

Marine Habitat Preferences of Marbled Murrelets in Haida Gwaii, BC

**by
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Abstract

Effective spatial planning for seabirds depends on understanding what influences foraging habitat choices. I used a long running at-sea survey dataset (1997-2018) to develop a baseline understanding of marine habitat preferences of Marbled murrelets (*Brachyramphus marmoratus*) in Haida Gwaii, British Columbia, Canada. Persistence hotspot mapping showcased how distributions have remained similar over time. Murrelet usage was positively associated with being closer to streams, shallower waters, higher proportions of sandy sediment and closer proximity to abundant potential nesting habitat. Additional surveys conducted in 2018 and 2019 identified stratified water as a dynamic variable that positively influenced counts. Finally, an experiment utilizing avian deterrent kites showed that a lower daily proportion of murrelets were counted in locations adjacent to kites when they were flying than when they were not. Overall, my study shows that static variables are primary influencers of Marbled murrelet marine distribution, but dynamic variables such as thermal mixing and predator occurrence also play roles.

Keywords: Marine Habitat; Habitat Preference; Marbled Murrelet; Fine-Scale Habitat; Hotspot Persistence; Predator Distribution Response

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Chapter 1.

General Introduction

Knowing where an animal is and understanding why it is there is fundamental to ecology. Habitat preference studies, or habitat selection studies, seek to understand the behavioural responses individuals use to select habitat, which influences their survival and fitness (Block and Brennan 1993; Jones 2001). Ecologists have conceptualized the way an individual selects habitat as scale dependant and hierarchical, with four order terms developed (Block and Brennan 1993).

A species' physical or geographical range is termed first-order selection. Within that, second-order selection is defined as the use of a home range. Within a home range, specific areas based on habitat components are selected for, labeled third-order selection. Finally, fourth-order selection is the choice of food items within a particular area or site. The geographic range of a species (first-order selection) will determine how sensitive a given organism is to extinction, in that the smaller the range, the more vulnerable a species will likely be (Gaston and Fuller 2009). Second-order selection can be examined by looking at high versus low use areas. An effective means to do this is through the creation of hotspot maps. A hotspot map for a species-area plot can be defined as the counted areas above a threshold compared to the other counted sites. (Veech 2000; Sussman et al. 2019). Third and fourth-order assessments are done through statistical modeling approaches, often by relating variables to binary (presence/absence) or count data (Bolker et al. 2009). The understanding of species' habitat preferences changes, not only as a factor of spatial scale, but also if the study is considering the system from a bottom-up or top-down viewpoint. Most species play role as both predator and prey. These role fluctuations lead to the possibility their distribution is controlled by a top-down system, a bottom-up system or both. In a bottom-up controlled system, prey distributions influence their predators' distributions (Hunt et al. 2002; Hipfner et al. 2012). With top-down controls, organisms are usually influenced by predator distributions through both lethal and non-lethal effects. Non-lethal effects, such as shifting locations based on fear of being depredated, can shift the prey species' locations to poorer foraging habitat (Cresswell 2008).

Habitat preference studies have many applications, one of which is to help create effective conservation management plans for species in need (Jones 2001). Many seabirds around the world are on the decline, with at-sea threats playing a major role (Dias et al. 2019). Marine habitat studies can help identify important at-sea habitat for marine protected areas, as well as provide biological insight into specific habitat requirements that can assist in spatial planning. The government of Canada has an interest in supporting such studies to help in the development of the Oceans Protection Plan (OPP). The OPP overarching aim is to protect Canadian coastal waters (Government of Canada 2020). The longer data are collected over time, the stronger our understanding of a given system becomes (Magurran et al. 2010). Therefore, it is hugely beneficial to use datasets collected over a long period of time to build a baseline understanding of how organisms interact with their environment. Laskeek Bay Conservation Society (LBCS) is a non-profit conservation organization that has been operating a long-term monitoring station in Haida Gwaii, British Columbia, Canada, since 1990 (Laskeek Bay Conservation Society 2020). The society has gathered the longest-running at-sea surveys in British Columbia, providing valuable information on the long-term trends of various species of interest.

One of the prominent seabirds that reside in the waters of Laskeek Bay is the Marbled murrelet (*Brachyramphus marmoratus*), a small seabird that is listed as threatened in Canada (Environment Canada 2014). Like all seabirds, Marbled murrelets use a dual habitat strategy during the summer months while breeding (Schreiber and Burger 2002). This means they spend time both in marine and terrestrial areas to rear their young during the breeding season. What separates this species from all other seabirds, except their sister species the Long-billed murrelet (*Brachyramphus perdix*), is their nesting dependence on old-growth forests, using the thick moss on branches as platforms to lay their single brood egg (Nelson and Hamer 1995b). Due to the harvesting of old-growth, much of the research and conservation efforts have had a terrestrial habitat focus (Environment Canada 2014). Despite these efforts, Marbled murrelet numbers continue to drop over large portions of their range (Bertram et al. 2015; Miller et al. 2012). Overfishing, pollution, human disturbance and climate change have induced changes to the waters within their home ranges and may also be contributing to the declining numbers (Trathan et al. 2014; Speckman, Piatt, and Springer 2004). This reinforces the need for marine habitat conservation planning in addition to terrestrial

conservation for this species. Marine habitat preference studies of Marbled murrelets have been conducted in the southern waters of California and Washington (Miller, Meyer, and Ralph 2002; Raphael et al. 2015; Lorenz et al. 2016), the southern region of British Columbia (Ronconi and Burger 2008; Yen, Huettmann, and Cooke 2004) and the in waters of Alaska (Barbaree, Nelson, and Dugger 2015; Kuletz, Labunski, and Speckman 2008; Haynes et al. 2011). This thesis provides the first comprehensive analyses of habitat preferences for Marbled murrelets in the unique region of Haida Gwaii.

I use the theory and motivation explained above to develop a thesis that explores marine habitat preferences for Marbled murrelets and test the underlying factors that drive these non-random patterns. The thesis is laid out as three data chapters. Firstly, I use the longest-running at-sea survey dataset in British Columbia to develop a baseline description of marine habitat patterns for this species in Haida Gwaii. I examine second-order habitat selection by creating a hotspot persistence map within the study area that provides a snapshot of areas that were consistently in use (or not) during the breeding season, summarizing data from 22 years of surveys. I then tested a set of potentially influencing variables (static and dynamic) on patterns, which is an exploration of third-order selection. In the third chapter, I quantify how closely murrelet distribution can be linked to general fish abundance and what dynamic oceanographic factors correlate with their foraging locations. This chapter addresses both third and fourth-order selection. In the final data chapter, I shift to a top-down view of murrelet use of space by testing whether the presence of avian predators influences distributional choice. This is done using a field experiment that utilized deterrent and Bald eagle (*Haliaeetus leucocephalus*) and Peregrine falcon (*Falco peregrinus*) kites and measured differences in murrelets' locations when kites were flying or were not flying. In my concluding chapter, I highlight the study's overarching findings and discuss how my results can contribute to management and conservation strategies for the threatened Marbled murrelet.

Chapter 2.

Marine Hotspot Persistence and Habitat Preferences of Marbled Murrelets from At-Sea Surveys (1997-2018)

2.1. Abstract

Baseline knowledge of habitat preferences is needed to build conservation recovery strategies for species of interest. I used the longest-running at-sea survey dataset available in British Columbia to examine hotspot persistence and habitat use of threatened Marbled murrelets (*Brachyramphus marmoratus*) at Laskeek Bay, Haida Gwaii, BC. The Laskeek Bay Conservation Society has been conducting sets of spring and summer surveys along fixed transect routes in open and shoreline waters from 1997–2018. I divided transects into 1 km long segments for analysis. Through hotspot persistence mapping, I found that murrelets consistently preferred shoreline transect routes and were repeatedly observed throughout the years within particular shoreline or shallow water segments. In 75 surveys conducted over 22 years, segments were assigned a “hotspot” status for a maximum of 64% and a minimum of 3%. In line with the visual findings of the hotspot map, AIC model selection, built from a series of general linear mixed models, supports murrelet preferences for marine areas that were shallow and closer to streams, had a closer proximity to abundant nesting habitat and were above sandy substrate. The top model containing these variables accounted for 22% of the variation in the dataset. These results highlight the importance of static environmental variables when considering the habitat needs of this species.

2.2. Introduction

Many seabird populations are declining around the globe, with at-sea threats playing a major role (International 2018; Dias et al. 2019). Marine habitat studies that gather baseline information are vital in creating effective management plans. Baseline environmental data can help detect future changes in the ecosystem and improve our understanding of changing environments and human activity to aid in the production of management plans (Government of Canada 2020). A growing approach to conducting

habitat preference studies is through tagging and tracking individuals (Grémillet and Boulinier 2009). These studies provide detailed information on movements but remain costly per device, and over a long-time frame, do not provide information on population-level aggregations. Therefore, traditional at-sea survey methods remain a cost-effective method for obtaining long-term information on distributions of seabird populations. Our interpretation of these at-sea surveys can be built around a habitat preference framework.

Habitat preference studies aim to understand behavioural responses that individuals use to select habitat that influence their survival and fitness (Block and Brennan 1993; Hutto 1985). The selection of habitat is scale-dependent and may be thought of as a hierarchical process (Block and Brennan 1993). In this scheme, first-order selection describes the physical or geographical range of a species. Within that is second-order selection, which is the selection of a home range. Once in their home range, an organism will occur disproportionately in specific areas based on habitat components, termed third-order selection. Finally, fourth-order selection is the choice of food items within a particular site. Spatial scales decrease as order increases, and temporal scales vary with each level. Assuming that the geographical range of a species is known, the first step towards understanding marine habitat preferences is locating high and low use areas, contributing to the description of their home range. This is frequently done through hotspot mapping. A species-area plot can be defined as counted areas that consistently appear above a threshold based on the other compared counts from a given site (Veech 2000; Sussman et al. 2019). These maps are necessary because the probability that a survey's observation at any given location is representative of true abundance at that location is low due to the high variability seabird surveys typically exhibit (Piatt et al. 2007). Once a baseline insight of spatial use is established, understanding the processes behind third and fourth-order selection can be done by quantifying the effects of underlying environmental factors on these non-random patterns (Block and Brennan 1993).

Marbled murrelets (*Brachyramphus marmoratus*) are Pacific coastal seabirds that nest high in the canopies of old-growth coniferous trees but spend the majority of their time foraging in coastal waters (Nelson 1997). In Canada, these birds have attained a threatened status due to the ongoing harvesting of old-growth forests in British Columbia by humans, which has substantially reduced the extent of their breeding

habitat (Environment Canada 2014). For this reason, the majority of research on the species has focused on understanding their terrestrial habitat needs and nesting requirements. Despite efforts to conserve this seabird through forest management, their numbers continue to drop over much of their range (Bertram et al. 2015; Miller et al. 2012). An additional factor contributing to this decline may be changes to their marine habitat, resulting from overfishing, pollution, human presence and/or climate change (Trathan et al. 2014; Speckman, Piatt, and Springer 2004).

Marbled murrelet's use of foraging habitat during the breeding seasons, and their relationships to physical marine characteristics, may vary among geographic regions (Haynes et al. 2011; Raphael et al. 2015; Yen, Huettmann, and Cooke 2004). Therefore, developing an in-depth knowledge about marine habitat requirements or preferences in specific areas will improve local and regional conservation planning. Studies that have looked at the marine habitat preferences and needs of this seabird have been mainly concentrated on the southern coastal regions of British Columbia (Ronconi and Burger 2008; Yen, Huettmann, and Cooke 2004), in the waters around Washington, Oregon and Central California (Miller et al. 2002; Raphael et al. 2015; Lorenz et al. 2016), and southern regions of Alaska (Barbaree, Nelson, and Dugger 2015; Kuletz, Labunski, and Speckman 2008; Haynes et al. 2011).

Currently, no studies have been conducted in the northern coastal islands of Haida Gwaii, BC, to determine marine spatial patterns and the environmental variables influencing the distribution in these waters. Waters in northern British Columbia are part of the cool Alaska Coastal Current and are also influenced by numerous coastal rivers (Hunt 1995). The boundaries between this regime and the warmer waters of the California current shift annually, strongly affecting regional pelagic seabird foraging and breeding performance (Bertram, Harfenist, and Smith 2005). In addition to this, Haida Gwaii borders the Hecate Strait, the channel that runs between Haida Gwaii and mainland British Columbia. Differences in the tides and currents along the strait create a unique marine habitat (Crawford et al. 1995). The geographic variability of potential marine habitats coupled with Haida Gwaii's distinct differences from other regions suggests that a regional assessment of murrelet habitat preferences is warranted to test the applicability of conclusions drawn from the models of marine habitat preferences generated elsewhere.

In this study, I describe spatial and temporal patterns of marine habitat selection of Marbled murrelets (hereafter “murrelets”) in Haida Gwaii, BC, and test for nesting, coastal, and bathymetric features that influence these patterns. I used the longest-running at-sea fixed transect dataset from Haida Gwaii (1997–2018) to create a hotspot persistence map to help visualize where birds have been repeatedly seen or are absent throughout the years, and test for the influences of environmental variables on these distributional choices.

2.3. Methods

2.3.1. Study Area & Species

Seabird surveys were conducted in Laskeek Bay, situated on the eastern side of Louise Island (52°56'25.89"N, 131°39'50.10"W), in the southern portion of Haida Gwaii, British Columbia, Canada (Figure 2.1). The study area encompasses a surface area of about 130 km² that includes a mixture of shallow areas and deep zones exceeding 200 meters. Boat traffic from tour, research and private vessels is occasionally present during spring and summer. Twenty-seven kilometers of coastline lies adjacent to the study area, with 10 streams of stream order 2 or higher (Gray 2010) that input freshwater into marine waters.

Haida Gwaii supports about 16% of British Columbia’s ca. 99,100 (72,600–125,600) breeding season individuals (Bertram et al. 2015; Environment Canada 2014). The breeding season can span late March through early September, though specific times can vary by region and individual pairs (Hamer and Nelson 1995; Loughheed et al. 2002; Tranquilla et al. 2005). Currently, no studies have examined the distributional preferences of murrelets during the breeding season in Haida Gwaii. Marine usage studies from other coastal regions show murrelets are more likely to be found in shallow water close to shorelines (Haynes et al. 2011; Lorenz, Raphael, and Bloxton 2016) and have been associated with sandy substrate (Haynes et al. 2011; Raphael et al. 2015), which serves as vital habitat for Pacific sand lance (*Ammodytes hexapterus*) (Ostrand et al. 2005). Pacific sand lance are important prey species for murrelets, along with other mid to high-level trophic species such as Northern anchovies (*Engraulis mordax*), Pacific sardines (*Sardinops sagax*), juvenile rockfish (*Sebastes spp.*) (Becker, Peery, and Beissinger 2007) and krill (*Thysanoessa spinifera* and *Euphausia pacifica*).

Murrelets sometimes hold prey in their bills for long periods of time until low light hours, and where topography is steep, then use streams as flyways to carry food for their offspring on old-growth nesting platforms (Ralph et al. 1995; Haynes et al. 2011; Meyer, Miller, and Ralph 2002). The majority of nest sites are found less than 30 kilometers from shore (Hull et al. 2001; Lorenz et al. 2017). Previous studies have related at-sea murrelet distributions to distances to potential nest sites or old-growth abundance at a spatial scale of 10s of kilometers (Raphael et al. 2015; Lorenz, Raphael, and Bloxton 2016; Yen, Huettmann, and Cooke 2004; Ronconi 2008, unpublished).

2.3.2. Sea-Survey Data Collection

The Laskeek Bay Conservation Society (LBCS) has been conducting annual sets of seabird surveys during seabird breeding seasons along fixed linear and shoreline transects since 1997 (Figure 2.1). A total of 90 surveys were completed during these years, with those in May and June prioritized (Figure 2.2). Each survey consists of 18 transects, 8 shoreline and 10 offshore (Figure 2.3), which have a mean length of 3.8 kilometers, ranging from 1.8 to 6.3. LBCS attempted to conduct the surveys over a four-month period (April–July) from 1997 to 2003, and over three months (May–July) from 2004 onwards. Surveys were only conducted on fair weather days (sea state 3 or less) and were comprised of all 18 transects in one day, unless weather turned, in which case a set of surveys would be conducted during two, usually consecutive, days.

Surveys were conducted by 2–4 participants traveling in a small aluminum skiff. Start and end times were recorded for each transect. Using a voice recorder, the primary observer identified all seabirds and dictated the number seen on the water, while the secondary observer drove the boat. Any additional surveyors would help with timing and GPS waypoint recordings and observations. Observations were made up to 50 meters on either side of the boat, for a summed transect width of 100 m. Birds seen on the water or just taking off from the water were recorded, and the location of the initial sighting was used. Birds landing on the water as a transect was being conducted were not treated as “on the water” sightings. From 1997–2008, locations were recorded as stopwatch times from the start of the transect. From 2009–2018, recordings of distance along the transect using a GPS unit were used to mark locations of bird observation points. The dynamic environmental variables cloud cover, precipitation, wind speed and time of day were recorded during surveys. Initial recordings were made at the start of a

survey day and updated at either the start or end of subsequent transects as conditions changed. After surveys, the voice recordings were transcribed to paper sheets and stored in binders.

2.3.3. Data Digitalization

I entered data from hard copy sheets into Excel spreadsheets before cleaning and reformatted the dataset in R and ArcGIS Pro using the R-ArcGIS bridging program. The translation of bird locations from spreadsheets to point features in ArcGIS was done using two approaches to accommodate the two methods used to mark bird locations. For stopwatch entries, I measured the total length of the transect, then divided by the total time taken to complete the transect to estimate average boat speed (meters/second). Each stopwatch point (seconds) was then multiplied by the boat speed to calculate the distance (meters along transect) at which birds were seen on the water. The ArcGIS Pro 2.3.0 “Make Route Event Layer” tool was used to translate these distances to coordinate points. Bird locations recorded with the GPS unit were entered directly. All surveys (1997–2018) were merged into one spatial dataset using the Merge tool (ArcGIS Pro 2.3.0) and saved as shapefiles.

2.3.4. Segmenting data

For hotspot analyses, I binned transects into 100 m x 1 km grid rectangles along routes over the survey area, producing 83 segments (Figure 2.3). The length was selected to enable analyses at a fine spatial scale but be long enough to result in measurable aggregations of murrelets. Because shoreline transect were not completely linear, most of these transect segments had small deviations from the standard 1 km size length (Figure 2.3). These differences in segment area were accounted for in our analyses.

2.3.5. Environmental Variables

To explore the effects of environmental characteristics on murrelet count distributions, I chose 6 spatial variables plus 4 dynamic variables that were recorded as surveys took place. Spatial variables were assembled from online sources or collected in the field to evaluate their influence on murrelet distribution through the years (Table 1;

detailed maps in Appendix A). Static spatial coastal variables were: distance to shoreline ($SHORE_{dist}$), distance to sandy shoreline ($SANDSH_{dist}$), distance to streams ($STREAM_{dist}$) and an index measuring the proximity and abundance of potential nesting habitat ($NEST_{index}$). Static oceanographic variables were ocean depth and percent sand bottom substrate ($SAND_{bottom}$). The contemporaneous dynamic variables were: time of day ($TIME$), percent cloud cover ($CLOUD_{cover}$), precipitation ($RAIN$) and wind speed ($Wind_{speed}$).

I collected depth and seafloor sediment data in the summer of 2019 primarily to quantify murrelet associations with percent sandy bottom (based on Wentworth scale). Collection points for sediment bottom were established at 1-kilometer intervals along the transects. Collection points occurred within a given segment (Appendix, Figure A1). Pacific sand lance have predominantly been found to bury in sandy sediment in waters 60 meters depth or less (Ostrand et al. 2005), so collections were made down to 60m as the maximum depth. I attached 60 meters of crab line to a Petite Ponar grab to obtain the sediment, stored these samples in small buckets and brought them back to base camp. For a single point, the grab was dropped three times. If no sand or only rock was collected after the 3rd drop, we assumed zero percent sand. Points along the transect that exceeded 60 meters were assigned a category of “Deep” and were assigned zero percent sand. I dried the collected sediment on a wood-burning stove (low heat) for 24–48 hours. After this drying step, samples were shaken through a sieve series (4 mm, 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm) for approximately 15 minutes, then weighed and recorded. I categorized sediment as sand if it was ≥ 0.063 mm and ≤ 2 mm. An assumption was made that the location of sediments at collection points remained constant for the study period. For ocean depth, a Lawrence Elite Yi 7 sonar “Fish Finder” was used to record continuously along transect lines. The mean depth recording per transect segment was used for the analysis (Appendix, Figure A2).

Potential nesting habitat data adjacent to the transects were taken from a three-class habitat suitability map provided by the B.C Ministry of Environment (Mather et al. 2010). For this study, potential nesting habitat was defined as any forested area where murrelets could nest, with all levels of nesting suitability (Class 1–3) treated with equal weight. Following Ronconi (2008), I created an index testing relationships between murrelet counts and nesting habitat proximity and abundance, using inverse distance weighting (IDW) in ArcGIS pro 2.3 (Appendix, Figure A3). IDW requires point features to

generate predictions, so I turned the potential nesting habitat polygon layer into a series of points on the islands surrounding Laskeek Bay by overlaying a hexagon net (each 866,024 m²) on the nesting habitat layer. The nesting habitat area that was contained within a hexagon was then transformed to a centroid point within each hexagon. I screened three potential commuting distances to identify the most appropriate spatial scale to calculate potential nesting habitat index values. A 5, 15 and 30 km radius from each centroid transect point was used to create a maximum radius of potential nesting habitat, as these are typical commuting distances for murrelets (Hull et al. 2001; Lorenz et al. 2017). To find which spatial scale was appropriate, I plotted the mean relationship of murrelet counts per segment to the nesting index of each given radius. The nesting index using a 5 km maximum distance had the strongest relationship to murrelet counts and therefore used in the subsequent candidate models. I treated this layer as static because, after inspection from google earth pro images, less than 4 km² of forest was harvested within the 5 km buffer zone between 1997–2003, and no harvesting was detected within the potential nesting area from 2004 onward.

The remaining environmental variables were collected from online sources: Shoreline was mapped using the physical shore-zone polygon from the GeoBC database (<https://catalogue.data.gov.bc.ca/dataset/shore-unit-classifications-line>). Details on classification are given in Howes, Harper, and Owens (2005). The distance to the shoreline and the shoreline type that contained sandy substrate was calculated from the cell segment center using the “Near” tool in ArcGIS Pro 2.3.0. Stream data were taken from the British Columbia Stream Atlas Network (<https://catalogue.data.gov.bc.ca/dataset/freshwater-atlas-stream-network>). I tested for relationships between murrelet distribution and streams by calculating the distance from the center of a given segment to each stream head of order 2 or higher (Appendix, Figure A4; Gray 2010).

2.3.6. Hotspot Persistence Analysis

To examine spatio-temporal variation in murrelet distributions, I implemented a hotspot persistence method (Sussman et al. 2019). The method creates a map that defines hotspots for each survey, then calculates the percentage of surveys in which each segment was a hotspot. May and June surveys had been surveyed consistently from 1997–2018. Therefore, I only used these months to build the hotspot map, reducing

the total number of surveys to 75. For each survey, three steps were taken to classify segments as hotspots. Firstly, an effort corrected count (ECC) was applied to raw counts to correct for small deviations in segment size resulting from the non-linearity of shoreline transects and their exact lengths. The ECC was calculated by dividing total counts within a segment by the area of the segment. Second, a two-parameter gamma distribution was fit to the ECC by summing the counts within grid segments for each unique survey day (*fitdistrplus* package in R). Finally, a segment was identified as a hotspot if the ECC value was above the 75th percentile for a given survey day. This procedure effectively standardizes surveys for the total number of murrelets present and weighs each survey equally regardless of the total counts. After applying these steps to each survey event over the 22-year period, I calculated the percent of surveys each segment was identified as a hotspot, ranging from 0–100. The higher the percentage a segment was given, the more frequently the segment was considered a hotspot.

2.3.7. Habitat Preference Analysis

Before building candidate models of habitat usage, environmental variables were checked for collinearity by calculating all pairwise Pearson’s correlation coefficients. Significant correlations of $r \geq 0.7$ were found between: $STREAM_{dist}$ and $SANDSH_{dist}$, as well as depth and $SHORE_{dist}$. The spatial variables depth, $STREAM_{dist}$, $NEST_{index}$ and $SAND_{bottom}$, were kept for the subsequent analysis. Since I knew *a priori* from literature and preliminary examination that murrelets were substantially more abundant close to shore, we attempted to obtain a greater resolution of other variables by making a separate analysis that included only transects adjacent to Louise island (shoreline). I standardized and centred environmental variables by subtracting the mean and dividing by the standard deviation to directly compare the magnitude of the effect size for the variables.

A series of generalized linear mixed models (GLMM) with an expected negative binomial distribution were used to analyze both the full bay and shoreline habitat selection (Appendix, Figure A5). All months available from 1997–2018 were used in this analysis. The GLMM framework handles non-normal response data and can account for nested, non-independent sampling (Brooks et al. 2017). All models used a negative binomial error distribution (log linked) fit to a “nbinom2” family, which assumes variance increases quadratically with the mean ($s^2 = m(1 + m/q)$, with $q > 0$). This type of

distribution was chosen due to count data being overdispersed (Brooks et al. 2017). Models were fit in R 3.61 using the glmmTMB function in the TMB package. This function fits models using the Laplace approximation to integrate over random effects (Brooks et al. 2017).

Two sets of candidate models were assembled *a priori*, divided into all combinations of static variables, and then all combinations of dynamic variables. Each candidate model contained the random effects of year, Julian day, transect segment nested within transects. The effort correction (offset) was included as the length surveyed within each segment. The full list of the candidate models is shown in Table 2.2. Top models were selected using the lowest Akaike information criterion, which all top models with Δ_i values less than 2 considered equal model weight (Anderson, Burnham, and White 1998; Richards 2005).

Variables from the top-scoring static and dynamic models, as well as the random effect coefficients previously listed, were then run to test their relative effects on murrelet counts. I assessed the significance of independent variables from top models, the Incidence Rate Ratios (IRR) and their 95% confidence intervals. The IRR indicates the change in the dependent variable in terms of a percentage increase or decrease, with the precise percentage determined by the amount of the IRR is above or below 1 (Cummings 2019). Values below 1 indicate a negative relationship, and counts above 1 indicate a positive relationship.

To account for spatial autocorrelation, I included the spatial “hierarchical” structure into the GLMM that specified that segments were nested within transects. This method assumes that the dependence of segments within their given transect is constant. I also tested for evidence of spatial autocorrelation after model construction using a correlogram test. In this type of test, a Moran’s I value is calculated over increasing spatial lags (Fortin, Dale, and Hoef 2002). To compare how well the spatial variables in the model accounted for spatial autocorrelation, I first summed all counts across years within their specified segment, then ran the correlogram test on the raw murrelet counts followed by a second correlogram test on the residuals from the spatial model. I then compared the results to see what changes in spatial relatedness occurred. Tests were run at increasing lags of 440 meters to a maximum distance of 9000 meters.

2.3.8. Model Performance

To evaluate model performance, I calculated marginal R^2_{GLMM} , which describes variance explained by fixed effects, and conditional R^2_{GLMM} , which describes the variance explained by both the fixed and random effects (Nakagawa and Schielzeth 2013). I then plotted the predicted values for each response variable with their associated 95% confidence intervals to evaluate the support for each variable at different numeric or categorical values for the given independent variable (Lüdecke 2018). These describe the marginal effects from the given GLMM model. When the marginal effects of a given variable are plotted, all other independent variables were set to zero to minimize their effects.

