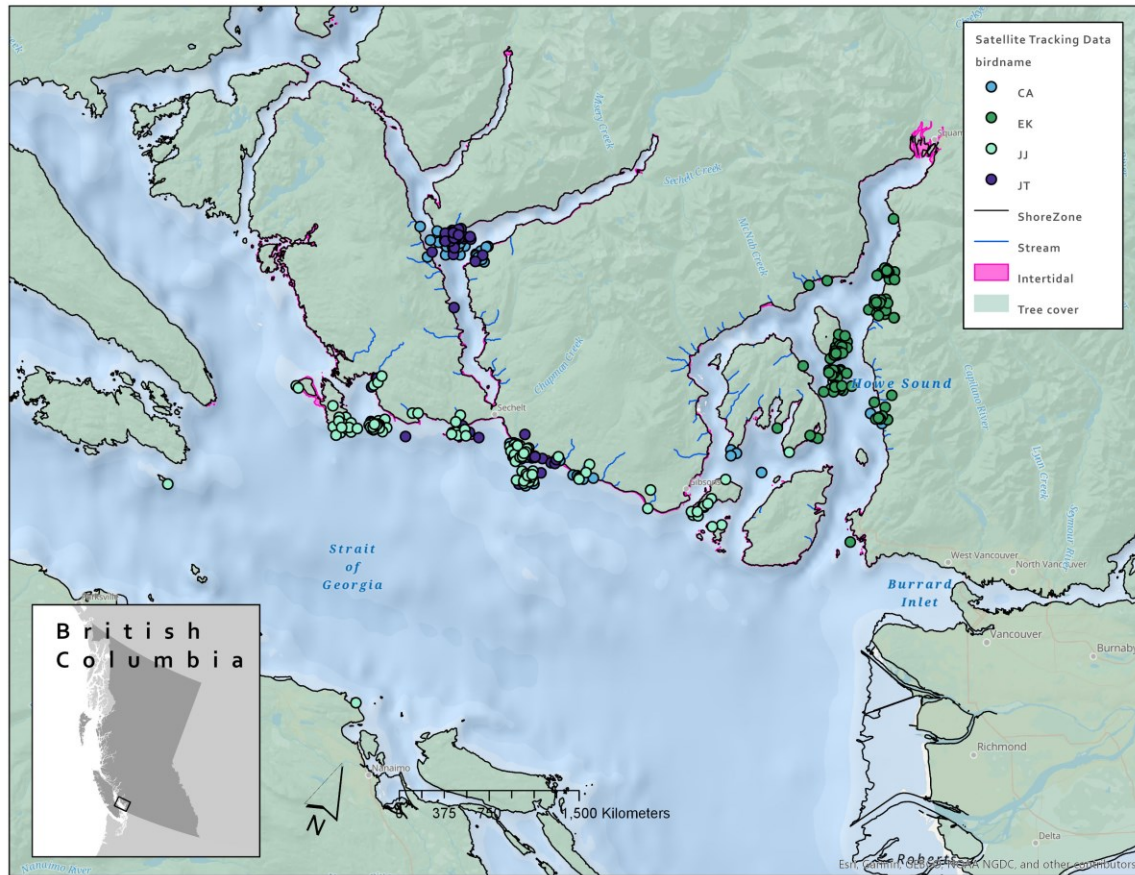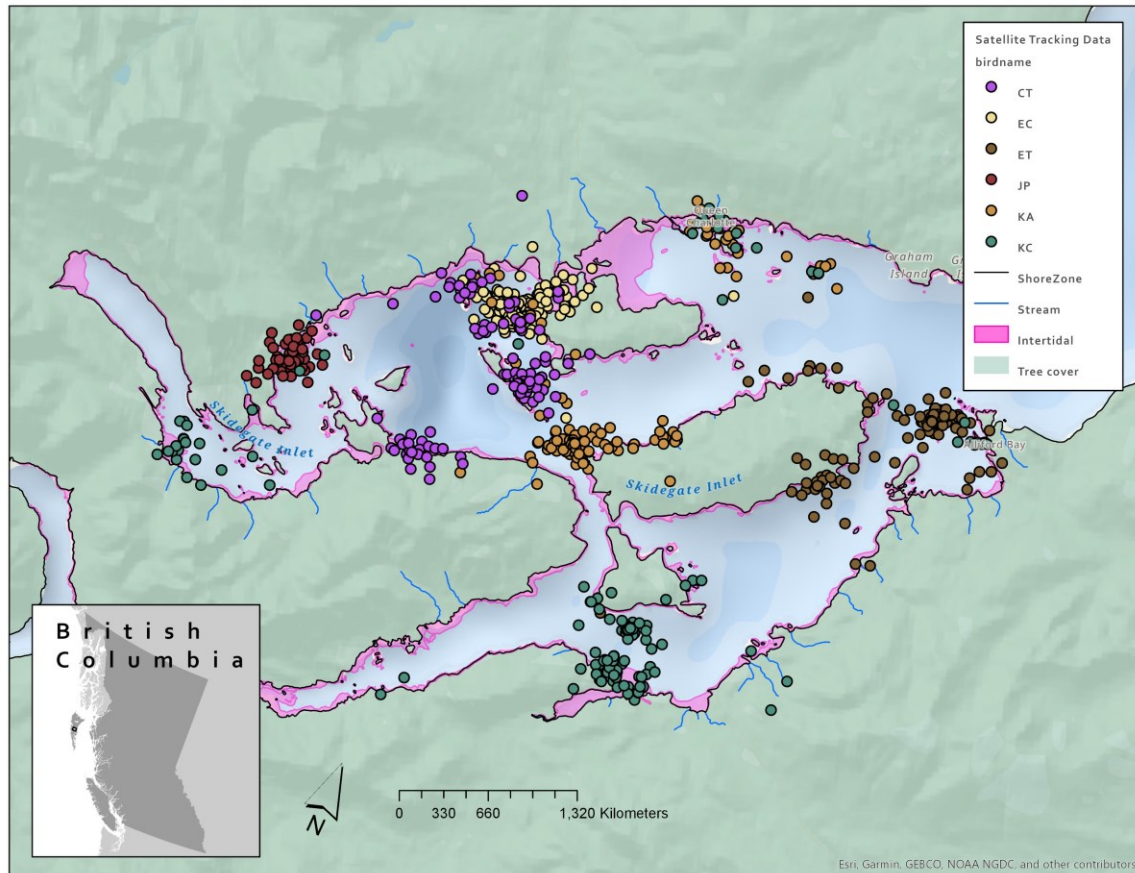
Figure A.2. Map of the Sunshine Coast study site showing processed satellite tracking data from four black oystercatchers across one year (March 2019-2021).
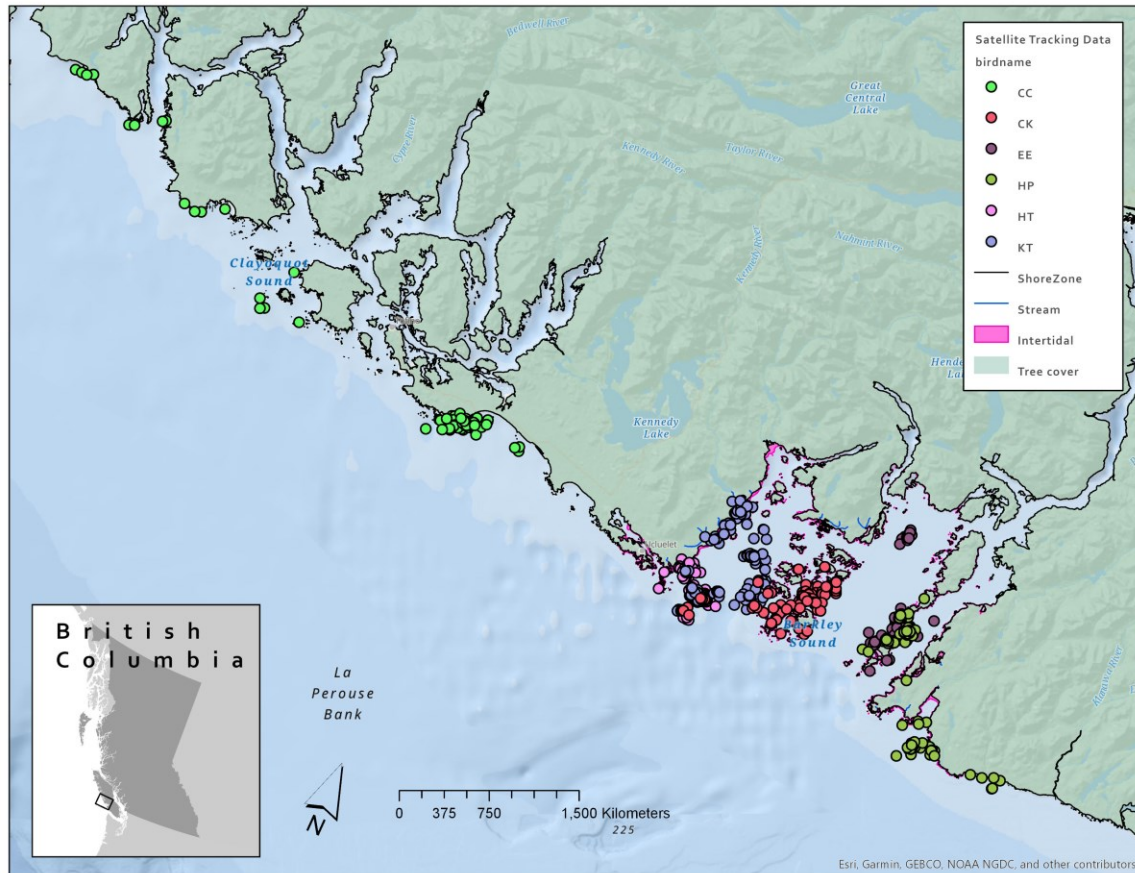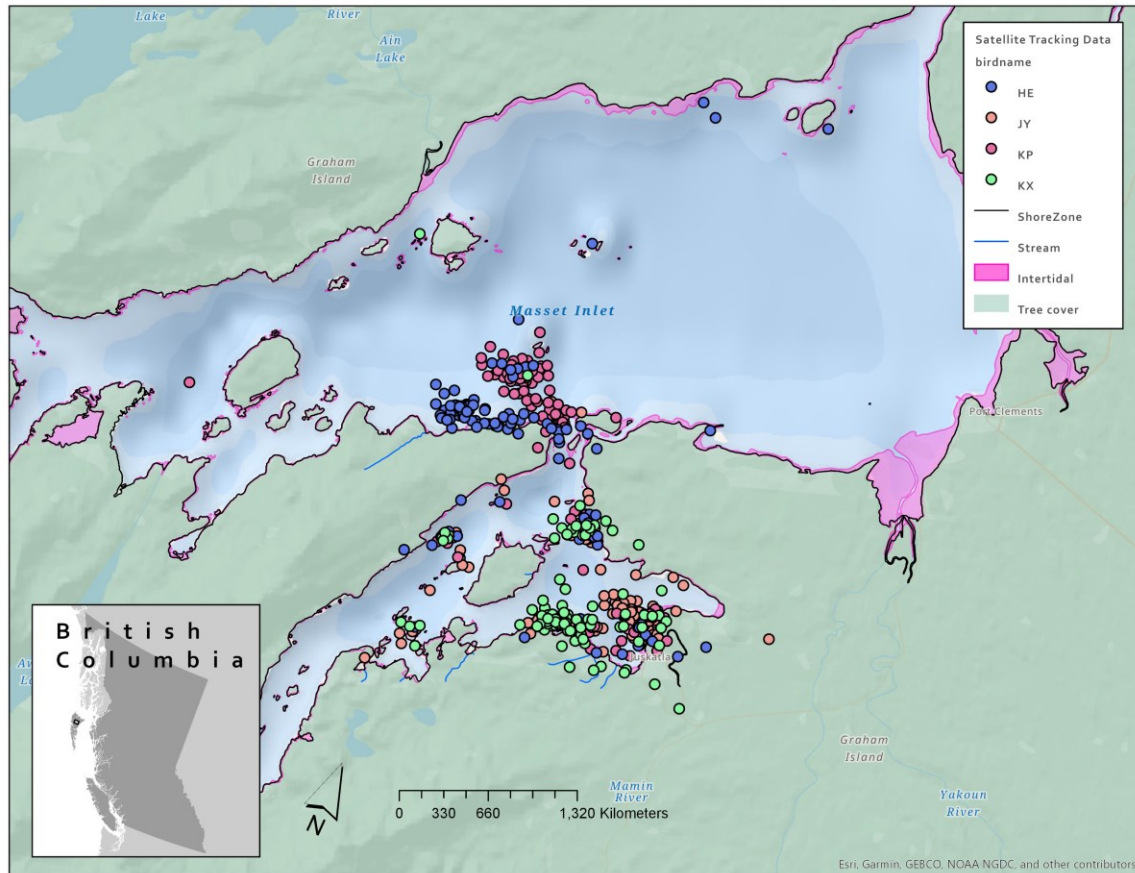
Figure A.3.   **Map of the Pacific Rim National Park study site showing processed satellite tracking data from six black oystercatchers across one year (March 2019-2021).**

Figure A.4. **Map of the Skidigate Inlet study site showing processed satellite tracking data from six black oystercatchers across one year (March 2019-2021). Note that the bird named JP only represents the first six months of tracking.**

Figure A.5. **Map of the Masset Inlet study site showing processed satellite tracking data from four black oystercatchers across one year (March 2019-2021).**