2.4. Results

2.4.1. Habitat Persistent Preference Heatmap

The average number of individuals sighted during a survey per segment was 1.16 birds, with counts ranging from 0 to 92 individuals during the months of May and June across the 22 years used for the map construction (Figure 2.4). The highest proportion of surveys a segment was deemed a hotspot was 0.64, and the lowest was 0.03. For the 8 inshore transects along Louise island, the lowest proportion of surveys a segment was a hotspot was 0.16, and the highest was 0.64, with a mean of 0.33. For the 10 linear offshore transects, the proportions ranged from 0.03–0.44 with a mean of 0.16. The majority of the segments categorized as hotspots repeatedly were on the south side of the shoreline. The furthest northwest transect had two segments that were persistently hotspots (>50% surveys), which were close to Cumshewa Head, a major landmass. It is evident that the further segments were situated from major landmasses, the less likely they were to be classified as hotspots.

2.4.2. Spatial Autocorrelation

I produced correlograms for both the raw murrelet counts and the residuals from the top static model. There was strong evidence of spatial autocorrelation of the raw counts (Figure 2.5), with positive autocorrelation linearly decreasing until 6000 meters. This linear pattern disappeared when model residual values were plotted (Figure 2.5),

indicating that the spatial variables implemented in the model accounted for the spatial autocorrelation in the raw data.

2.4.3. Habitat Preferences

For both the full bay and shoreline analyses, two sets of candidate models explored the influence of environmental variables on Marbled murrelet counts from at-sea surveys. The candidate models examining static variables for the full bay showed the strongest support for a single model. This top model ($\Delta AIC = 0$, $wt=0.93$; Table 2.3) included $DIST_{stream}$, depth, $SAND_{bottom}$ and $NEST_{index}$. The model received seven times more support than the next best model (Appendix Table A1). The marginal R^2_{GLMM} explained about 24% of the overall variance, and the conditional R^2_{GLMM} explained 52% of the variance. The candidate models for dynamic variables produced two candidate models with strong support with an $\Delta AIC_c < 2.0$ (Burnham and Anderson 2002; Tables 2.3). The top-ranked model included rain, time and wind speed, with rain and time present in both top models. The strongest dynamic model ($\Delta AIC = 0$, $wt=0.40$; Appendix Table A1) received 1.93 times the support of the next best model. In contrast to models of static variables, however, no models of dynamic variables alone provided strong predictive power in the absence of random effects; their marginal and conditional R^2_{GLMM} values indicated these models explained 1 % and 55% of the variance, respectively.

In the shoreline only analysis, four top models were selected from the static candidate models, which included $STREAM_{dist}$, depth and $SAND_{bottom}$ for the top-ranked model ($\Delta AIC = 0$, $wt=0.28$; Table 2.3). In all top models, the variable $STREAM_{dist}$ was consistent. In this top-ranked static model, the marginal R^2_{GLMM} value explains 5% of the variation, and the conditional R^2_{GLMM} denotes 54% of the variation. The dynamic candidate models for the shoreline analysis had four top models. $WIND_{speed}$ was present in all top models and was also the first ranked model ($\Delta AIC = 0$, $wt=0.25$). This top model had the marginal R^2_{GLMM} explaining 3% of the variance and the conditional R^2_{GLMM} explaining 55% of the variance. Based on the marginal R^2_{GLMM} values, it is evident that overall, the shoreline models explain the variance at a much lower rate than the full models for the static variables (Table 2.3).

The top static model from the full analysis (Table 2.4; Figure 2.6, 2.7, A6) indicates that murrelet counts significantly increase as their distance to streams and

water depth decreases (IRR = 0.50, 95% CI = 0.39–0.63; IRR= 0.66, 95% CI = 0.53–0.82, respectively). Counts of murrelets also increase as the percent of sand in ocean sediment increases (IRR= 1.16, 95% CI = 1.03–1.29) and more proximal to abundant potential nesting habitat (IRR = 1.23, 95% CI = 1.07–1.42). The top dynamic model revealed counts are significantly higher in the morning (IRR=1.32, 95% CI = 1.05–1.65) and when it rains (IRR=1.74, 95% CI = 1.05–2.82). The shoreline top model (Table 2.4; Figure 2.8, A6) indicates that murrelet counts significantly increase as the distance to streams and depth decrease (IRR=0.41, 95% CI = 0.25–0.68 and IRR = 0.46, 95% CI 0.21–0.99, respectively). Wind speeds influence the counts at their intermediate category (Figure 2.9), being significantly lower when speeds range from 6 to 10 knots (IRR = 0.49, 95% CI 0.30–0.78). The relationship of counts to wind suggests a positive association with light winds, negative correlation with intermediate winds and positive relationship for strong winds.

2.5. Discussion

The aim of this study was to better describe the marine distribution and understand habitat preferences of Marbled murrelets in Haida Gwaii. I used a long-term dataset (1997–2018) to complete two main objectives. I first created a hotspot persistence map to depict where birds have been repeatedly seen or absent throughout the years. I then tested for the influences of environmental variables on these distributional choices. The hotspot persistence map shows that murrelets repeatedly chose specific areas inshore and generally avoid some of the outer transect routes within Laskeek Bay. I analyzed habitat preference at two different scales, one containing the transects from the full bay area and one using only the transects along Louise island (shoreline). Overall, there is strong evidence that higher numbers of murrelets are found closer to streams, in shallow waters, in marine areas that contain sandy substrate and in areas more proximal to abundant potential nesting habitat. In models restricted to the shoreline transects, the predictive power of these variables weakens considerably. The role of the recorded weather and time variables were mixed. The full bay analysis indicated a higher murrelet count during the mornings and while it rains. The shoreline analysis indicated a higher count with increased cloud cover while it was raining, as well as a lower count when the winds were between 6–10 knots. In both the full and shoreline

analysis, these dynamic variables explained very little of the overall variance of the models.

2.5.1. Hotspot Persistence

The hotspot persistence map provides an effective visual snapshot of the murrelet distributional choices within Laskeek Bay over the last 22 years. The map clearly shows that murrelets prefer to use the inshore waters, but also that there is substantial variation in usage among the 1 km long inshore transect segments. The southern shoreside shows the strongest long-term usage for murrelets, but there are also segments in the northwestern waters close to Cumshua Head and one strong hotspot segment on the north end of Skedans Bay. As supported by the habitat preference model, these segments are within shallow waters that are often close to streams and potential nesting habitat or above sandy sediment that provide burying sites for Pacific sand lance. I also noted during my time surveying in this bay that the northern shoreline often contained large aggregates (often 50+ counted on one scan) of perched and low flying eagles actively foraging. Though the southern side also contained many active eagles, I never saw large aggregations of them along the shoreline, as observed on the southern end. It is, therefore, possible the southern end is also safer for murrelets to forage in. In the subsequent chapters (Chapters 3 and 4), I further explore what roles foraging and avian predator presence make on distributional decisions.

This is the first time this type of hotspot map analysis has been applied at such a localized scale to murrelets and is one of the few spatial depictions of local murrelet distribution. A kernel density analysis of space use of radio-tagged murrelets in southeast Alaska found concentrated hotspot patterns within specific bay areas (Barbaree, Nelson, and Dugger 2015), as did unpublished analyses of radio-tracked birds at Desolation and Clayoquot Sounds (Barrett 2008, personal communication). My map shows that murrelet spatial patterns can be depicted at a finely segmented scale, given sufficient survey data. It should be noted that the highest persistence determined in a kilometer-long segment was 64%, suggesting that dynamic oceanographic processes may be involved in birds' choices on a given day.

2.5.2. Distance to Streams

In both the full and shoreline analysis, there is a higher probability that murrelets use marine areas closer to streams. This relationship has been found in a number of other studies along the west coast (Haynes et al. 2011; Miller, Meyer, and Ralph 2002). Currently, there are two leading hypotheses to account for the relationship. The first is the utilization of streams as flyways to nesting sites. The reasoning is that it is more energetically efficient to forage and hold fish closer to the flyway stream heads when commuting to feed young (Becker and Beissinger 2003; Barbaree et al. 2014). This hypothesis may be more applicable to sites with more dramatic topography than is present around Laskeek Bay. The second hypothesis is that areas with freshwater and saltwater mixing will have higher productivity than areas that do not (Yen, Huettmann, and Cooke 2004). This means that these areas would be more valuable to murrelets in the quality of foraging opportunities available. It is likely that a combination of both hypotheses plays a role in their distribution choices to streams. In the subsequent chapter (Chapter 3), I find evidence stratified water close to streams may be valuable to murrelets, indicating that these streams are inputting nutrients that remain stagnant on the water's surface.

2.5.3. Percent Sand Bottom

Pacific sand lance are an important food source for murrelets, and are often found in coarse grain sand in shallow areas (Ostrand et al. 2005). Therefore, it is not surprising that various marine habitat studies have found that sandy shorelines and underwater substrate predict murrelet presence (Meyer, Miller, and Ralph 2002; Ronconi 2008, unpublished; Yen, Huettmann, and Cooke 2004). For this study, I tested for effects of the percent sand on murrelet counts to see what linear trends might arise and contribute to the overall model. I did find a significant positive trend of percent sandy sediment within segments on counts. This contributes to growing evidence that sandy sediment plays an important role in determining where murrelets are likely to forage. Four of the sediment collection points that fell between Vertical Point and Haswell Island had higher percentages of coarse grain sand, as do three points between Louise island and Cumshua inlet (Appendix, A7). These also are locations where I found high persistence of counts from the hotspot map.

2.5.4. Water Depth

Murrelets are thought to be midwater feeders (Drew, Piatt, and Hill 2013) and may dive down to 47 m (Nigel and Burger 1998). My results show that shallower waters are used by higher numbers of murrelets. This result also held true within the shoreline analysis, though overall model performance weakened considerably. Shallow waters have a higher probability of containing Pacific sand lance (Ostrand et al. 2005) and feeding schools of Herring coming inshore (Burkett 1995). Murrelets also forage on zooplankton species such as krill (Becker, Peery, and Beissinger 2007), which are preyed upon in shallow areas. Shallow areas in this bay often occur at short distances to shore. This correlation was accounted for by the addition of spatial random effects in the model and the addition of the shoreline analysis. Distance to shore has a separate function from foraging depth for murrelets, since foraging near land saves energy by minimizing travel time to nesting sites (Hull et al. 2001). The repeated support for shallow waters in the shoreline analysis further supports murrelets' affinity to shallower areas.

2.5.5. Potential Nesting Habitat

A positive relationship between the proximity and abundance of potential nesting habitat and murrelet water counts is present in these data. This relationship is strongest for the full bay evaluation and weaker for the shoreline analysis. This type of relationship has been documented a number of times (Yen, Huettmann, and Cooke 2004; Ronconi 2008; Raphael et al. 2015; Lorenz, Raphael, and Bloxton 2016), but my study showcases the relationship at a finer geographical scale than other studies. At first glance, it seems surprising that a bird that can have a nest to sea commuting distance of up to 145 km (Lorenz et al. 2017) would have a strong relationship to potential nesting habitat at a scale of 5 km or less. Potential reasoning for this could be the use of old-growth as cover when travelling to their nesting sites, though this has not been explicitly tested and is only speculation. Birds in Haida Gwaii may nest closer to the shorelines than at other study sites in the lower mainland or up in Alaska. There is very little information on the locations of nesting sites in Haida Gwaii, so this can not be ruled out. Future studies could radio-tag birds that forage in this bay to try and work out what the significance of this relationship actually means.

2.5.6. Time and weather variables

LBCS recorded a number of weather and time variables throughout their surveys, of which I analyzed wind speed, precipitation, time of day and percent cloud cover. These kinds of factors have been known to influence bird counts on the water for at-sea surveys (Tasker et al. 1984). My analysis shows weak evidence that these weather and time variables explain variance in the model, though some variables did come out as significant. Murrelet counts increased with precipitation, which was contrary to what was expected if rain obstructs visibility. Murrelets may be less active and prefer to stay on the water during periods of rainfall, though evidence of this behaviour has not been systematically checked. In the shoreline analysis, there was also some linkage to wind speed playing a role in their counts, though the trend was not linear, as lower murrelet counts were only significantly recorded when winds were at an intermediate strength. Winds can play a role in detectability due to water chop, which would lead to lower counts. I also found a higher number of birds being counted in the morning than the afternoon for the full, but not the shoreline only models. This contrasted with the survey results found in southern Alaska (Haynes et al. 2011), which observed a higher density of murrelets in the afternoon. The LBCS surveys were usually done prior to late afternoon and would have missed any late afternoon usage by murrelets.

2.5.7. Model Performance

I estimate how environmental static variables and weather variables relate to habitat preference through predictive modeling. This approach is important for the identification of suitable at-sea habitat (Oppel et al. 2012). After running models for static and dynamic variables of interest, I evaluate the predictive model performance by calculating the marginal and conditional R^2_{GLMM} values. I also graph partial models that plot the predicted values of a given variable with its associated 95 % confidence intervals while holding the other variables constant (Lüdecke 2018).

The marginal R^2_{GLMM} calculated that DISTstream, depth, SANDbottom and NESTindex and accounts for about 24% of the variation in the model, while the dynamic variables rain and time of day explains only 1% of the variation. When looking at the conditional R^2 values, we see some discrepancies in that when more fixed variables are added, conditional R^2 decreases slightly. This is due to the R^2_{GLMM} equation having a

variance error term in the denominator (Nakagawa and Schielzeth 2013). As different fixed variables are added, the error value can increase, leading to a lower R^2 value.

For a model that explains something as complex as marine habitat selection, the top static model explains a fair amount of murrelet habitat choices along the transects. There are however, critical dynamic variables that could not be added to this long-term dataset due to the scale of the analysis and data availability. Sea surface temperature, salinity and the amount of upwelling or vertical mixing an area has are among these dynamic variables that have previously been correlated to murrelet marine habitat usage (Becker and Beissinger 2003; Peery et al. 2009; Day and Nigro 2000) and could be contributing to the Laskeek Bay marine habitat choices. These ideas are explored further in Chapter 3.

2.5.8. Management implications

The Laskeek Bay data are the only long-term series available for Haida Gwaii, and this analysis has provided novel information for the area. The creation of a hotspot persistence map visually demonstrated how important specific survey areas remained through time. The results from the heatmap and the habitat preference analysis supported each other, as described in section 2.5.4, showing that both can be complementary tools in assessing habitat preferences. In addition to this, my static variable correlations of habitat preference analysis has supported previous findings in other coastal areas of spatial environmental variables deemed important for murrelets. The marine habitat preference analysis highlights the importance of streams, shallow areas, sandy substrate and nesting habitat, supporting the connectivity between marine and terrestrial features. The framework for this type of hotspot map and habitat analysis can also be applied to other seabird species that had been surveyed in Laskeek Bay.

This work can aid in the creation of a coastwide marine habitat suitability map for murrelets, facilitating effective policy decisions. The distribution of murrelets recorded and plotted during this study has also contributed to the Oceans Protection Plan, adding to the coastwide database of important marine foraging areas that will help improve emergency response readiness in case of an oil spill or shipping accidents.

2.6. Tables and Figures

Table 2.1 Static and Dynamic environmental variables used as covariates with respect to Marbled murrelets (*Brachyramphus marmoratus*) distribution.

Variable Type	Name	Definition	Significance
Static (Spatial)	Percent Sand Bottom (SAND _{bottom})	Static categorical variable; Categorized as sediment size (Wentworth scale) from point collected within segments.	Coarse grain sediment associated with Pacific Sand Lance habitat (Haynes, Ronconi, and Burger 2007)
	Depth (DEPTH)	Static numeric variable; Mean depth per segment (corrected to low tide level).	Affinity to shallower waters compared to heavier relatives who have the ability to dive deeper (Burkett 1995; Burger et al. 2008)
	Distance to sandy shoreline (SANDSH _{dist})	Static numeric variable; Midpoint of each segment to the nearest sandy shoreline was used.	Similar to Seafloor sediment, shoreline type (Sand/Gravel) can be used as a predictor to foraging fish habitat area (Haynes, Ronconi, and Burger 2007)
	Distance to streams (STREAM _{dist})	Static numeric variable; Measured as the distance from the center of a segment to stream mouth.	Have been observed to use streams/rivers as flyways to bring food to nests (Haynes et al. 2011)
	Index of potential nesting habitat (NEST _{index})	Static numeric variable; Distance from center of a segment to PNH edge.	Distance from nesting habitat correlates with marine distribution (Becker & Beissinger 2003; Ronconi 2008; Yen, Huettmann, and Cooke 2004)
	Distance to Shoreline (SHORE _{dist})	Static numeric variable; Measured as the distance from the center of the segment to shore.	Have found to be inshore foragers (Speich and Wahl 1995)
Dynamic (Temporal)	Percent Cloud Cover (CLOUD _{cover})	Dynamic numeric. Taken at the start of the day and updated throughout the survey if changes occur.	Environmental weather factors can influence bird detectability (Tasker et al. 1984; Hyrenbach et al. 2007)
	Precipitation (RAIN)	Dynamic binomial. Recorded as Yes or No precipitation at the start of day and updated thought survey if changes occur.	Environmental weather factors can influence bird detectability (Tasker et al. 1984; Hyrenbach et al. 2007)
	Wind Speed (Wind _{speed})	Dynamic categorical.	Environmental weather factors can influence bird detectability (Tasker et al. 1984; Hyrenbach et al. 2007)
	Time of Day (TIME)	Dynamic binomial; recorded as Morning (survey <12:00hrs) or Afternoon (survey >12:00 hrs)	Foraging behaviour depends on time of day (Haynes et al. 2011)

Table 2.2 Candidate models used to test static and dynamic variables of habitat preferences of Marbled murrelets. In addition to variables listed below, each model also included random effects of year, Julian day, transect segment nested within transects, and an offset of segment length.

<i>Model Type</i>	<i>Parameters</i>
<i>Static Models</i>	DIST _{stream}
	depth
	SAND _{bottom}
	NEST _{index}
	DIST _{stream} +depth
	DIST _{stream} +SAND _{bottom}
	DIST _{stream} +NEST _{index}
	depth+SAND _{bottom}
	depth+NEST _{index}
	SAND _{bottom} +NEST _{index}
	DIST _{stream} +depth+SAND _{bottom}
	depth+SAND _{bottom} +NEST _{index}
	DIST _{stream} +SAND _{bottom} +NEST _{index}
DIST _{stream} +depth+SAND _{bottom} +NEST _{index}	
<i>Dynamic Models</i>	CLOUD _{cover}
	rain
	WIND _{speed}
	time
	CLOUD _{cover} +rain
	Cloud _{cover} +WIND _{speed}
	CLOUD _{cover} +time
	rain+WIND _{speed}
	rain+time
	WIND _{speed} +time
	CLOUD _{cover} +rain+WIND _{speed}
	RAIN+WIND _{speed} +time
	CLOUD _{cover} +WIND _{speed} +time
	CLOUD _{cover} +WIND _{speed} +rain+time

Table 2.3 Top Models of marine habitat preferences in Laskeek Bay for *Brachyramphus marmoratus* during the nesting season between 1997 and 2018, using bird counts from at-sea surveys. The top models ($\Delta\text{AICc} < 2.0$) are reported for the full and shoreline only analysis. Models predict the average number of counts per segment and incorporate the year (n=22), Julian day (n=60) and segment (n=80) nested within transects (n=18) as random effects. K is the number of parameters estimated, AICc is the Akaike's Information Criterion, ΔAICc is the differences between the AICc of each model to the lowest AICc score, wt is the relative likelihood of each model in relation to all other models in the candidate set, marginal R² explains variance contributed by fixed factors and conditional R² describes the variance explained by both the fixed and random factors.

Parameter	K	AICc	ΔAICc	wt	Marginal R ²	Conditional R ²
Full analysis: Number of counts within segments (Static Models)						
STREAM _{dist} +DEPTH+SAND _{bottom} +NEST _{index}	10	10415.92	0.00	0.93	0.24	0.52
Full analysis: Number of counts within segments (Dynamic Models)						
rain+time	8	10449.86	0	0.40	0.01	0.55
rain+time+WIND _{speed}	10	10451.79	1.93	0.15	0.01	0.55
Shoreline analysis: Number of counts within segments (Static Models)						
STREAM _{dist} +depth+SAND _{bottom}	9	5050.61	0.00	0.28	0.05	0.54
STREAM _{dist} +depth+SAND _{bottom} +NEST _{index}	10	5050.84	0.24	0.25	0.06	0.54
STREAM _{dist} +SAND _{bottom}	8	5052.03	1.42	0.14	0.05	0.53
STREAM _{dist} +SAND _{bottom} +NEST _{index}	9	5052.25	1.64	0.12	0.06	0.54
Shoreline analysis: Number of counts within segments (Dynamic Models)						
WIND _{speed}	8	5059.81	0.00	0.25	0.03	0.55
CLOUD _{cover} +WIND _{speed}	9	5060.14	0.33	0.21	0.03	0.53
WIND _{speed} +rain	9	5061.04	1.23	0.13	0.02	0.55
CLOUD _{cover} +WIND _{speed} +rain	10	5061.63	1.82	0.10	0.03	0.54

Table 2.4 Incident rate ratio values of independent variables and their associated 95% Confidence Intervals (CI) from the top static and dynamic models for the full Laskeek Bay and Shoreline models of *Bachyramphus marmoratus* counts between 1997 and 2018 (April-July). CI's that do not overlap 1 are considered significant.

Predictors	Marbled Murrelet Counts	
	Incidence Rate Ratios	95% Confidence Intervals
Full Laskeek Bay Top Static Model		
depth	0.66	0.53–0.82
STREAM _{dist}	0.50	0.39–0.63
SAND _{bottom}	1.16	1.03–1.29
NEST _{index}	1.23	1.07–1.42
Full Laskeek Bay Top Dynamic Model		
Time [Morning]	1.32	1.05–1.65
Rain[Y]	1.74	1.05–2.86
Shoreline Top Static Model		
depth	0.46	0.21–0.99
STREAM _{dist}	0.41	0.25–0.68
SAND _{bottom}	1.12	1.01–1.25
Shoreline Top Dynamic Model		
WIND _{speed[6to10]}	0.49	0.30–0.78

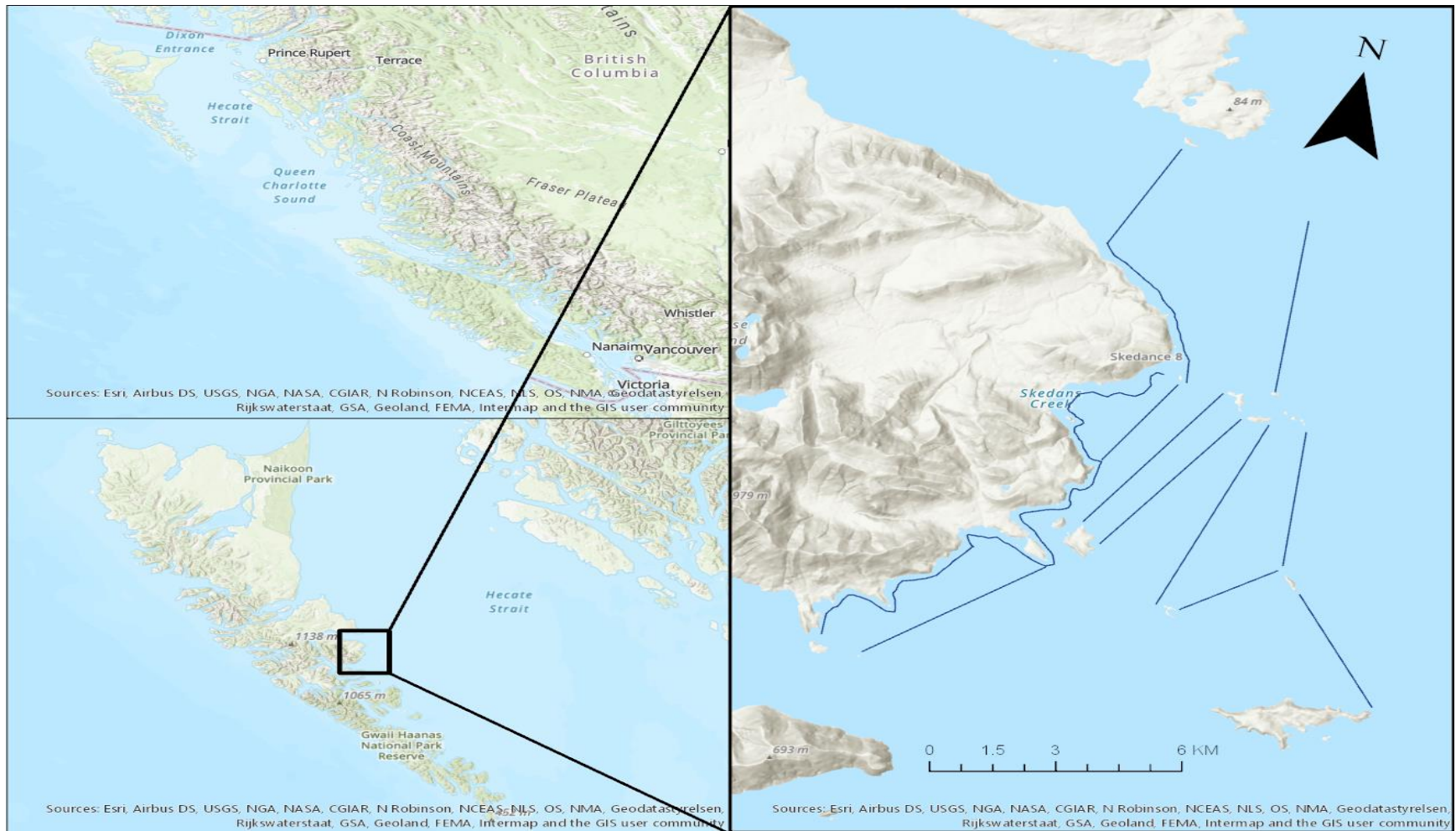


Figure 2.1 Top left illustrates the west coast of Canada, bottom left is a map of Haida Gwaii, and the right image focuses on Laskeek Bay with the shoreline and linear transects used to conduct sea-surveys.

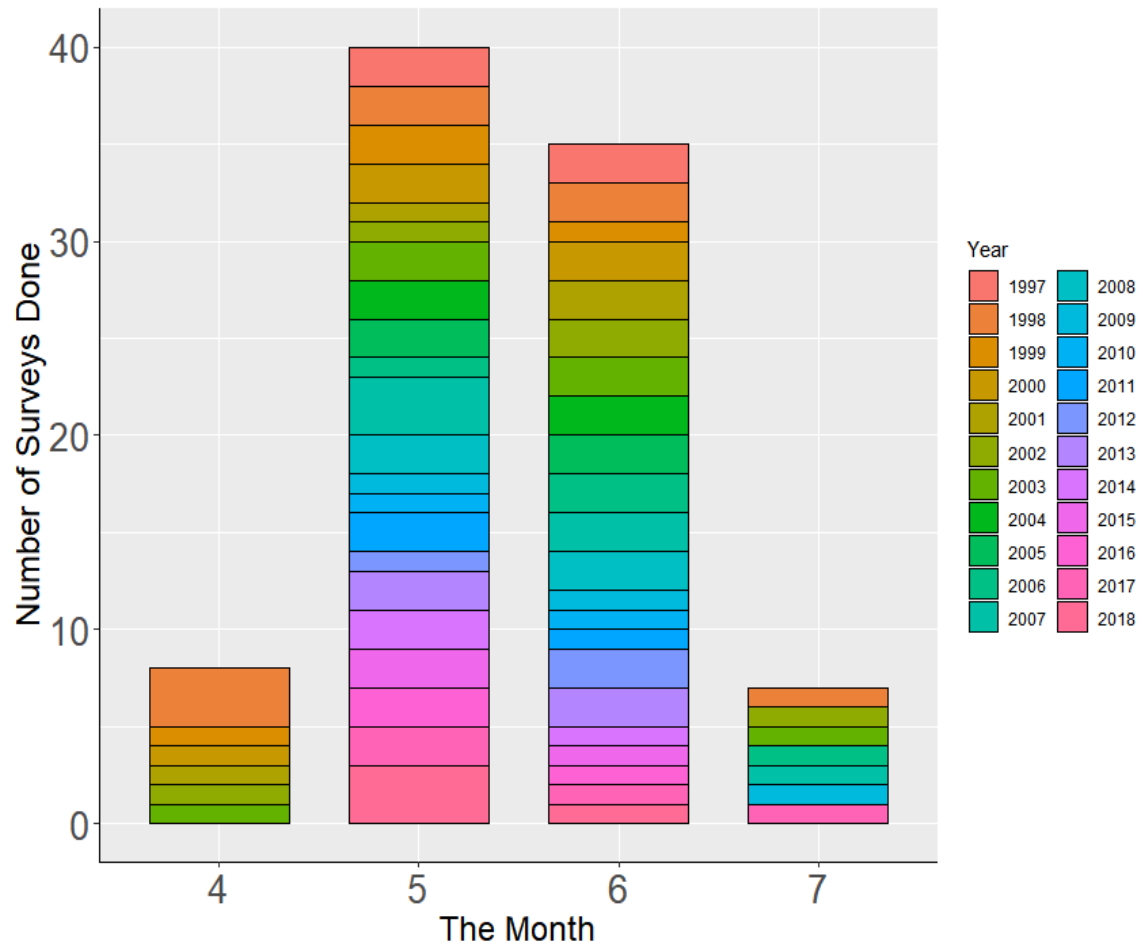


Figure 2.2 The number of seabird transect surveys completed by Laskeek Bay Conservation Society each year from 1997 to 2018 by month.

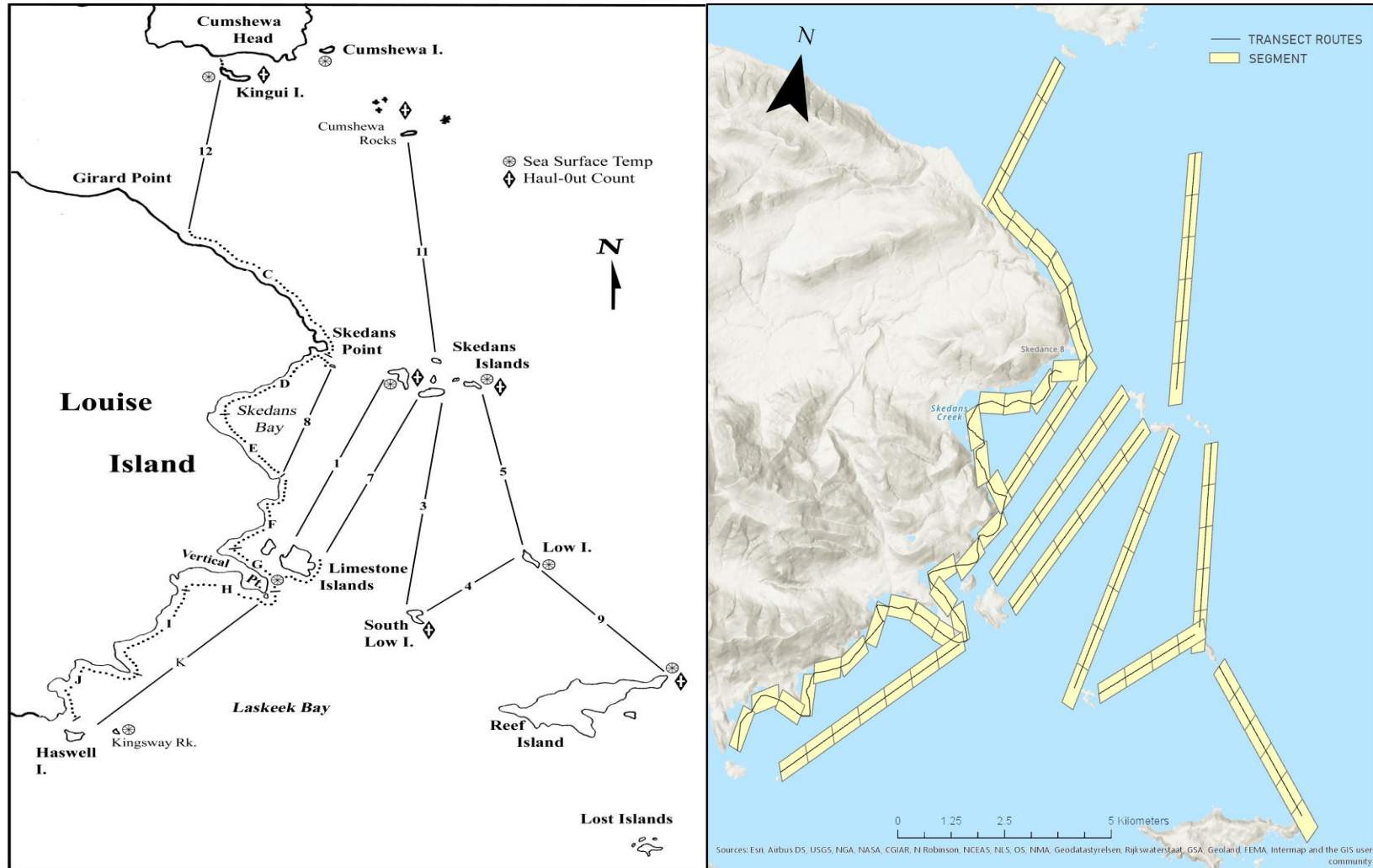


Figure 2.3 Comparison of survey routes set up by Laskeek Bay Conservation Society (left) and how transects were segmented into fine-scale segments (right) for analysis. Segments are depicted at 5 times the survey width of 100m.
 Source: (left) Laskeek Bay Conservation Society

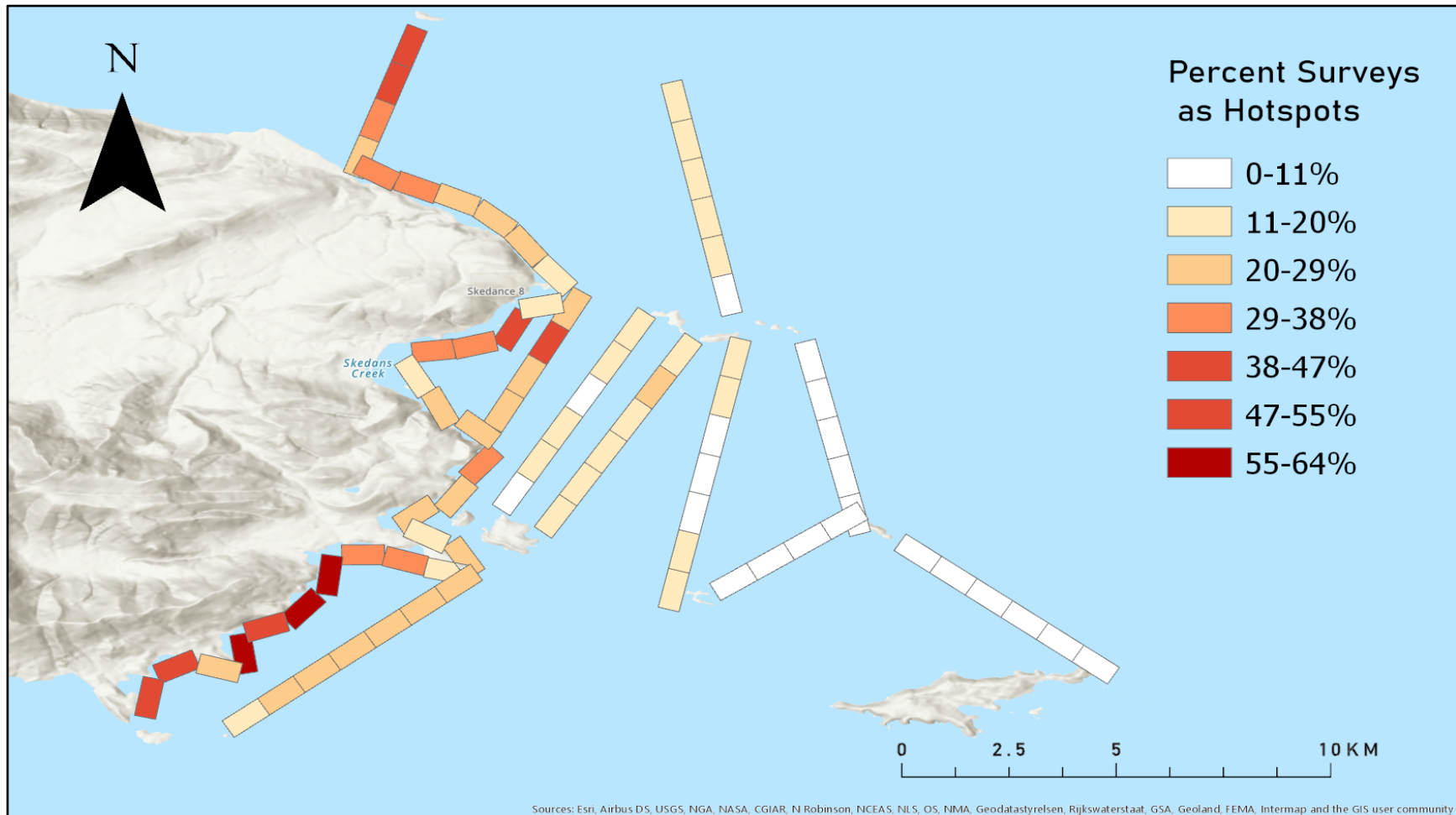


Figure 2.4 Map of Laskeek Bay showing the persistence of *Brachyramphus marmoratus* hotspots along transects broken up into ca. 1 km long segments. Percent surveys as hotspots is the proportion of surveys (n=75) taken in May and June between 1997 and 2018. A given segment was deemed a hotspot when the segment area-adjusted murrelet count was in the top 25% of the segments in each survey count.

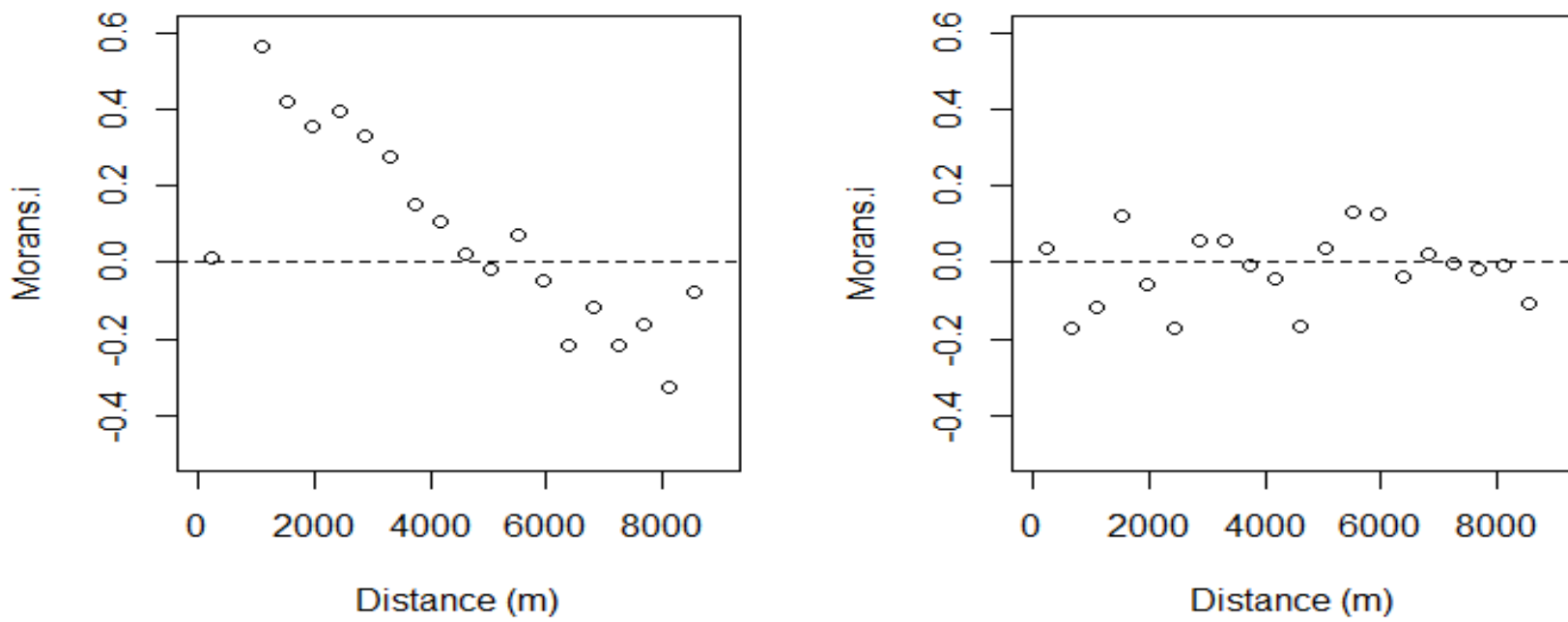


Figure 2.5 Correlograms showing Moran's I values over a range of distance lags (at 440 m intervals) for raw counts (left) and spatial model residuals (right) for *Brachyramphus marmoratus* counts summed across 22 years (1997 – 2018). Higher positive Moran's I values indicate increasing spatial autocorrelation.

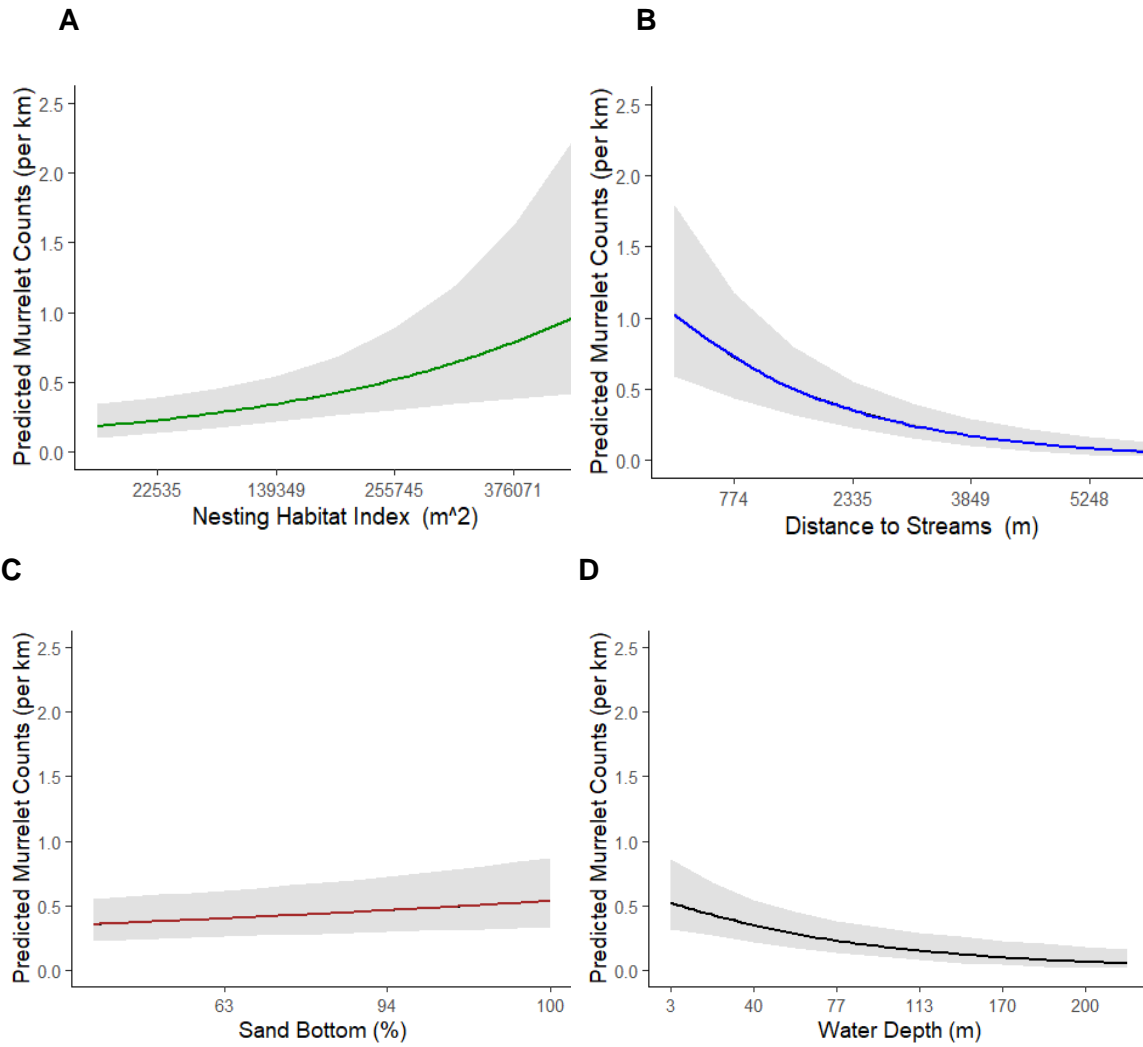


Figure 2.6 The conditional relationship from the top static model in the full bay analysis of (A) the nesting habitat index, (B) distance to streams, (C) percent sand bottom and (D) water depths versus the predicted number of *Brachyramphus marmoratus* counts with the associated 95% confidence intervals.

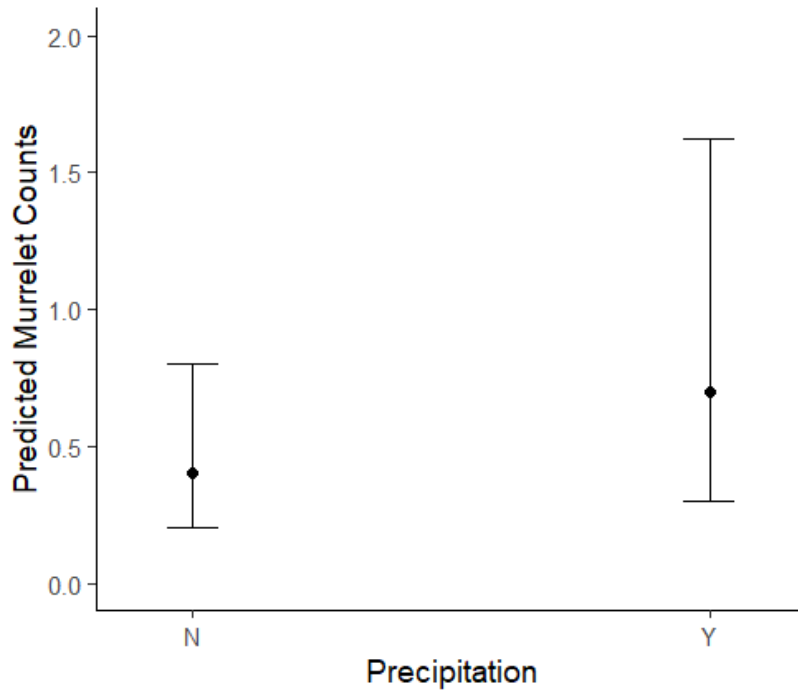
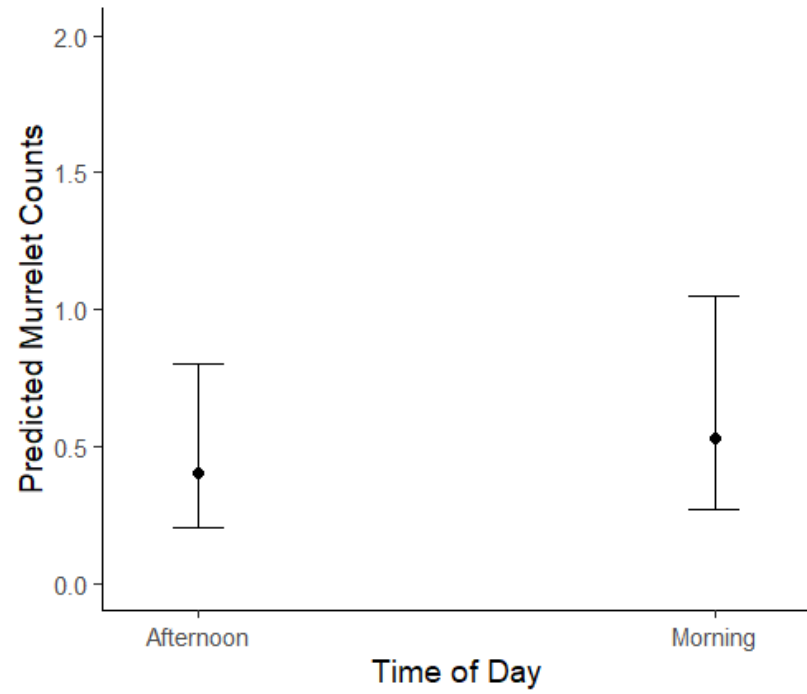
A**B**

Figure 2.7 The conditional relationship in the full bay analysis using variables from the top dynamic model of (A) time of day and (B) precipitation versus the predicted *Brachyramphus marmoratus* counts with their associated 95 % confidence intervals for full analysis.

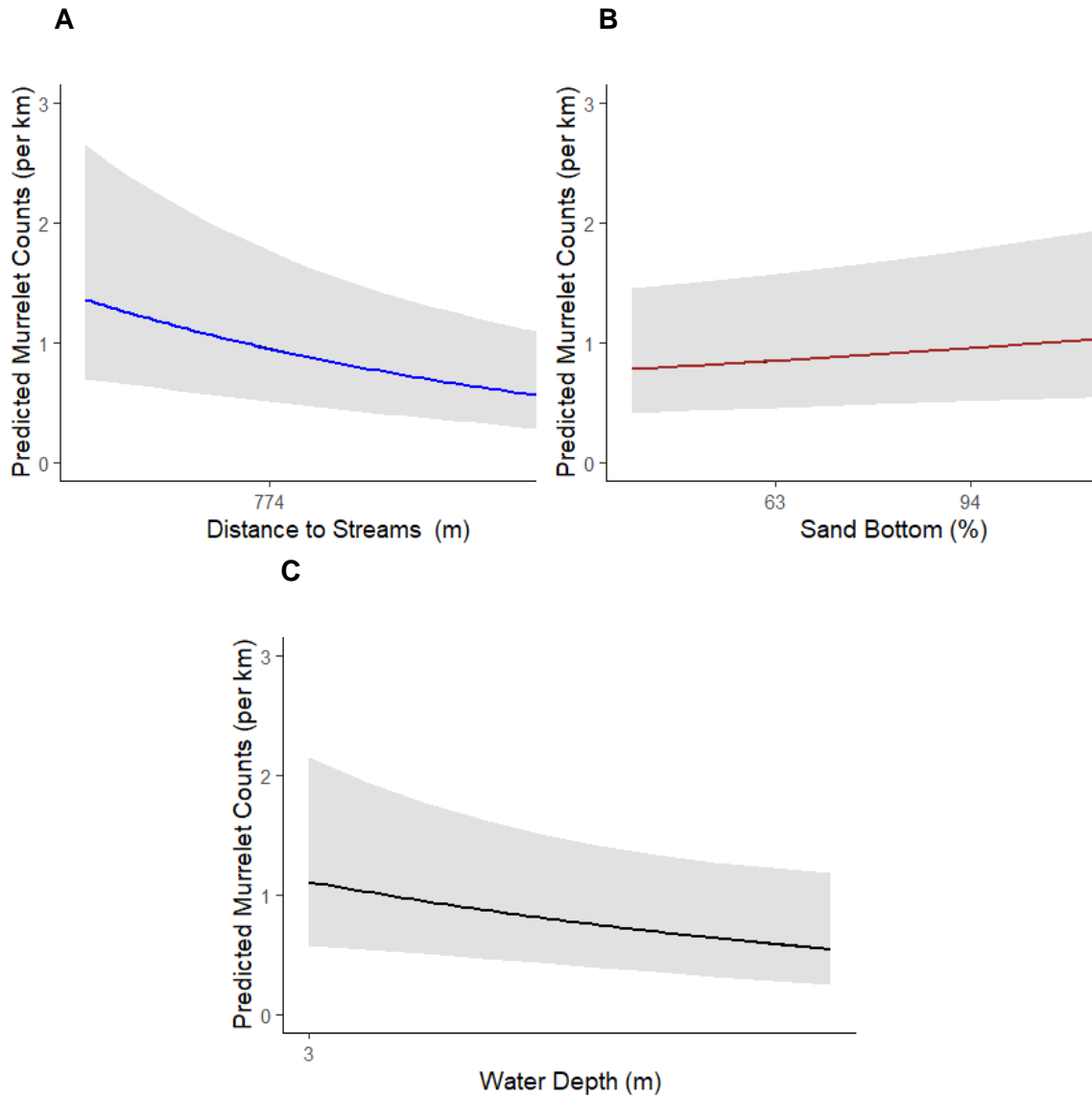


Figure 2.8 The conditional relationship in the shoreline only analysis using variables top static model of (A) distance to streams, (B) percent sand bottom and (C) water depths versus the predicted number of *Brachyramphus marmoratus* counts with the associated 95% confidence intervals.

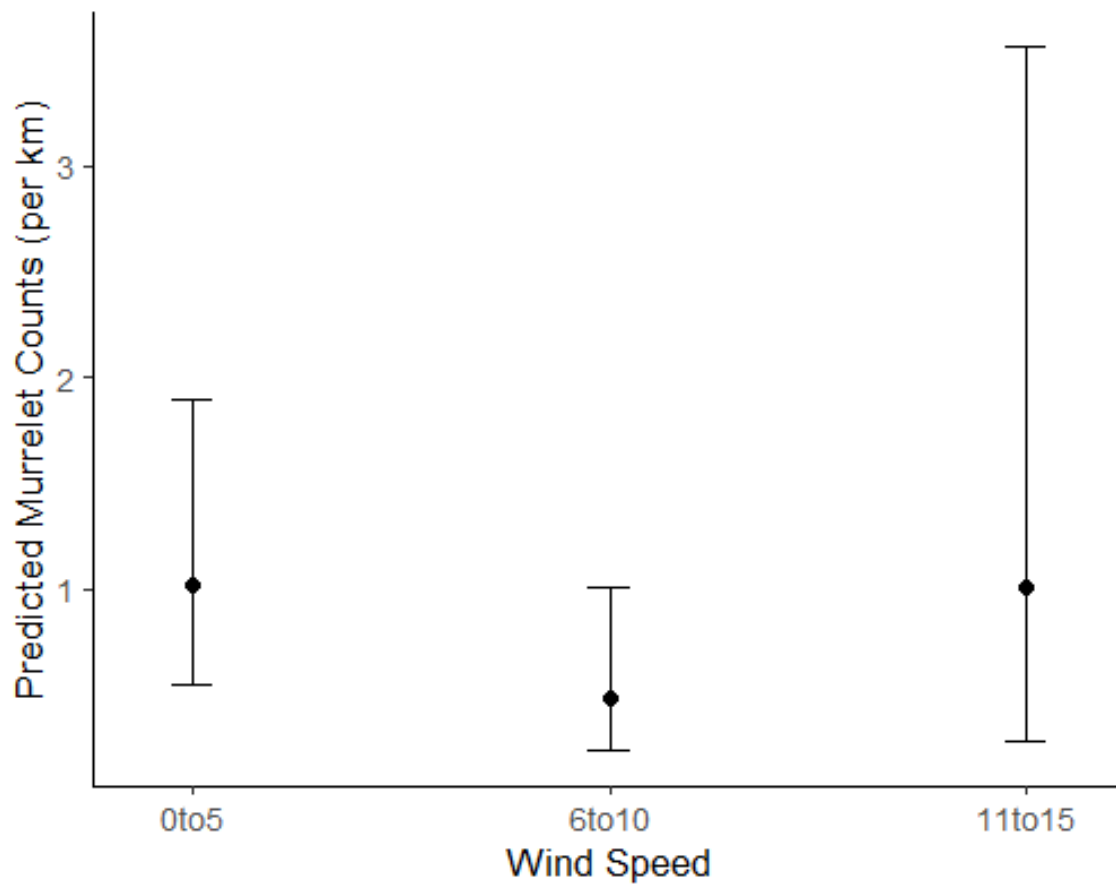


Figure 2.9 The conditional relationship from the shoreline analysis using variables from the top dynamic model between wind speed (knots) and predicted counts of *Brachyramphus marmoratus* and their associated 95% confidence intervals.

Chapter 3.

Prey and Oceanographic Dynamic Influences on Marbled Murrelet Marine Distribution in Laskeek Bay in Haida Gwaii, BC

3.1. Abstract

This study analyzes how Marbled murrelets (*Brachyramphus marmoratus*) used dynamic prey and oceanographic information to select marine habitat in conjunction with static environmental variables. I conducted At-Sea Surveys and collected concurrent bird-prey and oceanographic information in Laskeek Bay, located on the east side of the Haida Gwaii archipelago, British Columbia, Canada. Surveys were conducted during the murrelet breeding seasons (May–July) of 2018 and 2019. I hypothesized the murrelet distributions would have a tighter dependence on indirect oceanographic cues rather than direct visual prey cues, predicting that cooler sea surface temperatures and mixed thermal waters would increase the magnitude of murrelet counts. Secondly, I hypothesized that higher availability of prey would have an additive influence on the strength of association with static variables, predicting that a higher proportion of murrelets would be found closer to stream heads and potential nesting habitat when a higher number of prey schools occurred in the area. The habitat preference analysis showed that static variables (distance to streams, potential nesting habitat, depth and percent sand bottom) are stronger predictors than dynamic variables (thermal mixing, fish schools and sea surface temperature). Nonetheless, models that included both static and oceanic and prey variables outperformed those with static variables only. Stratified water was the dynamic variable most strongly related to variation in murrelet counts. Specifically, stratified water located closer to stream heads was related to higher counts, perhaps because they create productive and energy-efficient foraging areas for murrelets. Testing how associations changed with different levels of fish schools, I found a higher number of fish counts were weakly correlated with a higher number of murrelets closer to stream heads. This analysis demonstrates the interactive relationship between environmentally static variables and dynamic oceanographic and prey information and murrelet habitat preferences.

3.2. Introduction

Understanding how animals utilize surrounding conditions is done by analyzing spatial distribution and resource selection. Information from these types of studies is used to inform conservation management decisions. Predicting how predator populations are distributed with respect to prey populations has long been an underlying goal to help build this understanding (Hunt et al. 1999). For seabirds, marine locations based on recorded prey can be described as scale-dependent and hierarchical (Hunt et al. 1999; Becker and Beissinger 2003). At larger scales of tens to hundreds of kilometers, the distribution of birds at sea contains the suitable foraging prey within the bodies of water they are found in (Kuletz 2005). At smaller scales from about a kilometer to ten kilometers, seabirds forage at physical features where prey tend to be concentrated (Haynes et al. 2011). Finally, at the finest scales of meters to a kilometer, seabird distribution should reflect prey aggregation's actual locations (Becker and Beissinger 2003). How tightly seabird distributions are linked to potential prey can depend on the types of cues they use to locate their food, as well as the depth levels in which the prey reside (Schreiber and Burger 2002; Hunt et al. 1999). Seabirds that are labelled surface feeders often use direct visual cues (Stempniewicz et al. 2013). In contrast, seabirds that forage on prey that reside close to the seafloor will depend more heavily on indirect cues, such as sea surface temperature, tides, and currents to direct their foraging efforts (Guinet et al. 1997; Drew, Piatt, and Hill 2013).

Marbled murrelets (*Brachyramphus marmoratus*, hereafter “murrelets”) are midwater range pursuit diving seabirds that are non-colonial nesting in old-growth forests. The majority of nesters occur within ~30km of shorelines, but birds may travel up to 145 km inland (Lorenz et al. 2017). The harvest of old-growth forests has resulted in murrelets having a “threatened” status in Canada (Environment Canada 2014). However, evidence suggests that changes to marine habitat and prey availability also affect murrelet abundance in a given area, potentially influencing fluctuations in their population (Bertram et al. 2015; Yen, Huettmann, and Cooke 2004). Adjusting commuting distances between marine and terrestrial environments with changing conditions affects the amount of energy they expend. Theoretically, murrelets should be motivated to forage in areas close to their nesting sites to reduce commuting time and

predation risk during flight, potentially affecting the areas in which they forage or nest or both (Hull et al. 2001; Kuletz 2005; Barrett 2008, personal communication).

In the previous chapter, I used British Columbia's longest-running at-sea-surveys, based in Haida Gwaii, to explore how static and weather-related environmental variables influence murrelet distributions. Overall, results supported murrelet preferences for marine areas closer to streams, closer to abundant potential nesting habitat, and above sandy substrate. The positive correlation with streams and potential nesting site availability supports the theory that murrelets are foraging in an energetically efficient way with respect to commuting costs. The use of shallow depths and sandy substrate support preference for foraging in areas more likely to contain a higher concentration of foraging fish, such as the Pacific sand lance (*Ammodytes hexapterus*; PSL) (Ostrand et al. 2005). These findings were limited in that no concurrent bird-prey or oceanographic information was available at the scales necessary to incorporate into the analysis. There is evidence that murrelets in other regions adjust their foraging strategies and distribution choices with changing dynamic variables. For example, in the waters of California, murrelets adjusted their marine distribution based on sea surface temperature (SST), upwelling, and prey availability (Becker and Beissinger 2003). In another California study, radio marked murrelets adjusted their diving times to match the upwelling conditions (Peery et al. 2009). Upwelling is a type of vertical water column mixing that allows nutrients to move and become readily available at the water's surface (Peterson et al. 2007). Mixed thermal water is antonymous to stratified water, where no mixing occurs, and the water column layers contain different properties (Yoshiyama et al. 2009). A direct outcome of nutrient-rich waters is an increase in phytoplankton and, eventually, fish schools (Peterson et al. 2007). In southeastern Alaska's waters, the distribution of murrelets varied with the number of fish schools recorded at coarser scales (Haynes et al. 2011). To date, no such study has looked at these types of relationships for murrelets around Haida Gwaii.

My study aimed to investigate how murrelets are influenced by prey and oceanographic features relative to applicable static physical features in a bay facing the Hecate Strait, Haida Gwaii, BC. Based on the assumption that murrelets are midwater feeders, a tighter dependence on indirect oceanographic cues rather than direct visual prey cues is expected. Therefore, I predicted that cooler SST and mixed thermal waters would correlate with higher murrelet counts. Secondly, I hypothesized murrelets would

forage in such a manner to reduce their energetic travel costs, predicting that a higher proportion of murrelets would be found closer to stream heads and a higher abundance of potential nesting habitat, when prey schools were more numerous.

3.3. Methods

3.3.1. Study Species

Murrelets are opportunistic feeders (Burkett 1995); therefore, shifts in the abundance of different prey species may alter which groups are being consumed. To date, murrelets in Haida Gwaii have been recorded to eat Northern anchovies (*Engraulis mordax*), Capelin (*Mallotus villosus*), Shiner perch (*Cymatogaster aggregata*), Pacific sandfish (*Trichodon trichodon*), Pacific sand lance (PSL) (*Ammodytes hexapterus*), and Smelt (*Osmeridae*) (Vermeer and Morgan 1997). They have been observed in other areas to forage on Pacific herring (*Clupea pallasii*) and juvenile rockfish (*Sebastes spp*), which are also known to live in the waters around Haida Gwaii (Burkett 1995; Vermeer and Morgan 1997). Sealy (1975) recorded murrelets in Haida Gwaii eat a mix of forage fish and different Euphausiid species during the breeding season. He then noted a preference shift in these northern waters where Euphausiids dominated the murrelet diet in the early part of the breeding season (mid-April to mid-May), to an almost fully fish diet as the breeding season proceeded, with PSL being predominantly predated. Murrelet foraging choices may also be heavily influenced by indirect oceanographic variables in these waters. Strong tidal currents and tidal rapids have been found throughout the waters of Haida Gwaii (Vermeer and Morgan 1997). Upwelling mixes vertical water columns, upturning nutrients, attracting more life, and causing fish that are too weak to swim downward to be more accessible as prey (Hunt et al. 1999). Though not as dominant a force in Haida Gwaii as it is in the more southerly waters, upwelling can still be present (Peterson et al. 2007). Cooler temperature zones are also associated with higher productivity and murrelet presence (Chavez et al. 2003; Becker and Beissinger 2003; Ronconi 2008, unpublished). The temperature in Haida Gwaii is largely shaped by wind and bottom contours (Vermeer and Morgan 1997).

3.3.2. Study Area & At-Sea Surveys

I carried out a mix of linear and shoreline transect surveys in Laskeek Bay, facing Hecate Strait on the eastern side of Louise Island (52°56'25.89"N, 131°39'50.10"W), in the southern portion of Haida Gwaii, British Columbia, Canada. This bay has been a historically populated body of water for murrelets (see chapter 2 for details). All surveys were conducted during murrelet breeding seasons (May–July) of 2018 and 2019. I split the total number of transects run into two survey parts run on different dates within the same week. The survey termed “Part One” (Figure 3.1) consisted of 18.7 km length of shoreline and 18.6 km of outer transects, and the survey termed “Part Two” (Figure 3.1) consisted of 5.1 km of shoreline and 26.3 km length of outer transects. For May, June, and July in 2018 and 2019, 10 part one and 8 part two surveys were completed. Surveys started in the mornings between 06:30–07:30 and went until 12:00–13:00. Surveys were run from an 18 ft open aluminum skiff, travelling at a speed of 6 knots, with a minimum of two observers. The primary observer sat in the center of the skiff, and the secondary observer stood behind, driving the vessel. All birds were recorded within 50 m on either side of the boat, producing a 100 m wide transect. Birds that were seen flying and those landing in the transect area while boat surveys were underway were omitted. The surveys were only done on fair weather days (sea-state 0–3), as high waves and chop can limit birds' detectability on the water (Tasker et al. 1984).

3.3.3. Variables Measured

Murrelet counts, fish schools, and static and dynamic environmental variable data were binned into 100 m x 1 km long segments within transects (Chapter 2, Figure 2.3). Segments with no counts recorded for bird and fish school counts were assigned a value of zero. Table 3.1 provides a summary of the variables considered in the following analysis: details for those not covered below are provided in Chapter 2.

Prey Occurrence

The distribution of potential prey occurrence along the transect were recorded using Lowrance Elite Yi 7 sonar “Fish Finder,” simultaneously with sea-surveys. I used a Lowrance HST-DFSBL Transom-Mount Skimmer Transducer attached to the skiff's stern submerged 25 cm below the waterline. This transducer was set to 200 kHz for higher resolution and had a beam angle of 12 degrees. Sonar videos were recorded along

each transect as surveys were conducted, with the file stored for later processing. Processing sonar recordings along transect lines was done using Reefmaster 2.0 software, which allows the viewing of sonar videos and the vessel's location at any given time in the video. Prey occurrence was recorded as the number of fish schools observed at a given location down to a depth of 60 m (Haynes et al. 2009), binned into 1 km segments. I defined a fish school as a free-floating cloud on the screen, or ten or more individuals counted within 100 meters of one another. Since schooling is a visual phenomenon, I set ten individuals as a threshold value for scoring a school (Gautrais, Jost, and Theraulaz 2008). To assess the repeatability of fish school counting using these set parameters, two observers analyzed the same five transect videos of sonar records. I assessed these tabulations' repeatability using the intraclass correlation between observers in R 3.61 (Wolak, Fairbairn, and Paulsen 2012).

The number of fish schools within transect segments was used both as an independent variable predicting murrelet counts and as the dependent variable predicted itself by environmental variables. There are two methodological considerations associated with these usages. First, the transect width of fish recorded underwater by the sonar was smaller than that of the set transect width for bird recordings, giving the possibility of inflated bird counts to fish schools. However, this is a constant bias in all surveys. The second limitation is that the number of occurrences of fish schools does not account for the size of each fish school recorded, thereby does not consider the actual density prey in the water on a given survey.

Dynamic Environmental Variables

A temperature/salinity probe ± 0.1 (YSI pro 30) was used to record sea surface temperature (SST) and salinity (SSS) values. Sea surveys were paused at 1.5 km intervals along each transect, and the probe was submerged at 5-, 10- and 15-meter depths. ArcGIS Pro 2.3.0 was used to interpolate temperature points applying the "spline" tool with the tension setting to create continuous surface layers for temperature values. The temperature reading at 5 meters depth was treated as the SST, as temperature readings closer to the surface represent local heating rather than reflecting vertical mixing conditions (Sakuma et al. 2000). Each transect segment's center point was spatially joined to the corresponding temperature value for a given survey date. To examine the effect of thermal mixing (MIX), the difference between interpolated

temperature values 5 m and 10 m was calculated (Becker and Beissinger 2003). In correspondence with the temperature probe's accuracy, if a difference of 0.1 or higher was determined, then the point was classified as “stratified.” If a value of 0 or 0.1 was recorded, then the segment was classified “mixed.” Due to malfunctions with the salinity sensor, salinity readings were omitted from the analysis.

Static Environmental Variables

The analysis of long-term sea-surveys collected by LBCS presented in chapter two shows that a model using four static variables predicted the habitat distribution of murrelets. These variables were distance to streams ($STREAM_{dist}$), proximity to potential nesting habitat ($NEST_{index}$), ocean depth (depth) and percent sand bottom ($SAND_{bottom}$). Details on how these variables were collected and measured can be found in Section 2.3.5 of chapter two.

3.3.4. Habitat Preference Analysis

The collinearity of variables was checked using a Pearson's correlation before models were constructed. Variables were confirmed to be substantially uncorrelated ($r \leq 0.7$). I then standardized and centred variables of interest by subtracting the mean and dividing by the standard deviation, which allowed the magnitudes of the effect sizes to be directly compared.

A series of generalized linear mixed models (GLMM) with a negative binomial distribution were used to build all candidate models (Table 3.2). This type of distribution was selected to accommodate the overdispersed count response data (Brooks et al. 2017). Models were fit in R 3.61 using the `glmmTMB` function in the TMB package. For each candidate model, the random effect of year, Julian day, and segments nested within transects were included. An effort correction was also added to account for minor differences in route lengths among segments.

I assessed top models using Akaike information criterion (AIC), in which Δ_i values less than 2 were considered equal (Anderson, Burnham, and White 1998). For the selected top models, the Incidence Rate Ratios (IRR) and their associated 95% confidence intervals were calculated to evaluate significance. The IRR signifies a change in the dependent variable in terms of a percent increase or decrease, with the

precise percentage determined by how divergent the IRR value is from 1 (Cummings 2019). If the IRR occurs below the value of 1, then there is a negative correlation of the dependant variable on the independent, and if it is above 1, the correlation is positive.

A spatial “hierarchical” structure was built into the GLMM to help account for spatial autocorrelation. I modeled segments nested within transects (Appendix Figure B1), which assumes that all segments' dependence within their transect is constant. Patterns of spatial autocorrelation were first calculated and plotted on the raw data summed over 2018 and 2019. This plot was made using a correlogram test, which calculates Moran's I values over a range of spatial lags (Fortin, Dale, and Hoef 2002). The correlogram plot for the raw data was then compared to a subsequent correlogram plot of residuals from the model including all spatial variables (Table 3.1) to see how well the model's spatial components account for this type of autocorrelation.

Evaluating the Influence of Fish Abundance

To explore how productivity affected murrelet count relationships to the other environmental variables, I simulated predictive count values for each independent variable at two different fish school count levels. To do this, I used the `ggpredict` function from the `ggeffects` function in R 3.61 (Lüdecke 2018) to run predictive models for each independent variable. For each model, I specified that the model should run the predictive murrelet counts at both the upper and lower quartile of fish school counts. I then visually inspected the figures to look for changes in predicted values between the two fish school levels.

3.3.5. Model Performance

I calculated both marginal and conditional R^2_{GLMM} values to evaluate overall model performance (Nakagawa and Schielzeth 2013). These R^2_{GLMM} values estimate how well the fixed effects and the fixed and random effects together explain the variance that was measured, respectfully. The predicted values were plotted against the response variable with their associated 95% confidence interval for each independent variable of interest (Lüdecke 2018). To calculate each response variable's predicted values, I varied the independent variable of interest while all other factors were held constant at a value of zero.

3.4. Results

3.4.1. Temporal and Spatial Autocorrelation

The correlograms for both raw murrelet counts and the top model's residuals, with only static variables included, are shown in Figure 3.2. In the raw plot, positive spatial autocorrelation was present and linearly decreased until about 5000 m. There is no evidence of spatial autocorrelation for the residuals from the full static model, indicating that the model's hierarchical structure and static spatial components account for the spatial autocorrelation present.

The overall number of murrelets in 2018 (246) was almost four times lower than 2019 (926) (Appendix Figure B3). Similarly, the number of fish schools in 2018 (346) was lower by a factor of 2 compared to the 2019 field season (773) (Appendix Figure B3). I conducted a *post hoc* analysis by systematically building models that included the interaction of year to each fixed effect variable, to test if the relationship of murrelet counts to the variables changed. I found that in 2019 when overall murrelet counts were high, the relationships of variables all intensified, and the linear slope from that year appeared steeper but trended in the same direction.

3.4.2. Murrelet Habitat Preferences – models include fish schools as a predictor of murrelets

Two top models of murrelet habitat use were selected from the candidate list (Table 3.2; Appendix Table B1). The top-ranked model ($\Delta\text{AICc} = 0$, $\text{wt} = 0.36$; Table 3.3) included the variables SST, MIX, FISH_{school}, NEST_{index}, STREAM_{dist}, depth and SAND_{bottom}. Of the dynamic variables included in the top model, only the variable MIX was significant (IRR = 1.70, 95% CI 0.45–2.60). Contrary to my initial predictions, murrelet counts were significantly higher when water was stratified rather than mixed. I plotted the overall predicted distribution of stratified areas for the two field seasons with a kernel density plot (Appendix Figure B2). The majority of stratified recordings were concentrated inshore between vertical point and Haswell Island (Appendix Figure B2). As expected from previous modeling, there was also a significant relationship showing higher murrelet counts with shallower water depths (IRR = 0.51, 95% CI 0.33–0.80;

Figure 3.3) and decreasing distances to stream heads (IRR = 0.37, 95% CI 0.24–0.57; Figure 3.3).

The top model received 1.9 times more support than the second best candidate model. The second-ranked model did not include the variables SST and FISH_{school}. The fixed effect variables (marginal R^2_{GLMM}) for the top model explained about 44% of the variation, and the fixed and random effects (conditional R^2_{GLMM}) explain about 64% of the variation. The second top model explained 43% of the fixed effect variation and about 66% of the fixed and random effect variation. The top model includes all three dynamic variables (Table 3.3) and has 3.9 times more support, explaining about 2% more of the fixed variable variation than the candidate model that includes only the four static variables (Appendix B).

3.4.3. Fish Schools Connections

There was a high repeatability of fish school counts from the recordings. The two observers obtained an ICC score of 0.80 (95% CI = 0.63 – 0.90).

Models predicting fish school counts as a function of all environmental variables produced two top models (Table 3.3). The highest-ranking model included the variables MIX, SST, NEST_{index}, STREAM_{dist}, depth and SAND_{bottom}. For this top model, there was a significant correlation between shallow waters and fish schools (IRR=0.73, 95% CI = 0.62–0.87). In contrast with the murrelet habitat model, a higher number of fish schools were found when waters were mixed rather than stratified (IRR=0.78, 95% CI = 0.64–0.95).

To test whether the number of fish schools influenced the strength of association with stream heads and abundant potential nesting habitat, I simulated counts using the upper and lower quartiles of fish school count's. I did not find substantial visible differences in the strength of association when fish schools were high versus low (Figure 3.4).

3.5. Discussion

Predicting predator distributions in relation to prey is vital for understanding basic behaviour and implementing management strategies. I aimed to investigate how

murrelets are affected by prey and oceanographic features relative to key static physical features in a local bay in Haida Gwaii, BC. Based on energetic foraging theory (Hull et al. 2001) and previous studies (Becker and Beissinger 2003), I predicted that (1) cooler SST and mixed thermal waters would be the primary dynamic factors murrelets used to direct their marine distribution choices and (2) a higher proportion of murrelets would be found close to stream heads and abundance potential nesting habitat when prey schools were more numerous. Using data from two years of sea-surveys (2018 and 2019), I surveyed linear and shoreline transects within a local bay in Haida Gwaii in an attempt to gain evidence for my predictions. My findings indicated that stratified water is the dynamic variable that significantly increased murrelet counts, but all the dynamic variables (FISHschool, SST and MIX) contributed to the model that best explained their distribution. A higher number of fish schools did not change the strength of association to static variables. Overall, the static variables were far better predictors than the dynamic variables, but the oceanic and prey factors increased model performance.

3.5.1. Static and Dynamic Environmental Predictors

It is likely that both the hypotheses that (1) murrelets are foraging in an energetically efficient manner and (2) use indirect cues to select foraging sites, contributed to the results. Two years of data showed that a combination of factors were impacting murrelet's distribution decisions. Within Laskeek Bay, closer proximity to stream heads, shallow depths and stratified waters had the strongest roles and heavily influenced counts. The association with stratified water was unexpected, but further investigation leads to the possibility that stratified water and freshwater run-offs work together to create productive zones. A previous study in Kachemak Bay and Cook Inlet, Alaska, found a strong association between sheltered stratified waters with an inflow of freshwater from rivers and streams and pelagic schooling fish such as PSL and juvenile Herring (Abookire, Piatt, and Robards 2000). The authors believed that areas around river outflows have higher inputs of nutrients, coupled with the fact that stratified waters can create stability and promote primary productivity by keeping nutrients at the surface. Areas that contain both these components are more prone to an abundance of life. It is likely a similar phenomenon is occurring within Laskeek Bay, between Vertical Point and Haswell Island (Appendix, Figure B2). PSL and juvenile Herring are thought to be preferred prey when available in the summer months (Burkett 1995). Within Laskeek

Bay, murrelets have been observed to forage on PSL in the same areas dominated by freshwater run-offs and stratified water (Appendix, Figure A1).

I predicted a looser association with fish schools, under the assumption that murrelets relied on indirect environmental cues, and the model results supported this claim, though there are limitations to this interpretation. The absence of swim bladders in PSL makes it impossible for sonar to pick up readings of these schooling fish (Robards et al. 1999). A PSL was collected from a sediment pull, and anecdotal observations of murrelets holding a PSL in its mouth in Laskeek Bay during the 2019 field season were made. Predation of PSL by murrelets may be an explanatory factor as to why the variables influencing where the fish schools were distributed differed from those of the murrelets. If the sonar was picking up fish that were not of primary interest to murrelets, the association to the fish school variable weakens.

3.5.2. Influence of Fluctuations in Fish Schools

Sonar recordings do not record PSL schools (Robards et al. 1999), likely the primary prey of interest to murrelets, and therefore the remaining fish schools recorded were somewhat weakly associated with murrelets distribution. The information on the general number of fish schools was still informative as it gives a snapshot of how productive the transects and overall waters were at a given time.

2018 and 2019 had large parallel differences in the number of murrelets and the number of fish schools recorded. Though there were not enough years to test the significance of such an association, the waters' overall productivity on a given year may directly affect the overall number of murrelets that choose to reside within the bay. Similarly, Becker and Beissinger (2003) noticed that, based on their sonar data, there were less prey available at their California site in 1998. That same year, murrelets were distributed farther from the two primary breeding area flyways.

There is little evidence supporting my second prediction that when waters had more prey available, the strength of association to the static variables distance to streams and proximity to abundant potential nesting habitat increases. It is possible murrelets forage closer to the stream heads when fish school counts are higher, though this trend did not come out as significant. Contrary to my predictions, a higher magnitude

of murrelets were not found relative to higher $NEST_{index}$ values when fish school counts were high, compared to when fish counts were low. The $NEST_{index}$ measures the proximity and abundance of potential nesting habitat to a binned area on the water; therefore, it seemed likely that foraging in areas close to a high abundance of nesting sites would be energetically beneficial. However, the energetic benefits of staying closer to the higher index sites are small when considering the index values were created from a 5-meter buffer zone (Appendix Figure A2). Identification of murrelet nesting habitat has been notoriously complicated, with large variations in commuting distances (Lorenz et al. 2017). Studies that have found energetic constraints of nesting habitat and marine habitat have used radio-tagged birds that enable direct links between the two (Peery et al. 2009).

3.5.3. Management Implications

Inshore waters that are prone to stratification, and are in close proximity to freshwater inputs, can create ideal marine foraging habitat for Marbled murrelets. These sites are critical to murrelets during breeding seasons and can be identified as high-quality marine habitats in management planning. This study investigates an interactive relationship between environmentally static variables and dynamic oceanographic and prey variables with murrelet habitat preferences and emphasized the importance of static environmental variables. The parallel differences in overall murrelet and fish school numbers between years is an important consideration, especially when studying yearly population fluctuations. Future studies could focus on systematically testing inshore productivity and murrelet abundance. Understanding how murrelets respond to changing marine conditions can help pinpoint explanations for distributional shifts or population declines.

3.6. Tables and Figures

Table 3.1 Static, dynamic, and prey variables used as covariates with respect to *Brachyramphus marmoratus* counts and their associated definition and biological significance.

Variable Type	Name	Definition	Significance
Static (Spatial)	Percent Sand Bottom (SAND _{bottom})	Static categorical variable; Categorized as sediment size (Wentworth scale) from point collected within segments.	Coarse grain sediment is associated with Pacific sand lance habitat (Haynes, Ronconi, and Burger 2007).
	Water Depth (depth)	Static numeric variable; Mean depth per segment (corrected to low tide).	Affinity to shallower waters compared to heavier relatives who have the ability to dive deeper (Burkett 1995; Burger et al. 2008).
	Distance to streams (STREAM _{dist})	Static numeric variable; Measured as the distance from the center of a segment to the closest stream mouth.	Have been observed to use streams/rivers as flyways to bring food to nests (Peery et al. 2009).
	Index of potential nesting habitat (NEST _{index})	Static numeric Variable; Distance and abundance of nesting habitat converted to index values along transect routes with 5 km buffer.	Murrelets foraging closer to nesting habitat may be more energetically beneficial (Becker & Beissinger 2003; Ronconi 2008; Yen, Huettmann, and Cooke 2004).
Dynamic (Oceanographic and prey)	Sea Surface Temperature (SST)	Dynamic numeric; Interpolated from readings taken every 1.5 km along transects at 5 m depth.	Cooler SST has been linked to nutrient enhancement and prey aggregations (Chavez et al. 2003).
	Thermal Mixing (MIX)	Dynamic categorical; difference taken between temperature readings at 5m and 10m. sorted into “mixed” and “stratified.”	A mixed thermal layer can indicate nutrient mixing, which promotes productivity (Behrenfeld et al. 2006).
	Schools of Fish (FISH _{schools})	Dynamic numeric; Number and location of fish schools recorded along transects with Lawrence Elite Yi 7 sonar “Fish Finder.”	Higher occurrence of fish schools have correlated to murrelet distribution in reflecting productivity of waters (Haynes et al. 2011).

Table 3.2 Candidate models used to test the influence of the static and dynamic variables on the marine habitat preference of *Brachyramphus marmoratus*. Each model also included random effects of year, Julian day, and segments nested within transect, as well as the length of segments added as an offset term.

<i>Model Type</i>	<i>Parameters</i>
<i>Combined Models</i>	SST+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
	MIX+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
	FISH+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
	SST+MIX+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
	SST+FISH+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
	MIX+FISH+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
	SST+MIX+FISH+DIST _{stream} +depth+SAND _{bottom} +NEST _{index}
<i>Static Models</i>	DIST _{stream}
	depth
	SAND _{bottom}
	NEST _{index}
	DIST _{stream} +depth
	DIST _{stream} +SAND _{bottom}
	DIST _{stream} +NEST _{index}
	depth+SAND _{bottom}
	depth+NEST _{index}
	SAND _{bottom} +NEST _{index}
	DIST _{stream} +depth+SAND _{bottom}
	depth+SAND _{bottom} +NEST _{index}
	DIST _{stream} +SAND _{bottom} +NEST _{index}
DIST _{stream} +depth+SAND _{bottom} +NEST _{index}	
<i>Dynamic Models</i>	SST
	MIX
	FISH
	SST+MIX
	SST+FISH
	MIX+FISH
	SST+MIX+FISH

Table 3.3

Top Models of marine habitat preferences for Marbled murrelets (*Brachyramphus marmoratus*) and fish schools during murrelet nesting season in Laskeek Bay for 2018 and 2019, using counts from at-sea surveys. The top models ($\Delta\text{AICc} < 2.0$) are reported. Models predict the average number of counts per segment and incorporate the year ($n=2$), Julian day ($n=18$) and segment ($n=80$) nested within transects ($n=18$) as random effects. K is the number of parameters estimated, AICc is the Akaike's Information Criterion, ΔAICc is the differences between the AICc of each model to the lowest AICc score, wt is the likelihood of each model in relation to all other models in the candidate set, marginal R^2_{GLMM} explains variance contributed by fixed factors and conditional R^2_{GLMM} describes the variance explained by both the fixed and random factors.

Parameters	K	AICc	ΔAICc	Wt	Marginal R^2_{GLMM}	Conditional R^2_{GLMM}
Counts of Marbled murrelets per segment						
MIX+SST+FISH _{school} +NEST _{index} +STREAM _{dist} +depth+SAND _{bottom}	13	1794.253	0.000	0.370	0.438	0.642
MIX+NEST _{index} +STREAM _{dist} +depth+SAND _{bottom}	11	1796.144	1.891	0.144	0.427	0.658
Counts of fish school per segment						
MIX+SST+NEST _{index} +STREAM _{dist} +depth+SAND _{bottom}	12	2315.69	0.000	0.370	0.149	0.362
MIX+NEST _{index} +STREAM _{dist} +depth+SAND _{bottom}	11	2315.996	0.306	0.144	0.139	0.351

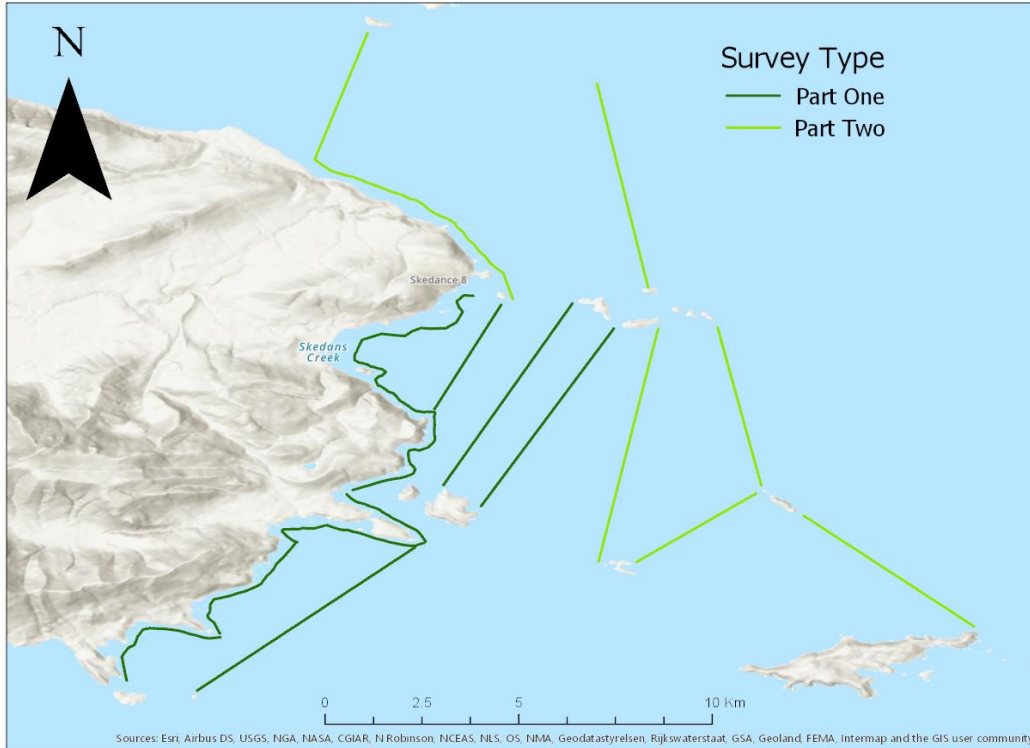


Figure 3.1 Transect routes for sea-surveys in Laskeek Bay. Surveys were split between two days within the same week. Dark green represents part one survey routes, and the light green represents part two survey routes.

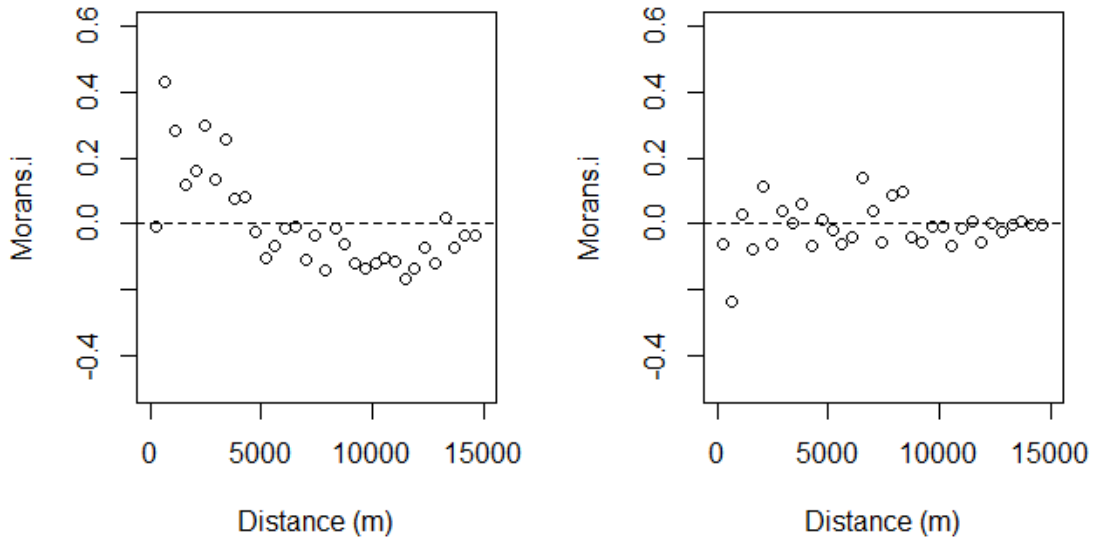


Figure 3.2 Correlograms showing the Morans I values at increasing distance lags (440 m) for raw *Brachyramphus marmoratus* counts (left) and spatial model residuals (right) for counts summed across 2018 and 2019. Increasing positive Morans I values indicate increasing spatial autocorrelation.

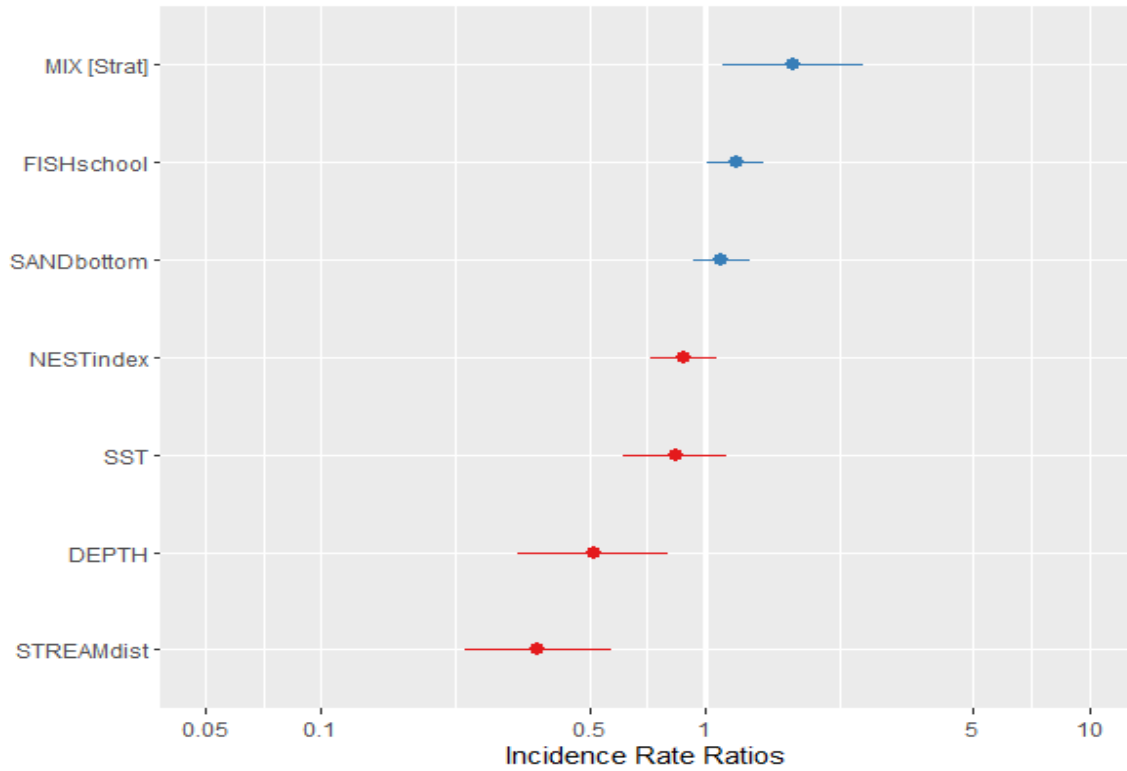


Figure 3.3 Incident rate ratio values of independent variables and their associated 95% confidence intervals, from the top model of *Brachyramphus marmoratus* counts in Laskeek Bay between 2018 and 2019 breeding season (May–July). Confidence intervals that do not overlap 1 are considered significant; red signifies a negative correlation to counts, and blue is a positive correlation.

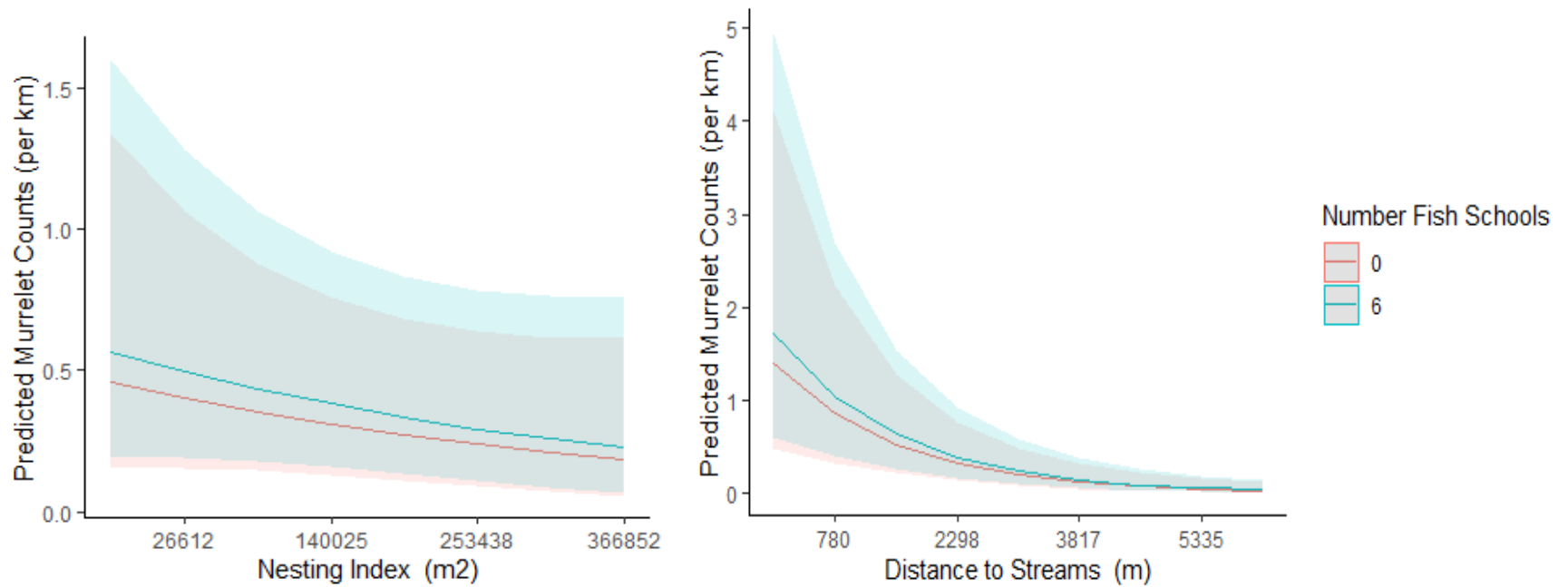


Figure 3.4 Conditional relationships between (A) potential nesting habitat index and (B) distance to stream heads to the predicted probability of *Brachyramphus marmoratus* counts within segments using the top-ranked model from the habitat preference analysis. For both (A) and (B), the blue line represents 6 FISH_{school} counts held constant, and the red line represents 0 FISH_{school} counts held constant within the model. Bands indicate 95% confidence intervals.

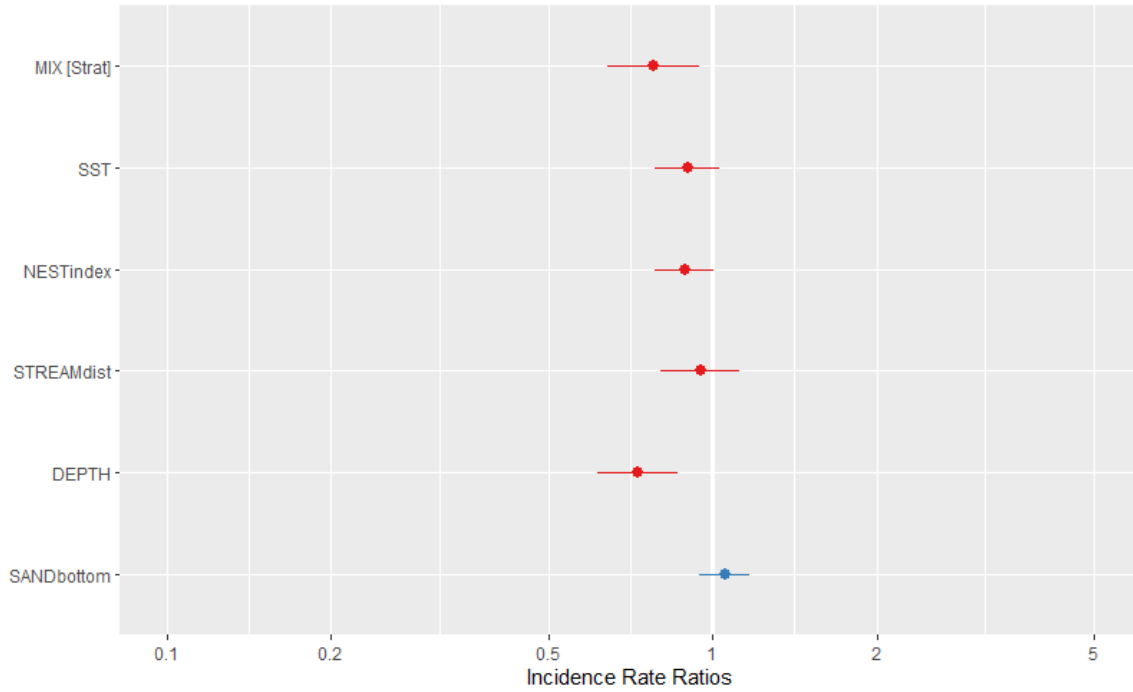


Figure 3.5 Incident rate ratio values of independent variables and their associated 95% confidence intervals, from the top model of $FISH_{school}$ counts in Laskeek Bay between 2018 and 2019 murrelet breeding season (May–July). Confidence intervals that do not overlap 1 are deemed significant; red implies a negative correlation to counts and blue a positive correlation.

Chapter 4.

Avian Predator Avoidance by Marbled Murrelets at Sea: A Field Experiment

4.1. Abstract

The influence of non-lethal effects of predators on seabirds' marine distributions has received little attention, with a bottom-up framework historically shaping such studies. The aim of this study was to measure distributional changes of Marbled murrelets (*Brachyramphus marmoratus*) when avian predators were present. I conducted a field experiment using deterrent decoys (kites) that mimicked flying Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons (*Falco peregrinus*). Paired at-sea surveys along set transects were conducted within the same week, one with kites flying and one without. Observers recorded locations and counts of murrelets on the water, real eagles seen, and fish schools present. I predicted that (1) the total number of murrelets counted along the shoreline waters would be lower when avian kites were flying and/or (2) on the days kites flew, a higher proportion of birds would be counted on the outer rather than shoreline waters and/or, (3) along the shoreline, a lower proportion of murrelets would be counted in sections kites were flying, compared with those present in the same sections on days they were not. I found evidence of fewer murrelets along the shoreline area due to real avian presence, but no effect of kites detected in this metric. However, within shoreline ones, a lower proportion of murrelets were found within 350 radius areas of sites when kites were flown than when they were not. I discuss how incorporating avian predator avoidance can influence the interpretation and future monitoring of murrelets during at-sea surveys and thereby aid management decisions.

4.2. Introduction

Our understanding of predator-prey relationships has historically been measured by consumption rates, otherwise known as lethal effects (Abrams 1993; Cresswell 2011). Harder to understand is how non-lethal effects (such as scaring prey) can affect a prey's immediate behaviour and long term survival (Lima 1998). False assumptions can be made that if the lethal effects of a given predator on prey are low, then the non-lethal

effects should also be minimal. However, the opposite is likely the case; if predator avoidance is an active prey strategy, one should expect a low mortality rate that can be directly attributed to their behaviour (Sih 1986). Measuring the life history costs of non-lethal effects is difficult, but the costs to a species life history should not be underestimated. When prey species make the decision to increase their immediate survival, they are often diverting their energy away from their own growth, reproduction, and base fitness (Lima 1998; Harris 1980).

The impact predators have had on seabird life history is undeniable. This group of birds has evolved to spend the majority of their lives out on water, coming to land for breeding purposes only, often breeding on isolated cliffs and islands. This strategy has largely been credited to the evolutionary pressures of predator avoidance (Schreiber and Burger 2002). Though seabirds are generally less vulnerable on the water, they still face a number of prospective predators that they must navigate around (Riedman and Estes 1988; DeGange and Nelson 1982; Mallory et al. 2004; Paine, Wootton, and Boersma 1990). Despite this, the vast majority of studies investigating the distribution of seabirds at-sea approach their studies from only a bottom-up framework, though researchers are becoming aware of this bias (Hipfner et al. 2012).

Marbled murrelets (hereafter “murrelets”) are small non-colonial seabirds that forage on inshore marine waters along the North American Pacific coast (Environment Canada 2014). Due to their dependence on old-growth forests for nesting, predation studies have had a terrestrial focus, particularly with nest predation (Nelson and Hamer 1995a; Mark and Naslund 1994; Malt and Lank 2007). What is less known are the non-lethal effects predators have on the adult murrelet population. Avian predators, such as the Bald eagle (*Haliaeetus leucocephalus*, hereafter “eagles”), are occasionally thought to predate adults from the water. Evidence of predation has been found when radio collars from adult tagged murrelets were found in the nests of eagles (SFU murrelet project, unpublished). These birds are an abundant predator in the northern Pacific Ocean (Hodges 2011) and have been linked to local foraging distribution changes in various waterbird species (Middleton, Butler, and Davidson 2018). Peregrine falcons (*Falco peregrinus*) are another important avian raptor known to predate on murrelets and have also been shown to have non-lethal effects on a variety of seabirds (Paine, Wootton, and Boersma 1990). Though not as widespread as eagles, the presence of these birds can be significant. Ydenberg et al. (2004) showed that an increase in

Peregrine numbers led to a change in stopover choices made by Western sandpipers, consequently affecting sandpiper census counts. No studies have looked at the non-lethal effects of the presence of raptors on murrelets, though their influence can be hypothesized. In southern British Columbia, murrelets have been observed to forage offshore in the evenings, early in the breeding season, at specific sites (Tranquilla et al. 2005), raising the possibility an increase in evening predation risk could be causing the distributional change.

My aim in this study was to determine if the visual presence of avian raptors causes local distributional changes of murrelets along the shoreline of a bay in Haida Gwaii, British Columbia, Canada. With the use of avian kites situated along a coastline, I predicted (1) the total number of murrelets counted in the shoreline waters would be lower when avian kites were flying and/or (2) on the days kites flew, a higher proportion of birds would be counted on outer rather than shoreline waters when compared to days kites did not fly, and/or, (3) along the shoreline, a lower proportion of murrelets would be counted in sections where kites were flying, compared with those present in the same sections on the days they were not. I also counted numbers of real eagles present and tested for their effects in thesis data.

4.3. Methods

4.3.1. Field Site

This study was conducted during May, June and July of 2018 and 2019 along the inshore waters of Louise Island (52°53'12.7"N 131°39'21.5"W), situated in Haida Gwaii, BC, Canada. The experiment covered about 10.5 km of shoreline between Haswell Island and Vertical Point (Figure 4.1). This shoreline has long stretches of rocky cliffs made of limestone and basalt, interwoven with scattered beaches. The nearshore waters adjacent to the island ranged in depth from 2–52 meters and contained a mix of fine and coarse grain sand, and rocky sediment along the water bottom (Appendix Figures A1 and A4). This area had been observed during the summer months since 1997 to be consistently populated by foraging murrelets (Chapter 2).

4.3.2. Field Experiment Set-Up and Surveys

Three treatments were tested along the study area's shoreline (Table 4.1). The first treatment, KITE_{down} was an at-sea survey conducted with no disturbances to the experimental area. The second, KITE_{up}, included two factors that had the potential to impact murrelet behaviour, as it included both the visual presence of the kites as well as prior disturbance along the shoreline caused by the vessel when setting up kites. To test for a prior disturbance effect only, a third treatment, BOAT, re-created the boat disturbance that took place when kites were raised, without actually raising any kites.

At the start of each field season, kite stands were built consisting of extendable 5-meter fiberglass poles (Appendix, Figure C1). The poles were distributed at cliff shoreline sites along Louise Island (Figure 4.1), where they remained for the duration of the season. To mimic predator presence, I flew both commercially available eagle and Peregrine falcon kites used to deter birds from airports or other locations (Margo Supplies LTD; Appendix, Figure C2). Ten kite stands were set along the shoreline, with five along the north side of the shoreline and five along the south side (Figure 4.1). The kite types initially alternated between eagles and falcons, but due to the eagle kites being resilient to tearing and damage, by the third survey of the first year of the experiment, all falcons were replaced with eagle kites. I lack statistical power to test for potential effect differences between the eagle and falcon kites, and they are treated as equivalent throughout this study.

For KITE_{up} treatments, setup began 06:30–07:00 in the mornings. Starting from the North end of the shoreline, we systematically approached each stand from the boat, with one individual jumping onto the shoreline, then attaching and raising the kite. After all kites were setup, we took a 30–45-minute break before beginning the survey. The actual surveys took place between 10:30 and 14:00 hrs. In 2018, the KITE_{up} treatment involved all 10 kites flying on a survey day. In 2019, experimental surveys involved the BOAT treatment on half the area and the KITE_{up} treatment on the other half. For these surveys, kites were raised from only one half of the shoreline (5 North or 5 South locations, Figure 4.1). Along the other half of the shoreline, which contained the other 5 kites, stands sites were approached by the boat to simulate this disturbance without actually raising kites. I alternated which side of the shoreline would get the KITE_{up} or BOAT treatment between surveys. In both years, the experimental surveys were paired

with a KITE_{down} treatment survey done on a separate day within the same week. All three survey treatments were run within the same general daily time frame.

At-sea survey methods were consistent between treatments and were done as shoreline transects along Louise Island, as well as one outer linear transect parallel to the island (Figure 4.1), which was situated about 1.1 km away from the shoreline. Two observers were used for the surveys, the primary observer, positioned in the center of the vessel, and the secondary observer, who was also driving. Boat speed was set to a constant 6 knots, with murrelet counts and georeferenced locations recorded up to 50 meters from either side of the boat. Birds flying or landing in the transect while surveys were being conducted were not included in the counts. In addition to recording murrelets, real eagle sightings and fish schools were also recorded. Any eagle perched along the shoreline and visible from the boat or flying directly overhead were recorded for real eagle sightings. Fish schools were recorded using a Lowrance Elite Yi 7 sonar “Fish Finder” as surveys were conducted. A Lowrance HST-DFSBL Transom-Mount Skimmer Transducer was attached to the stern of the skiff and was submerged 25 cm below the waterline. This transducer was set to 200 kHz for higher resolution and had a beam angle of 12 degrees. Sonar videos were recorded and processed after surveys were finished. Using the software Reefmaster 2.0, I defined a fish school as a free-floating cloud seen on the screen or 10 or more individuals counted within 100 meters of one another (details are given in chapter 3 on fish school counting protocols).

4.3.3. Data Analysis

The data specified a shoreline transect or an outer transect split into north and south sides (Figure 4.1). This structure was used for the subsequent analyses.

I first explored if fewer murrelets were counted along the shoreline when kites were flying compared to when they were not. To do this, I calculated the difference between variable values from each paired treatment trials (KITE_{up} and KITE_{down}) that were run within the same week (Table 4.2). I used the paired trials to build a linear mixed model using the lme4 package in R 3.61 (Bates et al. 2014). For this model, the dependent variable was differences in counts of murrelets, while predictor variables were differences in fish schools and real eagles between treatment trials. Shoreside (North or South) was set as a random variable. The differences between KITE_{up} and

KITE_{down} trials were calculated by subtracting KITE_{up} counts from KITE_{down}; thus, positive values indicate a stronger kite effect, meaning a lower number of murrelets, fish schools or real eagle counts between the paired surveys during the KITE_{up} treatment. 95% confidence intervals were computed to test for significance. The effect of boat disturbance on the overall counts along the shoreline was analyzed by repeating the above procedure, between the BOAT and KITE_{down} treatment. Subtracting BOAT treatment from KITE_{down} produces positive values if fewer birds were present during surveys with boat disturbance.

I then examined whether a higher proportion of murrelets were counted along the outer marine transects on the day's kites flew compared to when they did not. To control for variation in counts between days that could distort differences in local distributions, I re-scaled murrelets and fish school counts to proportions on outer transects, pooled over North or South shoreside on a given day. Using the paired treatment design detailed above, the differences in proportions were calculated by subtracting values of KITE_{down} from KITE_{up} treatments, or KITE_{down} from BOAT treatments. For the real eagle variable, raw count sums from each trial were used to calculate the difference between paired treatments and shoreside was used as a random variable. Positive values indicate a greater number of murrelets or fish schools along the outer transect during days kites flew. For the real eagle variable, positive values indicate fewer eagles when kites were flying compared to days they were not. 95% confidence intervals were computed to test for significance. Similar to the previous analysis of counts, a linear mixed model, using the lme4 package, was implemented to look for effects on differences of proportions in KITE_{up} versus KITE_{down} treatments and BOAT versus KITE_{down} treatments.

Finally, to explore if more murrelets would be found in areas farther away from the kites within the shoreline area on days kites flew compared to when they did not, 350-meter radius buffer zones were drawn around each kite location (Figure 4.2). As with the onshore-offshore analysis, counts were re-scaled as proportional counts at locations within a given day. The re-scaled counts that fell within a given buffer zone were summed. The proportion of re-scaled counts within the buffers of a given shoreside relative to the overall re-scaled onshore counts for that trial was calculated, tagged with its appropriate treatment. Thus, proportions closer to one indicated a higher proportion of murrelets within the buffer zones during a given treatment. These calculations were done for murrelets, fish schools and real eagle sightings. The differences between

KITE_{up} and KITE_{down} trials were calculated by subtracting KITE_{up} from KITE_{down} proportions. Positive differences thus indicate fewer murrelets resided within the buffer zones on days with kite disturbance than when kites were not flying, with the same procedure done for fish school and real eagle re-scaled counts. These calculated differences of paired trials were analyzed when building the linear mixed model, with shoreside (North or South) set as a random variable, using the lme4 package. The 95% confidence interval was computed to test the significance of the fixed effects. The effect of boat disturbance within buffer zones was assessed by repeating the above methods and re-running the model, between BOAT and KITE_{down} treatments. Subtracting BOAT treatment from KITE_{down} would yield positive values if fewer birds were present within the buffer zones with boat disturbance.

To examine potential differences between yearly counts of murrelets, fish schools, and real eagles were first summed and manually inspected. There was not enough power in the model to add a yearly interaction term. However, I did plot the yearly difference values of the overall counts along the shoreline, differences in the proportion of murrelets on the outer transect, as well as the proportion of murrelets outside the buffer zones, when kites flew and when they did not. These plots were made to visually check for any major differences.

4.4. Results

A total of 161 murrelets were counted in 2018, and 1415 birds in 2019. When correcting for survey effort, I calculated there were about five times the number of murrelets in the second year compared with the first.

I found no evidence that the presence of the boat prior to surveys had any effect on murrelet distributions. The variance of the murrelet count differences between KITE_{down} and BOAT was large (-10.54 ± 21.16) and was found to be statistically insignificant (95% CI = $-60.12 - 38.95$). There was also no evidence that murrelets re-distribute outside the buffer zones (0.13 ± 0.37 ; 95% CI = $-0.55 - 0.27$) or to the outer transect when there was boat disturbance (-0.04 ± 0.02 ; 95% CI = $-0.01 - 0.09$).

The analysis of the effects of kites on total counts along the shoreline produced mixed results. Over both years, there were fewer murrelets when kites flew than when

they did not (3.04 ± 4.47). An overall higher difference was detected in 2018, but not in 2019 (Figure 4.4). The pooled difference was not statistically significant (95% CI = $-5.31 - 11.48$), with one large negative value (more murrelets with kites present) in 2019 strongly influencing the results (Figure 4.3, 4.4). Counts along the shoreline were significantly negatively correlated with real eagle counts (-4.80 ± 1.54 ; 95% CI = $-7.67 - 1.93$; Figure 4.5) in both years (Figure 4.6). I found a statistically insignificant correlation between counts and the number of fish schools (95% CI = $-0.03 - 2.76$). There was no significant effect of the kites' presence on real eagle sightings (95% CI = $-0.10 - 3.02$).

With respect to potential movements offshore, no evidence was found that higher proportions of murrelets were found on the outer transect when kites flew (0.00 ± 0.01 , 95% CI = $-0.01 - 0.02$; Figure 4.7). There was also no indication that real eagles or fish schools were associated with any significant differences in the murrelet proportions on the outer transect (95% CI = $-0.00 - 0.00$; 95% CI = $-0.06 - 0.08$). When murrelet proportion differences on the outer transects were examined by year, there was more variability in 2019, but both years had differences that remained close to zero (Appendix, Figure C4).

Within the inshore transects, a lower proportion of murrelets was found in the buffer zones when kites were flying than when they were not (0.21 ± 0.12), and this trend was significant (95% CI = $0.02 - 0.40$; Figure 4.8). The difference in the proportion of fish schools and the proportion of real eagles in the buffers did not significantly affect murrelets' local redistribution away from the kites (95% CI = $-1.70 - 0.43$, 95% CI = $-0.54 - 0.27$; respectively). When plotting these differences by year, I found a relatively similar range and trend with the majority of paired surveys in both years, indicating a lower number of murrelets within the kite buffer zones when kites flew (Appendix, Figure C5).

4.5. Discussion

Our understanding of seabird marine distribution has primarily been tested and explored using a bottom-up framework, with consideration of how top-down variables influence these groups of birds on marine waters developing only recently (Hipfner et al. 2012). This study used at-sea surveys of a small seabird, the Marbled murrelet, to experimentally test if the presence of avian predators would influence murrelets' overall presence and/or local distribution on the water. I predicted (1) the total number of

murrelets counted along the shoreline waters would be lower when avian kites were flying and/or (2) on the days kites flew, a higher proportion of birds would be counted on the outer waters compared to days kites did fly. Finally, I predicted (3) that a lower proportion of murrelets would be counted along the shoreline around sites when kites were present compared to days when kites were absent. A potential confounding artifact from boat disturbance when raising kites prior to conducting the surveys was not found to have a detectable effect on murrelet distribution and will not be considered in the subsequent discussion.

My findings support the hypothesis that murrelets do redistribute in the presence of potential predators. In both years of the experiment, the presence of real eagles was negatively related to inshore murrelet counts, and murrelets appear to have avoided inshore areas immediately adjacent to kite stands when kites flew. In 2018, but not 2019, the presence of kites also lowered the total number of murrelets censused along the shoreline. Both methodological and biological factors may account for the apparent annual difference. Methodologically, in 2018, the kite stimulus along the entire shoreline was stronger, with all 10 being flown along the 10.5 km of shoreline on a given day, whereas in 2019 only 5 kites were flying, along half the shoreline, on a given day. Although we analyzed the responses treating north or south shoreside independently, there may in fact be an interaction between treatments. Biologically, having ca. 5 times more murrelets present in 2019 could have provided the birds with a heightened sense of security, reducing offshore movements. In many species, the risk of predation decreases as group sizes increases, and it has been observed in a number of studies that vigilance and skittish behaviour decreases in larger groups (Elgar 1989; Lima and Dill 1990).

Kites caused a lower number of murrelets to be counted in zones along the shoreline within kite buffer zones, but the same did not hold when real eagles were used to measure these distributional differences. The absence of a correlation of real eagles to murrelet counts may be due to noise with respect to how real eagles were recorded. Real eagles' exact locations were challenging to mark, as they were recorded either from tree sightings along the shoreline or flying overhead. All waypoint recordings were marked from the boat, which did not capture their exact location. Additionally, for sightings of those flying overhead, the nature of their location was dynamic and impossible to capture completely. In contrast, knowing the precise location of kites and

the ability to mark birds seen on the water at their precise location enabled me to measure the correlation of avian predator presence to local murrelet distribution with greater certainty. This provides direct evidence that murrelets do react to avian predators in their marine habitat. This study provides a unique way to experimentally test the effects of predation on seabirds' marine distribution. Other studies have observed that the indirect threat of avian predators can cause seabirds to redistribute at a fine-scale or change their immediate behaviour in the presence of predators (Addison, Ydenberg, and Smith 2007), but this approach directly tests these correlations.

The negative correlation between real eagle and murrelet counts close to the shoreline, found in both years, is compelling evidence that avian predators can cause murrelets to leave productive foraging areas to mitigate predation risk. Of the three potential responses to the experiment measured, redistribution within inshore areas was most strongly supported. This suggests that the birds were trying to manage risk and reward by remaining in more productive areas rather than opting for even safer but potentially less productive sites. Though there is no previous work that has directly correlated eagle to murrelet counts, Whitworth et al. (2000) did observe a difference in murrelets offshore between sites in southeast Alaska, with no conclusive explanation for their observation. It is possible that the two sites had differences in predators, which caused the two groups to behave differently. I tried to capture an offshore shift in murrelets by looking at changes between the shoreline and the outer transect but did not find any, nor when looking at correlations to real eagles. The narrow transect strip (100 m), placed over 1 km from the shoreline, may not have been sufficient to capture an offshore movement. For instance, Middleton, Butler, and Davidson (2018) used three parallel transects at increasing distances offshore when measuring the distributional shift in diving birds caused by Bald eagles. It is also possible that murrelets relocated to other parts of the shoreline not included in the surveys.

Conclusion and Implications

Overall, this paper provides evidence that murrelets react to avian predators by either leaving entire shoreline areas or moving away at a finer scale to safer zones. These results have implications on how at-sea surveys can be more effectively conducted, as well as current and future management implications for Marbled murrelets. Eagles have been making a strong recovery in numbers over the last few

decades, and therefore understanding the consequence of their presence to seabirds is a necessity (Hipfner et al. 2012). Taking eagle presence into account when conducting shoreline at-sea surveys is an effective and easy way to reduce unexplained variation in counts. At-sea surveys have been a key tool in supporting management decisions in the United States for Marbled murrelets and have been used by the Northwest Forest Plan team to look at population trends since 2007 (McIver et al. 2019). The team has broken up the waters along Washington, Oregon, and California into 5 zones. Though the team does count murrelets at various distances from the shoreline, the birds could be choosing to move into different zones if the threat of avian predation in a given year or time is too large, which would translate to variations in the populations between years. I suggest that looking at past avian predator population counts within each zone maybe useful, to see if there are any negative correlations. I also recommend that future surveys take avian predators into account when conducting surveys along the shoreline. Future research should also repeat this experiment in other regions and for other seabird species, to see if results hold true under different parameters.

4.6. Figures and Tables

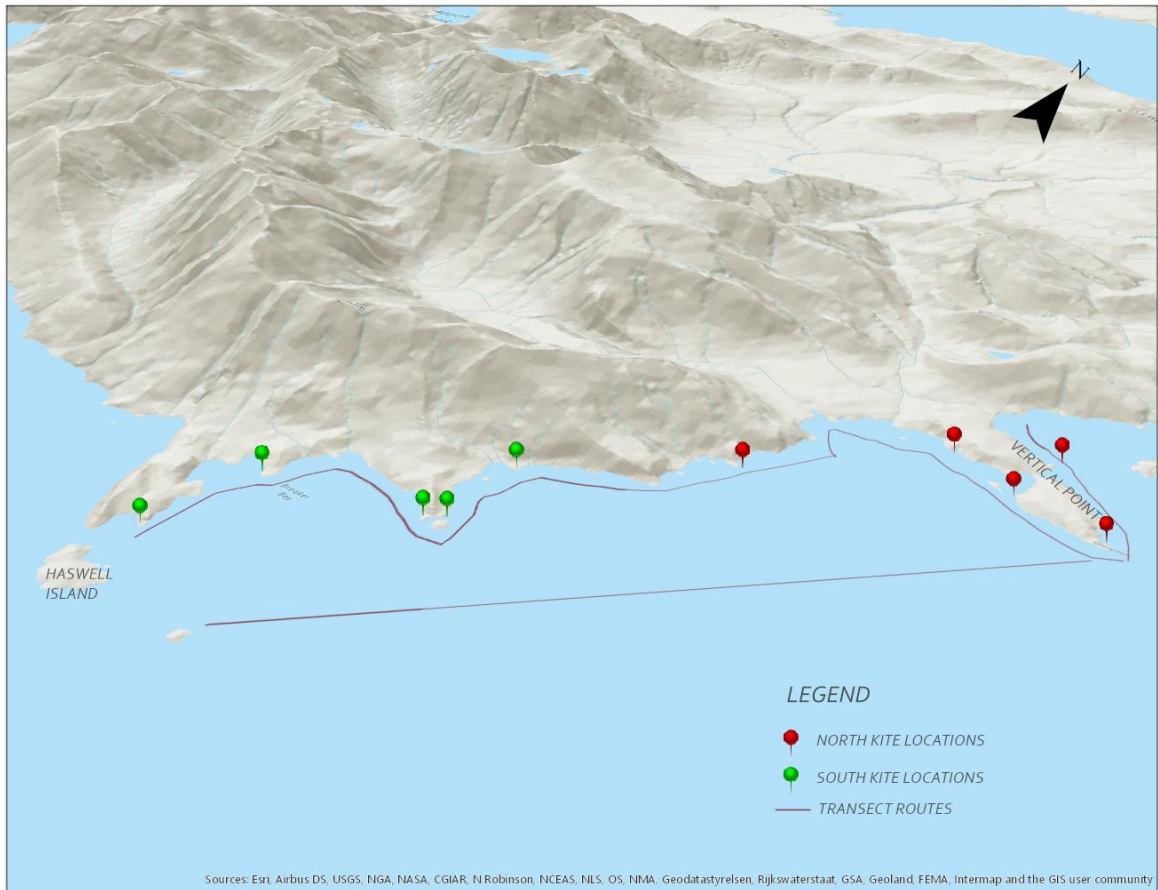


Figure 4.1 Study area in Haida Gwaii, British Columbia, Canada. Avian kite locations marked. 5 kites were positioned on the south side of the shoreline, and 5 kites were distributed along the north side. Shoreline transects tally to 10.5 km.

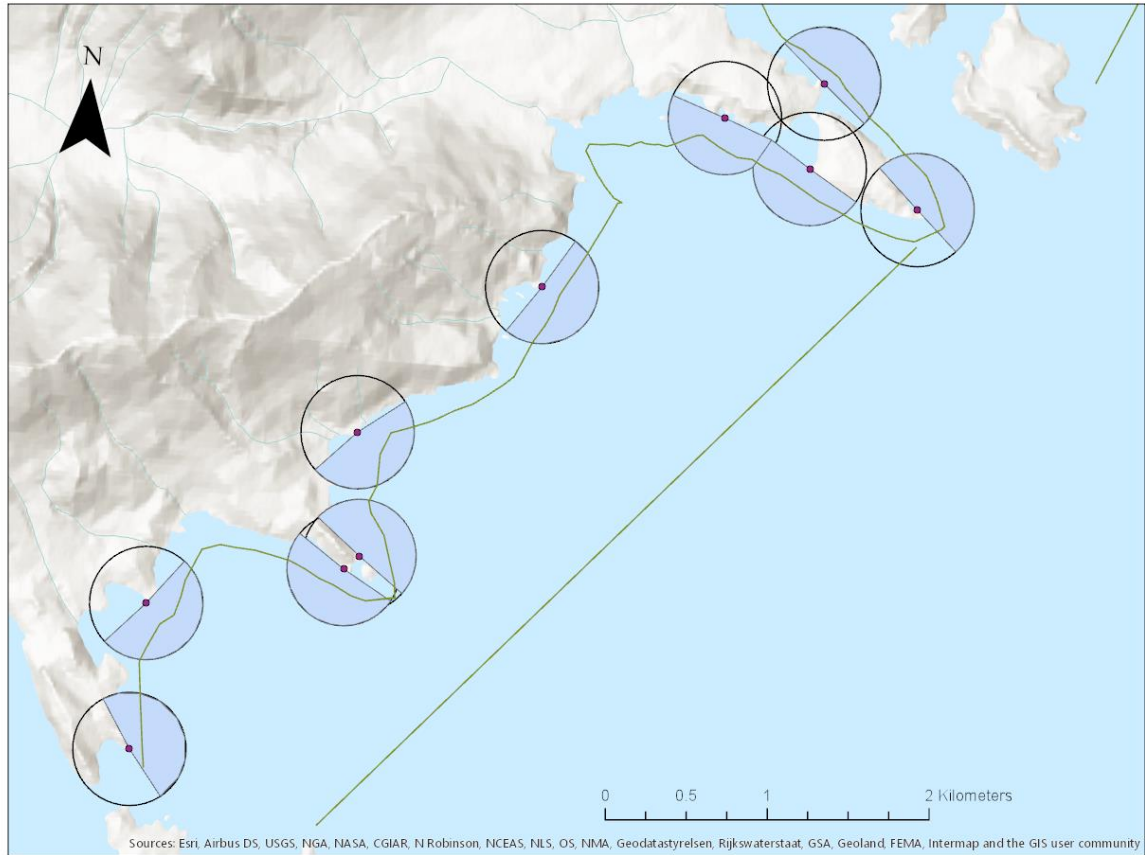


Figure 4.2 Buffer zones around avian kites with sea-survey transects. Each buffer has a radius of 350-meters. Half crescents were applied, with the half that contained the visible deterrent to the water line used. Points that fell within the visible crescent were tallied and divided by the overall counts in the study area on a given survey.

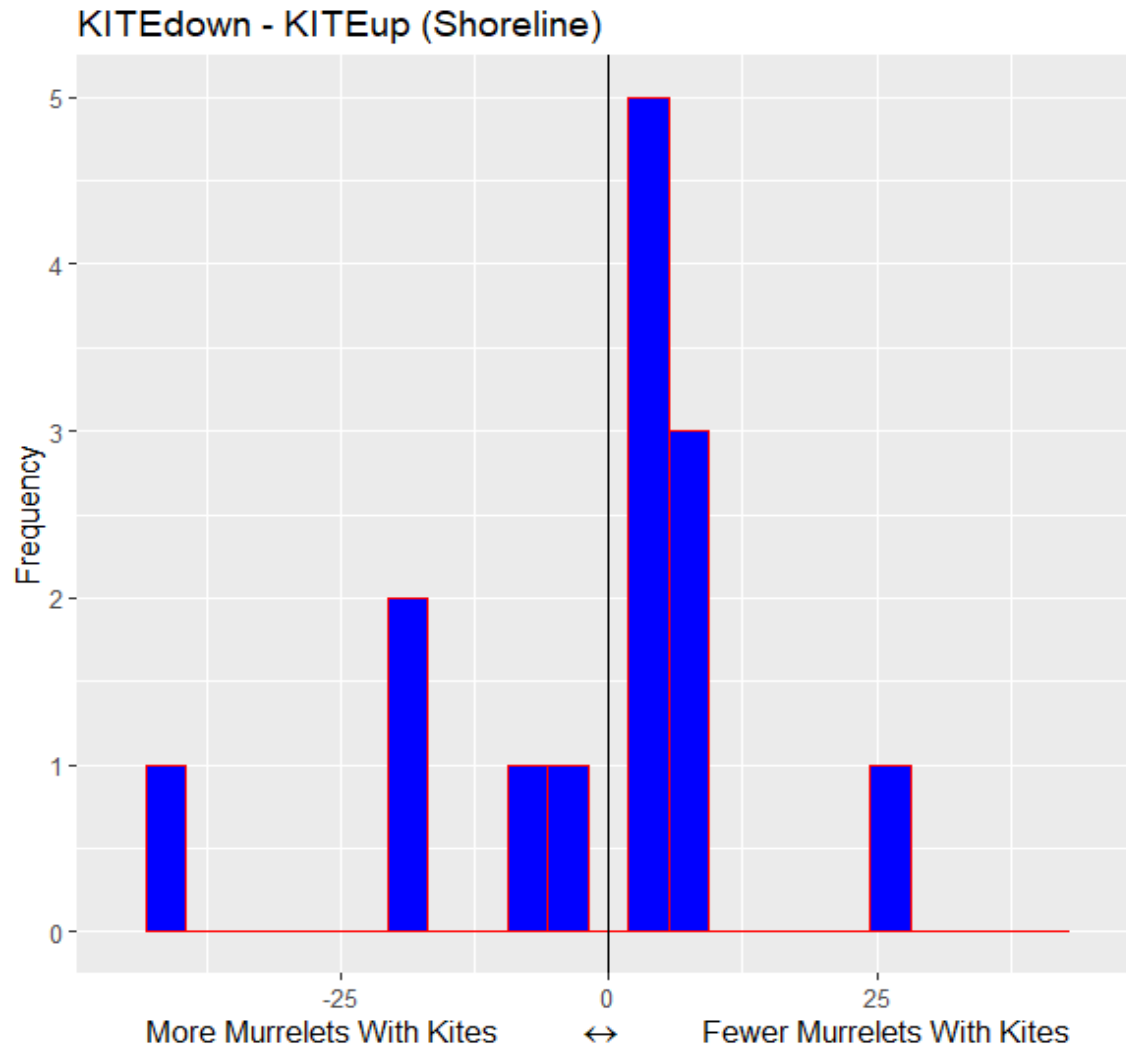


Figure 4.3 *Brachyramphus marmoratus* (murrelet) count differences along the shoreline between paired surveys (n=14) of when kites were flying (KITE_{up}) to when they were not (KITE_{down}). A positive difference indicates fewer murrelets present when kites were flying.

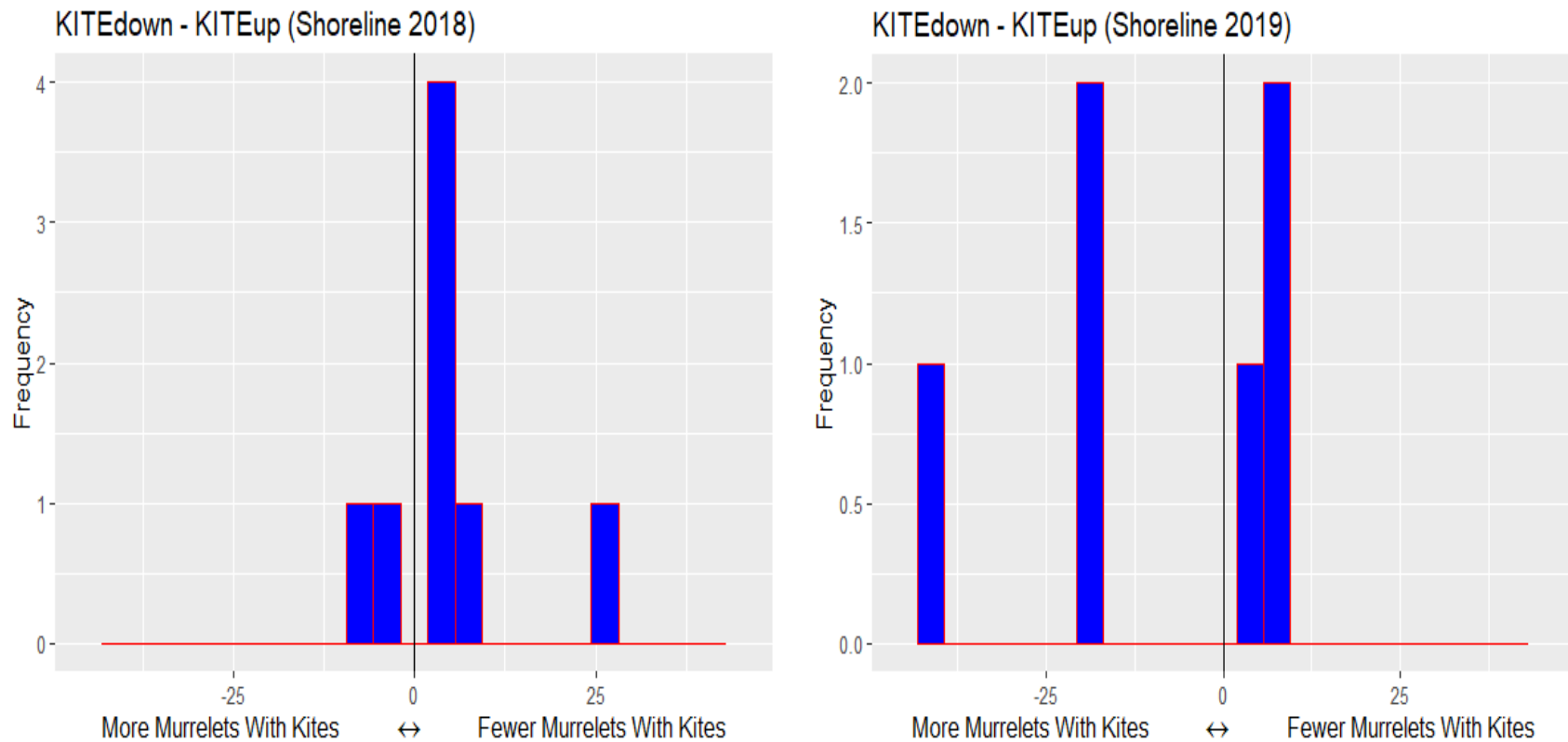


Figure 4.4 *Brachyramphus marmoratus* (murrelet) count differences along the shoreline, between paired surveys, split by year, of when kites were flying (KITE_{up}) to when they were not (KITE_{down}). A positive difference indicates fewer murrelets present when kites were flying.

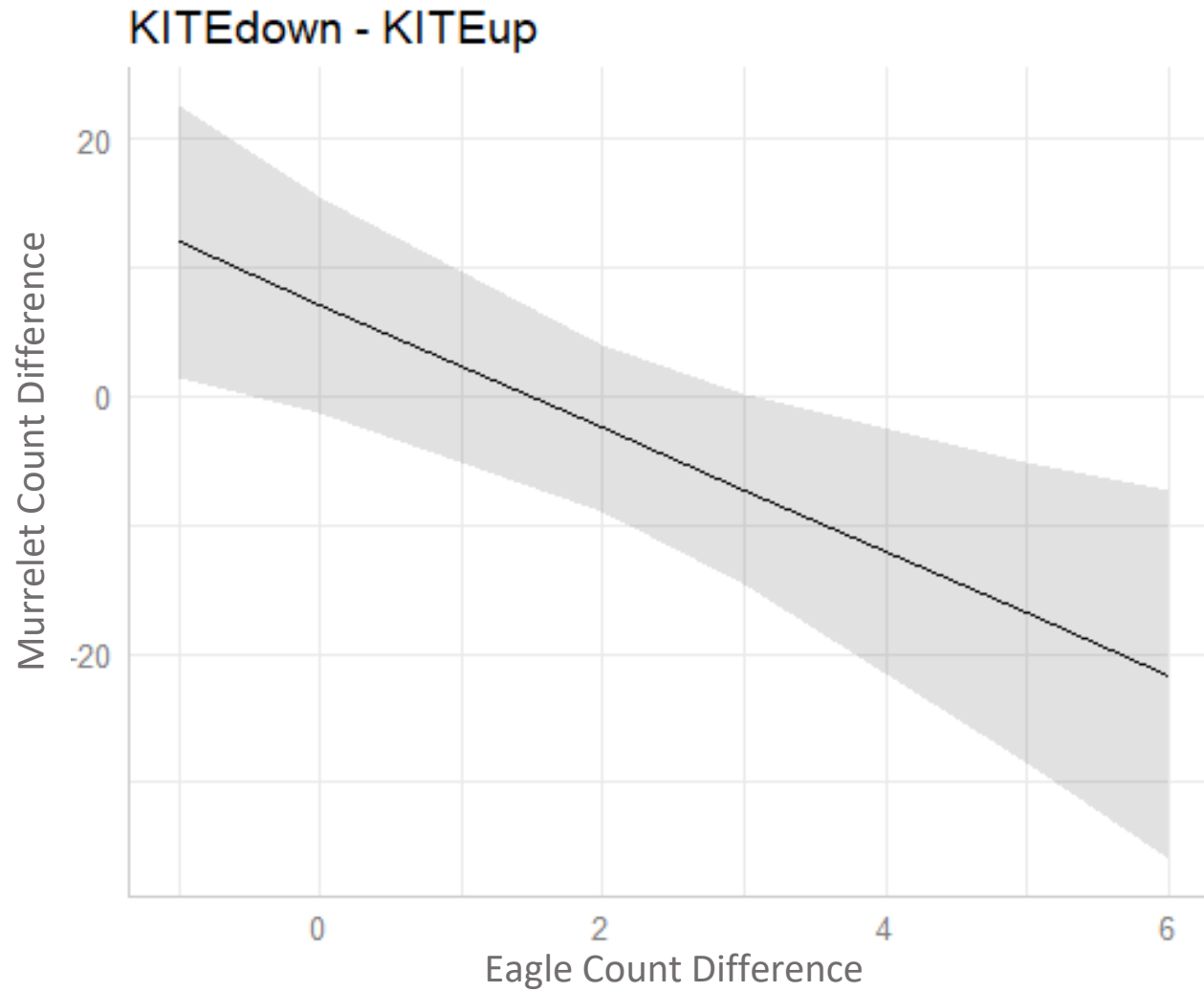


Figure 4.5 Conditional relationship between Bald eagles (*Haliaeetus leucocephalus*) and Marbled murrelets (*Brachyramphus marmoratus*) counts from the linear mixed model.

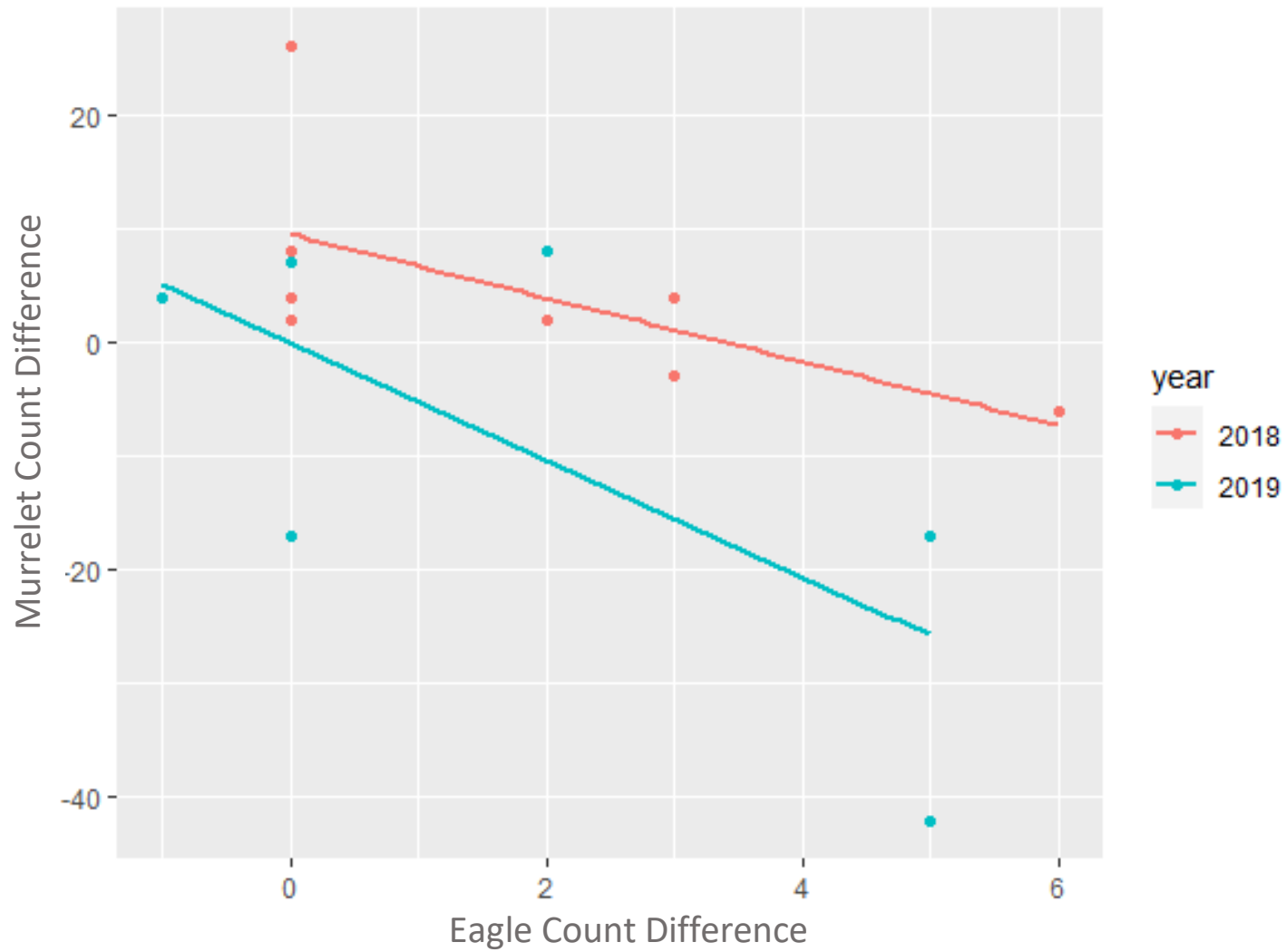


Figure 4.6 Scatter plot of the differences in Bald eagle (*Haliaeetus leucocephalus*) and Marbled murrelet (*Brachyramphus marmoratus*) counts of paired surveys (n=14) with a line of best fit drawn for the two years of study.

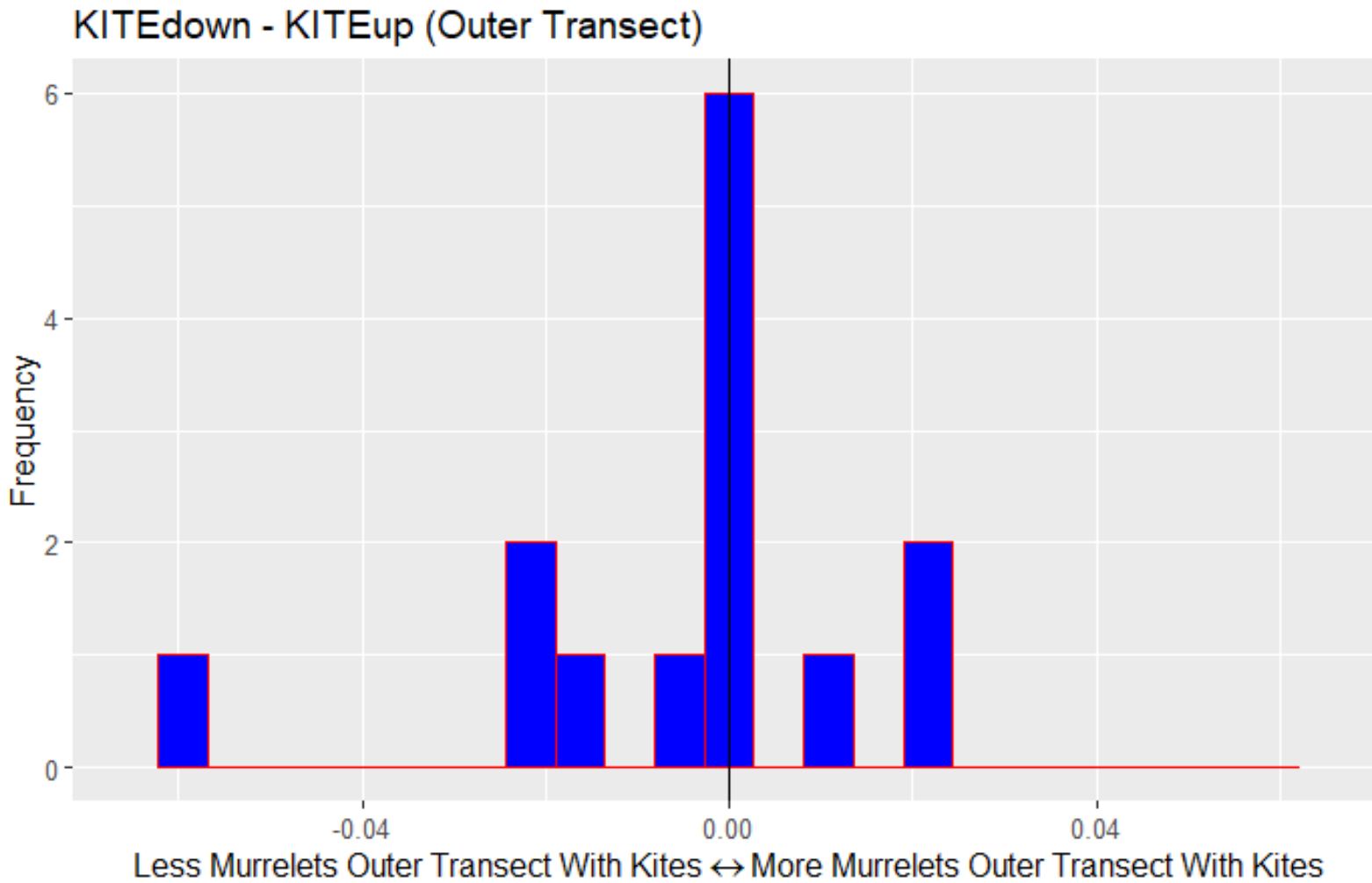


Figure 4.7 The difference in the proportion of murrelets (*Brachyramphus marmoratus*) that were situated along the outer transect when kites were flying (KITE_{up}) from when they were not (KITE_{down}) between paired treatment trials (n=14). Positive values indicate more murrelets along the outer transect when kites were flying.

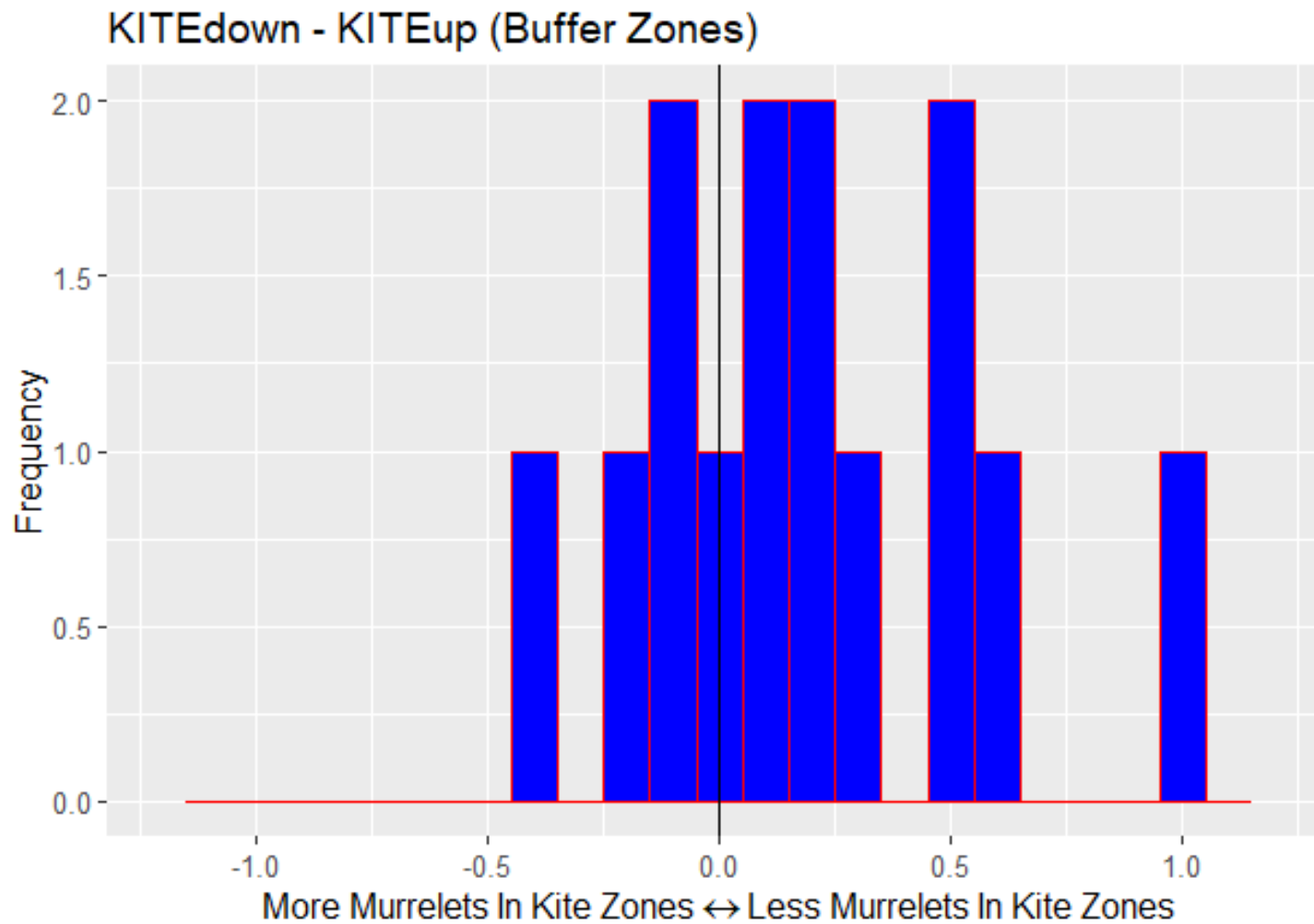


Figure 4.8 The difference in the proportion of murrelets (*Brachyramphus marmoratus*) that were situated within kite buffer zones when kites were flying (KITE_{up}) from when they were not (KITE_{down}) between paired treatment trials (n=14). Positive values indicate fewer murrelets in buffer areas when kites were flying.

Table 4.1 Experiment treatment names, descriptions and years implemented.

Treatment Name	Description	Years Treatment Run
KITE _{up}	Kites fly during the survey, and pre-survey boat disturbance occurs.	2018+2019
KITE _{down}	No kites flying and no boat disturbance prior to surveys.	2018+2019
BOAT	Boat disturbance along water prior to surveys.	2018

Table 4.2 Paired treatment categories used to assess whether avian kites and boat disturbance effect murrelets (*Brachyramphus marmoratus*). All paired treatment surveys were done within the same week (7 days) and grouped by shoreside as BOAT and KITE_{up} treatments run as one survey but treatments split by shoreside in 2019.

Treatment Pairs	Number of Paired Trials	Description
KITE _{down} + BOAT (South)	3	Difference for each paired treatment calculated by subtracting observations from BOAT by KITE _{down} observations for south shoreside.
KITE _{down} + BOAT (North)	3	Difference for each paired treatment calculated by subtracting observations from BOAT by observations from KITE _{down} for north shoreside.
KITE _{down} + KITE _{up} (South)	7	Difference for each paired treatment calculated by subtracting observations from KITE _{up} by observations from KITE _{down} for south shoreside.
KITE _{down} + KITE _{up} (North)	7	Difference for each paired treatment calculated by subtracting observations from KITE _{up} by observations from KITE _{down} for north shoreside.

Chapter 5.

General Conclusions

I have presented three data chapters that used at-sea surveys to investigate marine spatial patterns of Marbled murrelets in Laskeek Bay, Haida Gwaii, British Columbia, Canada. In Chapter 2, I used B.C.'s longest-running at-sea survey dataset (1997–2018) to create a hotspot persistence map and test potentially influencing environmental variables. This produced a baseline understanding of their marine habitat in the area. For Chapter 3, I extended my habitat preference investigation by running two years of summer surveys (May–July; 2018–2019) to see how closely murrelets were distributed in relation to potential prey and dynamic oceanographic variables. Lastly, In Chapter 4, I used an experimental approach over two seasons (May–July; 2018–2019) to see how avian predators along the shoreline changed the overall counts and local distribution of murrelets on the water.

My thesis has revealed a layered story that visualizes and explains Marbled murrelet marine distribution in Laskeek Bay. The results from Chapter 2 imply that hotspot mapping at a fine-scale is an effective way to visualize and plot murrelet distribution, and these patterns were primarily linked to static environmental variables. I found that murrelets were counted on the water at a higher rate in areas closer to streams, in shallower areas, over sediment that contained a higher percentage of sand and in areas that were close to abundant potential nesting habitat. The two years of at-sea surveys (2018 and 2019) conducted with concurrent bird-prey and dynamic oceanographic information showed that dynamic oceanographic variables are not as strongly linked to murrelet count as static variables but play a role. Thermal mixing was the strongest dynamic predictor variable, with murrelets having higher counts in stratified waters. I speculated stratified water close to freshwater inputs helps to create a productive zone for foraging. I also had visual confirmation that murrelets were foraging on Pacific sand lance (PSL) in Laskeek Bay, and this was also reaffirmed when I found sediment ideal for PSL with a specimen buried within the sand. The final data chapter indicated avian predators' effect murrelet distribution and counts on at-sea surveys. Murrelets were counted along the shoreline farther away from the experimental avian

kites when flying, compared to when they were not. There was also some indication that murrelets will leave entire foraging areas when enough avian predators are present.

My findings provide useful information for conservation initiatives, such as the Oceans Protection Plan (OPP) and the Canadian federal recovery strategy for Marbled murrelets. I used the longest-running at-sea survey dataset to build a hotspot map that can be directly applied to the OPP's development of a coastwide seabird database to help emergency response planning in case of oil spills or shipping accidents (Government of Canada 2020). Results from the marine habitat preference models support previous marine studies done in other regions by reaffirming the importance of static environmental variables. The thesis highlights the importance of considering both terrestrial and marine features when managers consider which areas to protect for Marbled murrelet marine foraging. The addition of stratified water as a vital feature reinforces how valuable regional assessments of habitat preferences are. This thesis also supports the link between PSL and murrelets, showing that this forage fish may largely drive their selection of marine habitat features and that Laskeek Bay holds important habitat for PSL that likely supports an abundance of different species. I also demonstrate that static and dynamic features work together to provide favourable habitat, so insight into both when investigating local marine environments is necessary to have a complete understanding of what drives foraging choices. The final chapter shows that avian predators in an area should be considered when looking at population trends and changes in the distribution for murrelets. An easy way to reduce unknown variance for at-sea surveys would be to take avian predators into account when conducting surveys along the shoreline.

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Appendix A.

Supplementary Material for Chapter 2

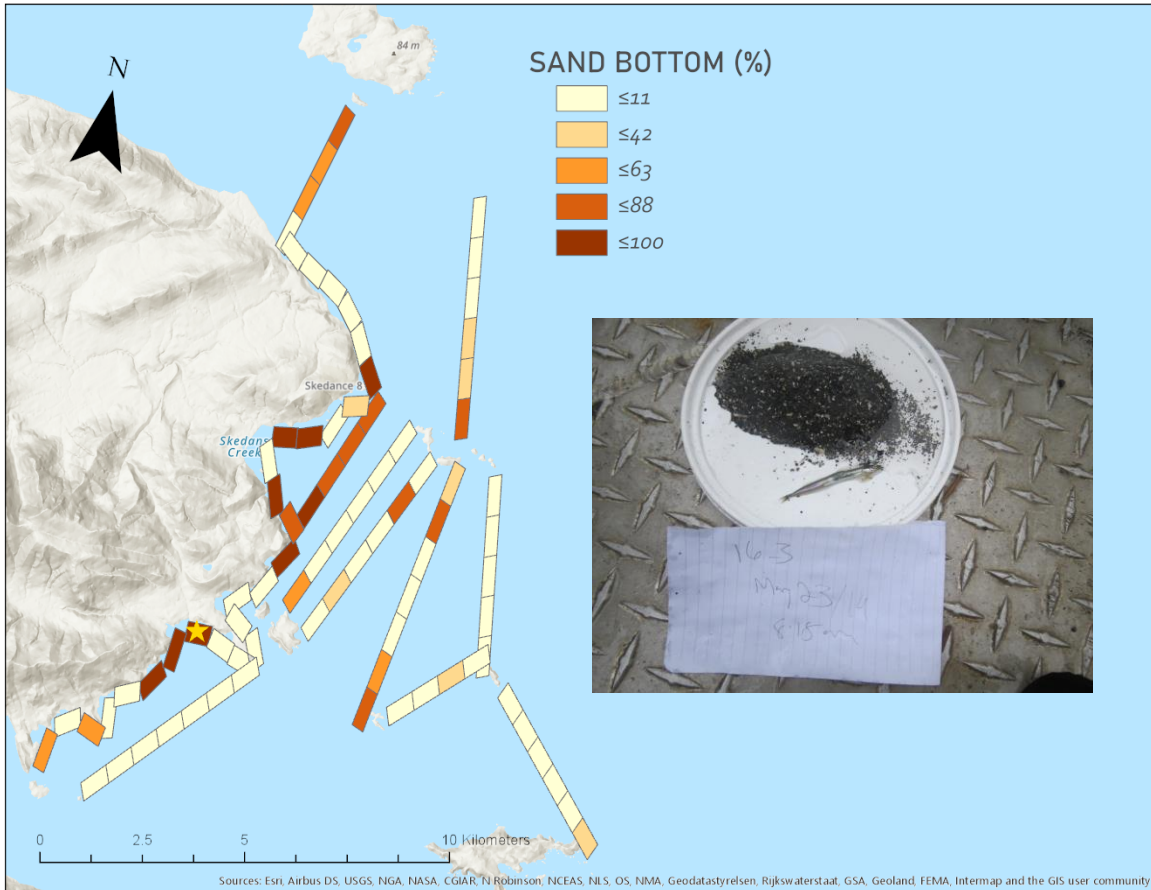


Figure A1 Percent sand bottom in Laskeek Bay, Haida Gwaii, BC. Samples were taken with a petite ponar. A maximum of three replicas were taken within each segment to find sediment. Points below 60 meters assumed to be zero percent sand, as it is the below-normal diving range for marbled murrelets and not ideal for Pacific sand lance. Star represents point Pacific sand lance was found in ponar grab.

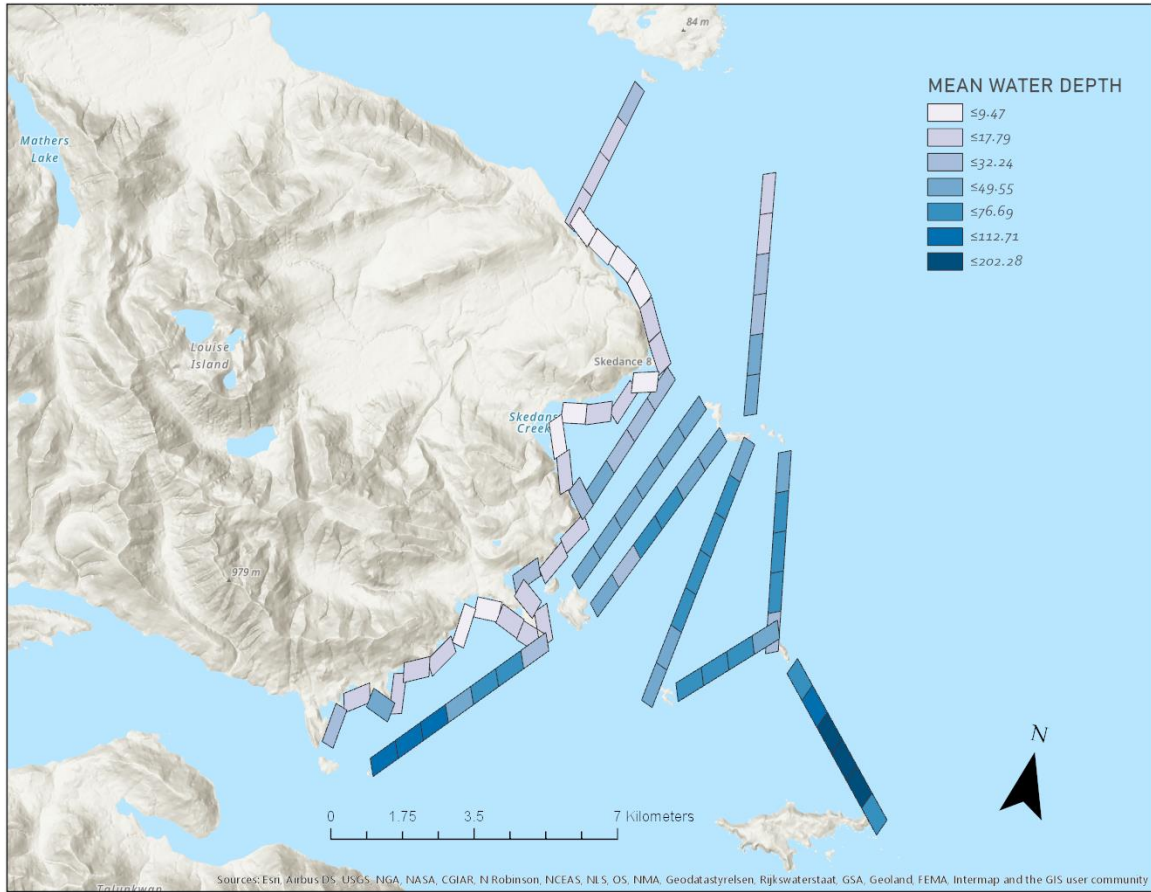


Figure A2 Mean water depth values along transects in Laskeek Bay, Haida Gwaii, British Columbia. Transects split into 1 km long segments with mean depth points from Lawrence Fish Finder calculated per segment.

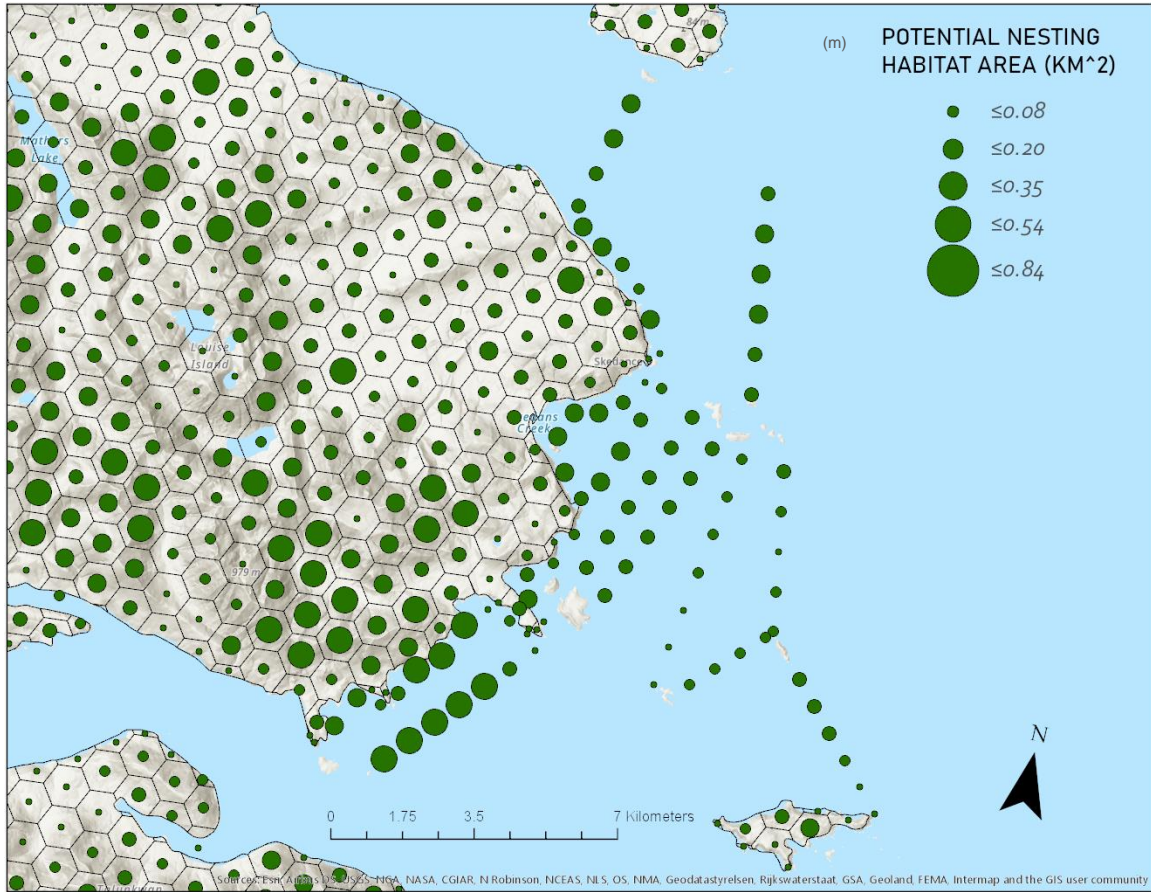


Figure A3 Potential Nesting Habitat (PNH) of *Brachyramphus marmoratus* within Laskeek Bay, Haida Gwaii, BC. PNH polygon cut into hexagon segments (866025 m²), and the area within hexagons transformed into points. Inverse distance weighting (IDW) used at each kilometer segment point along transects to calculate index value, using a 5 km radius from each segment centroid point.

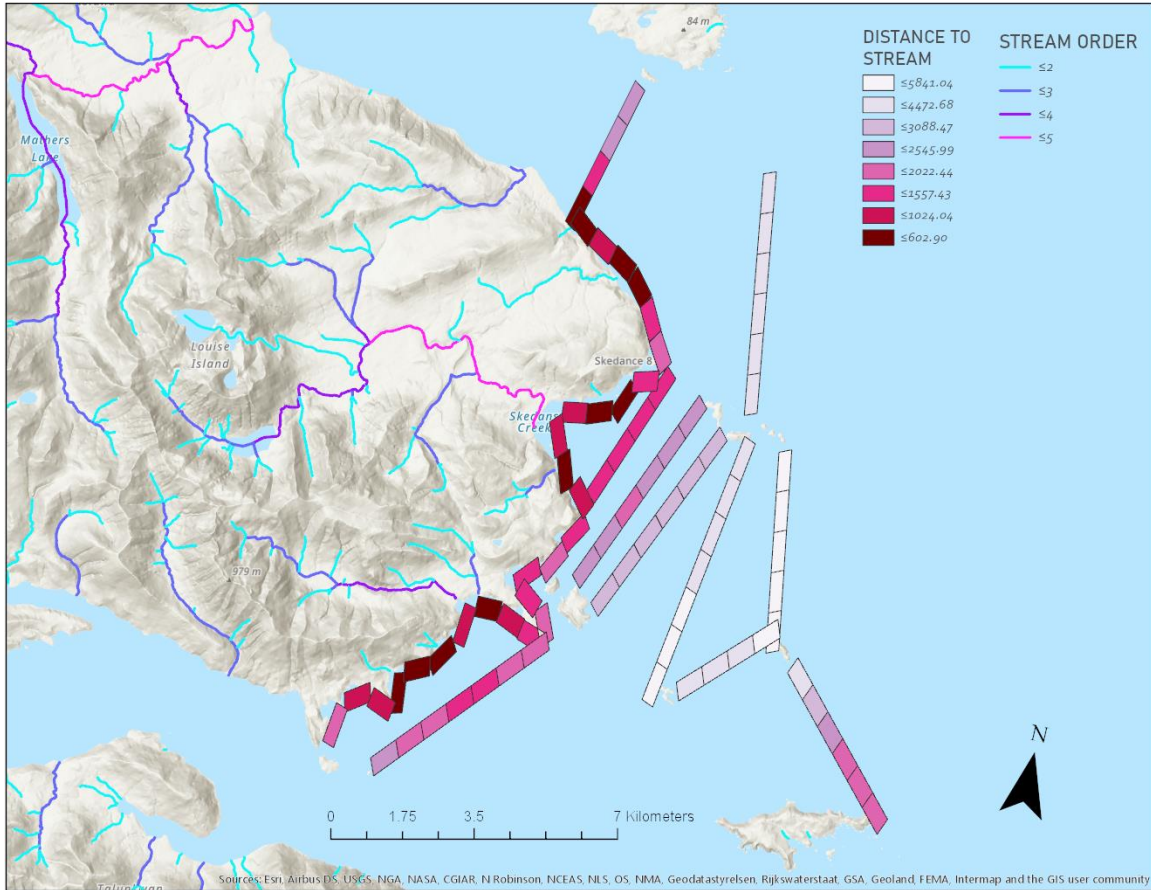


Figure A4 Streams of order two and higher around Laskeek Bay, Haida Gwaii, BC. Distance to streams calculated from each segment's centroid point to stream head, with all stream orders treated with equal weight. Dark red represents closer proximity to stream head, and lighter colours represent segments farther away, measured in meters.

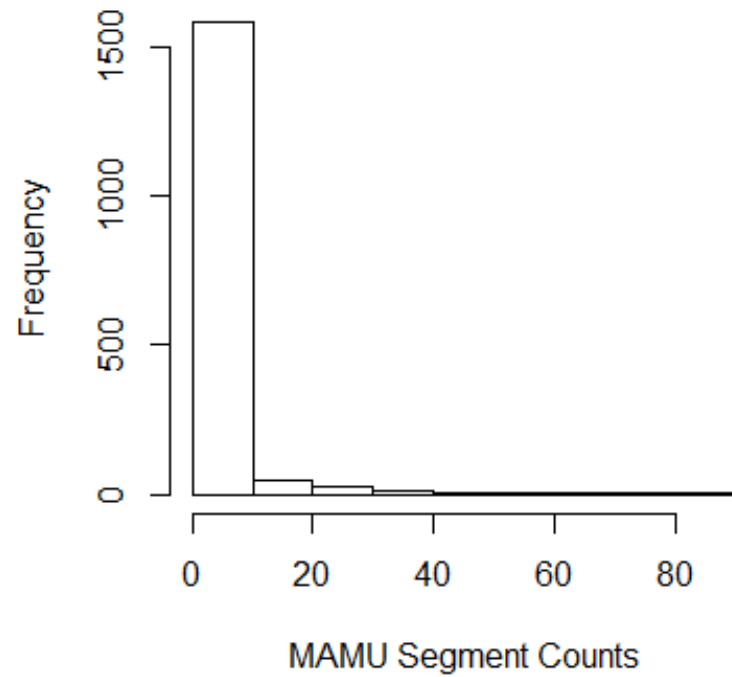
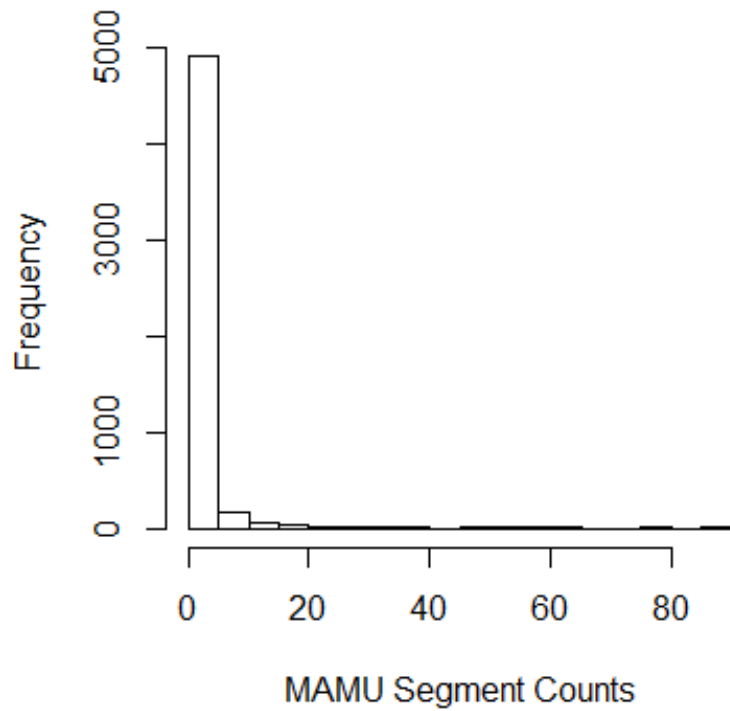


Figure A5 Distribution of *Brachyramphus marmoratus* counts within transect segments from 1997 to 2018 for full bay (left) and shoreline (right).

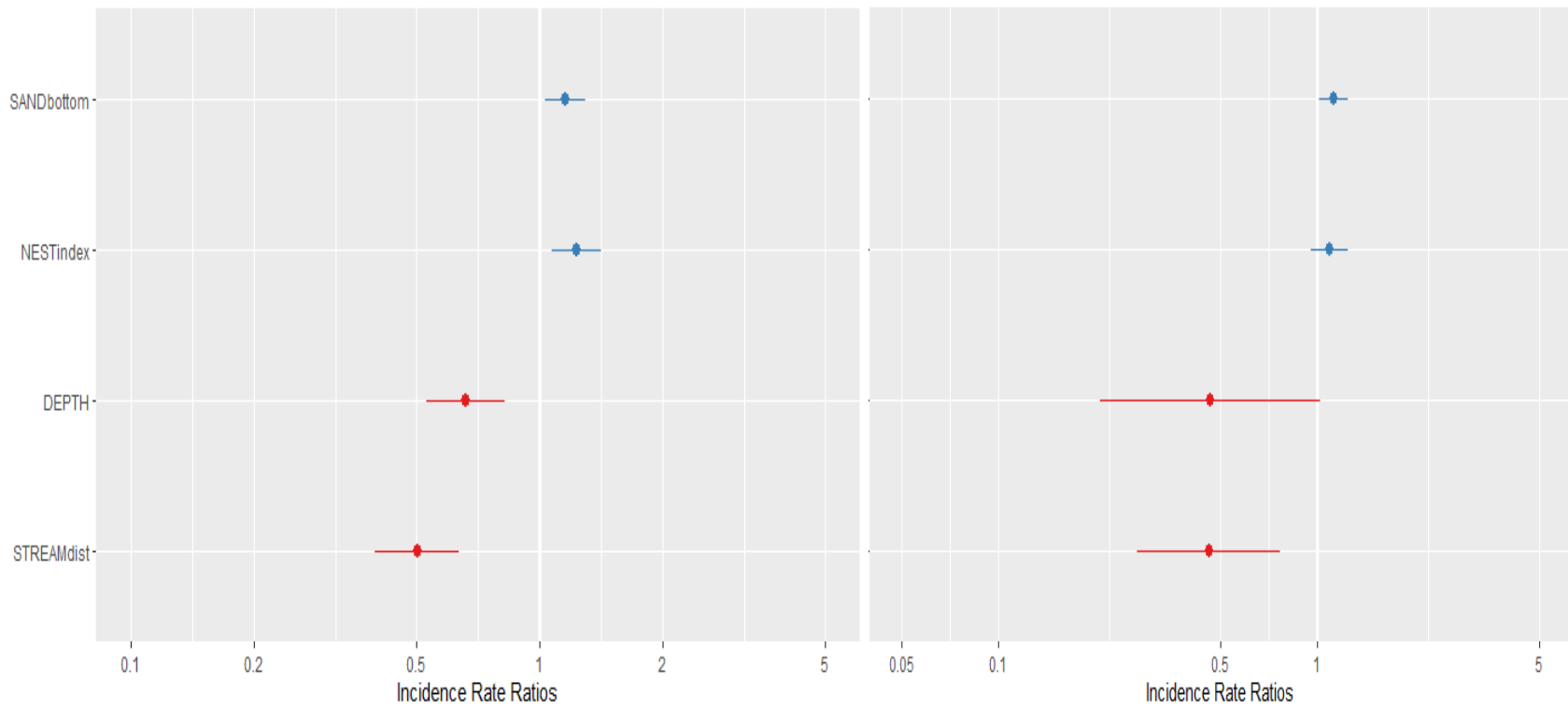


Figure A6 Incident rate ratio values of independent variables and their associated 95% confidence intervals, from the static modes of *Brachyramphus marmoratus* counts in Laskeek Bay between 1997 and 2018 (April-July). The Full model (Left) encompasses all transects within the bay and is a mix of shoreline and outer water. The shoreline model (Right) only includes shoreline transects along Louise island. Confidence intervals that do not overlap 1 are considered significant. Red signifies a negative correlation to counts, and blue is a positive correlation.

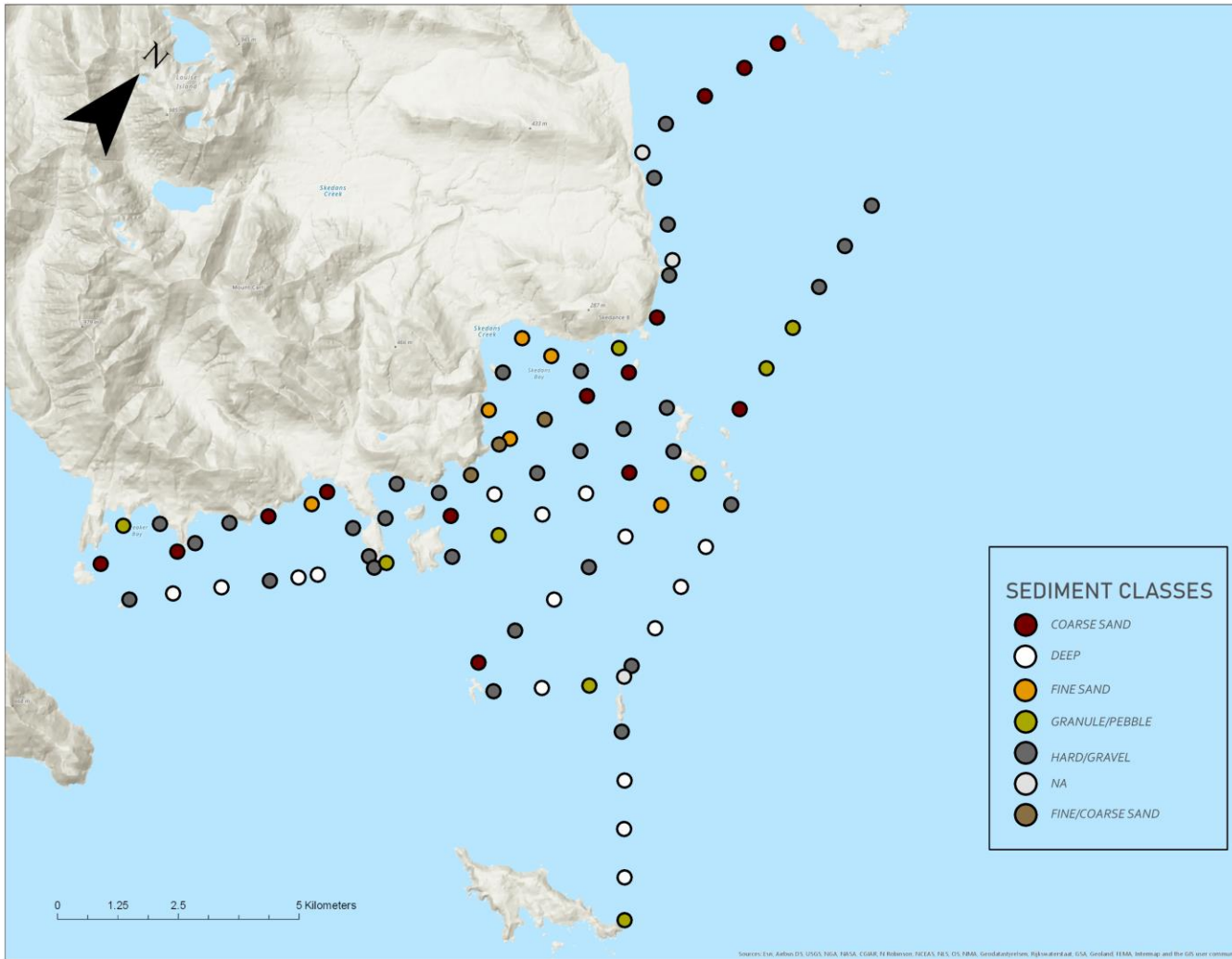


Figure A7 Sediment collection points with associated classification based on the Wentworth scale in Laskeek Bay, Haida Gwaii, BC. Those with two classification names indicate an equal mix of those two classes in sediment collected.

Table A1 Full candidate models of marine habitat preferences for *Brachyramphus marmoratus* during nesting season in Laskeek Bay between 1997 and 2018. Models predict the average number of counts per segment and incorporate the year (n=22), Julian day (n=60) and segment (n=80) nested within transects (n=18) as random effects. K is the number of parameters estimated, AICc is the Akaike's Information Criterion, Δ AICc is the differences between the AICc of each model to the lowest AICc score, wt is the likelihood of each model in relation to all other models in the candidate set, marginal R² explains variance contributed by fixed factors and conditional R² describes the variance explained by both the fixed and random factors.

Parameter	K	AICc	Δ AICc	wt	Marginal R ²	Conditional R ²
Full analysis: Number of counts within segments (Static Models)						
STREAM _{dist} +DEPTH+SAND _{bottom} +NEST _{index}	10	10415.92	0.00	0.93	0.24	0.52
STREAM _{dist} +DEPTH+SAND _{bottom}	9	10421.87	5.96	0.05	0.23	0.52
STREAM _{dist} +DEPTH	8	10424.59	8.68	0.01	0.22	0.52
STREAM _{dist} +SAND _{bottom} +NEST _{index}	9	10426.15	10.23	0.01	0.19	0.52
STREAM _{dist} +NEST _{index}	8	10430.91	15.00	0.00	0.17	0.52
STREAM _{dist} +SAND _{bottom}	8	10431.42	15.51	0.00	0.18	0.52
STREAM _{dist}	7	10434.87	18.95	0.00	0.16	0.52
DEPTH+SAND _{bottom} +NEST _{index}	9	10438.82	22.90	0.00	0.09	0.50
DEPTH+NEST _{index}	8	10442.08	26.17	0.00	0.07	0.50
SAND _{bottom} +NEST _{index}	8	10445.95	30.04	0.00	0.03	0.52
DEPTH+SAND _{bottom}	8	10448.12	32.20	0.00	0.06	0.50
NEST _{index}	7	10449.06	33.15	0.00	0.02	0.53
DEPTH	7	10449.97	34.05	0.00	0.05	0.50
SAND _{bottom}	7	10454.59	38.67	0.00	0.00	0.53

Parameter	K	AICc	Δ AICc	wt	Marginal R ²	Conditional R ²
Full analysis: Number of counts within segments (Dynamic Models)						
rain+time	8	10449.86	0	0.40	0.01	0.55
rain+time+WIND _{speed}	10	10451.79	1.93	0.15	0.01	0.55
time	7	10452.71	2.85	0.10	0.00	0.55
CLOUD _{cover} +rain+time+WIND _{speed}	11	10453.47	3.61	0.07	0.01	0.55
rain	7	10453.59	3.73	0.06	0.00	0.54
CLOUD _{cover} +time	8	10453.89	4.03	0.05	0.01	0.55
time+WIND _{speed}	9	10454.55	4.69	0.04	0.01	0.55
rain+WIND _{speed}	9	10454.62	4.77	0.04	0.00	0.54
CLOUD _{cover} +rain	8	10455.29	5.43	0.03	0.00	0.54
CLOUD _{cover} +time+WIND _{speed}	10	10455.81	5.95	0.02	0.01	0.55
CLOUD _{cover} +rain+WIND _{speed}	10	10456.28	6.42	0.02	0.01	0.54
CLOUD _{cover}	7	10457.54	7.68	0.01	0.00	0.54
WIND _{speed}	8	10457.66	7.80	0.01	0.00	0.54
CLOUD _{cover} + WIND _{speed}	9	10458.87	9.01	0.00	0.00	0.54
Shoreline analysis: Number of counts within segments (Static Models)						
STREAM _{dist} +depth+SAND _{bottom}	9	5050.61	0.00	0.28	0.05	0.54
STREAM _{dist} +depth+SAND _{bottom} +NEST _{index}	10	5050.84	0.24	0.25	0.06	0.54
STREAM _{dist} +SAND _{bottom}	8	5052.03	1.42	0.14	0.05	0.53
STREAM _{dist} +SAND _{bottom} +NEST _{index}	9	5052.25	1.64	0.12	0.06	0.54
STREAM _{dist} +depth	8	5053.02	2.41	0.08	0.04	0.53
STREAM _{dist}	7	5053.57	2.97	0.06	0.04	0.53
STREAM _{dist} +NEST _{index}	8	5054.43	3.82	0.04	0.05	0.53
depth+SAND _{bottom} +NEST _{index}	9	5056.51	5.90	0.01	0.04	0.54

Parameter	K	AICc	Δ AICc	wt	Marginal R ²	Conditional R ²
depth+SAND _{bottom}	8	5058.92	8.31	0.00	0.03	0.54
depth+NEST _{index}	8	5059.49	8.88	0.00	0.03	0.54
SAND _{bottom} +NEST _{index}	8	5060.25	9.65	0.00	0.03	0.54
depth	7	5061.01	10.41	0.00	0.02	0.54
NEST _{index}	7	5061.94	11.33	0.00	0.02	0.53
SAND _{bottom}	7	5063.78	13.18	0.00	0.01	0.53
Shoreline analysis: Number of counts within segments (Dynamic Models)						
WIND _{speed}	8	5059.81	0.00	0.25	0.03	0.55
CLOUD _{cover} +WIND _{speed}	9	5060.14	0.33	0.21	0.03	0.53
WIND _{speed} +rain	9	5061.04	1.23	0.13	0.02	0.55
CLOUD _{cover} +WIND _{speed} +rain	10	5061.63	1.82	0.10	0.03	0.54
WIND _{speed} +time	9	5061.81	2.00	0.09	0.02	0.55
CLOUD _{cover} +WIND _{speed} +time	10	5062.16	2.35	0.08	0.03	0.53
WIND _{speed} +time+rain	10	5063.06	3.25	0.05	0.02	0.55
CLOUD _{cover} +WIND _{speed} +time+rain	11	5063.65	3.84	0.04	0.03	0.54
CLOUD _{cover}	7	5064.98	5.17	0.02	0.01	0.52
rain	7	5066.39	6.58	0.01	0.00	0.54
time	7	5066.41	6.60	0.01	0.00	0.54
CLOUD _{cover} +time	8	5066.80	6.99	0.01	0.01	0.52
CLOUD _{cover} +rain	8	5066.85	7.04	0.01	0.01	0.52
time+rain	8	5068.15	8.34	0.00	0.00	0.54

Appendix B.

Supplementary Material for Chapter 3

Table B1 Complete set of candidate models of marine habitat preferences for *Brachyramphus marmoratus* during nesting season in Laskeek Bay in 2018 and 2019. Models predict the average number of counts per segment and incorporate the year (n=2), Julian day (n=18) and segment (n=80) nested within transects (n=18) as random effects. K= number of parameters estimated, AICc = Akaike's Information Criterion, Δ AICc = differences between AICc of each model to the lowest AICc score, wt = likelihood of each model in relation to all other models in the candidate set, marginal R² = variance contributed by fixed factors and conditional R² = the variance explained by both the fixed and random factors.

Parameters	K	AICc	Δ AICc	Wt	Marginal R ²	Conditional R ²
MIX+SST+FISH _{school} +NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	13	1794.25	0.00	0.37	0.44	0.64
MIX+NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	11	1796.14	1.89	0.14	0.43	0.66
MIX+SST+NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	12	1796.62	2.37	0.11	0.43	0.66
FISH _{school} +NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	11	1796.77	2.51	0.11	0.42	0.65
STREAM _{dist} +DEPTH	8	1797.53	3.27	0.07	0.41	0.67
NEST _{index} +STREAM _{dist} +DEPTH	9	1797.94	3.69	0.06	0.41	0.66
NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	10	1798.14	3.89	0.05	0.41	0.66
SST+FISH _{school} +NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	12	1798.34	4.09	0.05	0.43	0.65
SST+NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	11	1799.51	5.25	0.03	0.42	0.66
STREAM _{dist} +SAND _{bottom}	8	1803.86	9.61	0.00	0.32	0.65
NEST _{index} +STREAM _{dist} +SAND _{bottom}	9	1804.42	10.17	0.00	0.34	0.65
STREAM _{dist}	7	1804.47	10.22	0.00	0.31	0.65
NEST _{index} +STREAM _{dist}	8	1804.82	10.57	0.00	0.33	0.654

Parameters	K	AICc	Δ AICc	Wt	Marginal R2	Conditional R2
DEPTH	7	1809.09	14.83	0.00	0.21	0.673
DEPTH+SAND _{bottom}	8	1809.14	14.88	0.00	0.21	0.667
NEST _{index} +DEPTH	8	1811.08	16.83	0.00	0.21	0.673
NEST _{index} +DEPTH+SAND _{bottom}	9	1811.16	16.91	0.00	0.21	0.667
MIX+FISH _{school}	8	1813.56	19.31	0.00	0.01	0.694
MIX+SST+FISH _{school}	9	1814.62	20.36	0.00	0.02	0.693
MIX	7	1815.80	21.55	0.00	0.01	0.715
MIX+SST	8	1816.68	22.42	0.00	0.01	0.714
FISH _{school}	7	1817.06	22.80	0.00	0.00	0.692
SAND _{bottom}	7	1817.92	23.67	0.00	0.00	0.699
NULL	6	1818.09	23.84	0.00	0.00	0.71
SST+FISH _{school}	8	1818.86	24.61	0.00	0.01	0.692
SST	7	1819.74	25.49	0.00	0.00	0.709
NEST _{index} +SAND _{bottom}	8	1819.95	25.69	0.00	0.00	0.698
NEST _{index}	7	1820.13	25.88	0.00	0.00	0.71

Table B2

Complete set of candidate models of marine habitat preferences for general fish school occurrence counts during *Brachyramphus marmoratus* nesting season in Laskeek Bay in 2018 and 2019. Models predict average number of counts per segment and incorporate the year (n=2), Julian day (n=18) and segment (n=80) nested within transects (n=18) as random effects. K= number of parameters estimated, AICc = Akaike's Information Criterion, Δ AICc = differences between AICc of each model to the lowest AICc score, wt = likelihood of each model in relation to all other models in the candidate set, marginal R² = variance contributed by fixed factors and conditional R² = the variance explained by both the fixed and random factors.

Parameters	K	AICc	Δ AICc	Wt	Marginal R ²	Conditional R ²
MIX+SST+NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	12	2315.69	0.00	0.41	0.15	0.36
MIX+NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	11	2315.97	0.31	0.35	0.14	0.35
NEST _{index} +DEPTH	8	2319.66	3.97	0.06	0.12	0.35
SST+NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	11	2320.06	4.37	0.06	0.14	0.35
NEST _{index} +DEPTH+SAND _{bottom}	9	2320.71	5.02	0.03	0.13	0.35
DEPTH	7	2320.80	5.11	0.03	0.11	0.35
NEST _{index} +STREAM _{dist} +DEPTH	9	2321.12	5.43	0.03	0.12	0.36
DEPTH+SAND _{bottom}	8	2321.99	6.30	0.02	0.11	0.35
NEST _{index} +STREAM _{dist} +DEPTH+SAND _{bottom}	10	2322.32	6.63	0.01	0.12	0.34
STREAM _{dist} +DEPTH	8	2322.83	7.14	0.01	0.11	0.35
MIX	7	2327.28	11.59	0.00	0.01	0.34
MIX+SST	8	2327.40	11.71	0.00	0.03	0.35
SST	7	2332.14	16.45	0.00	0.01	0.36
NEST _{index} +STREAM _{dist}	8	2332.95	17.26	0.00	0.03	0.33
NEST _{index} +STREAM _{dist} +SAND _{bottom}	9	2333.24	17.55	0.00	0.04	0.32
NEST _{index} +SAND _{bottom}	8	2333.54	17.85	0.00	0.02	0.33
NEST _{index}	7	2333.62	17.93	0.00	0.01	0.34
NULL	6	2333.81	18.12	0.00	0.00	0.34
SAND _{bottom}	7	2333.82	18.13	0.00	0.01	0.33
STREAM _{dist}	7	2334.76	19.07	0.00	0.01	0.33
STREAM _{dist} +SAND _{bottom}	8	2335.03	19.33	0.00	0.02	0.33

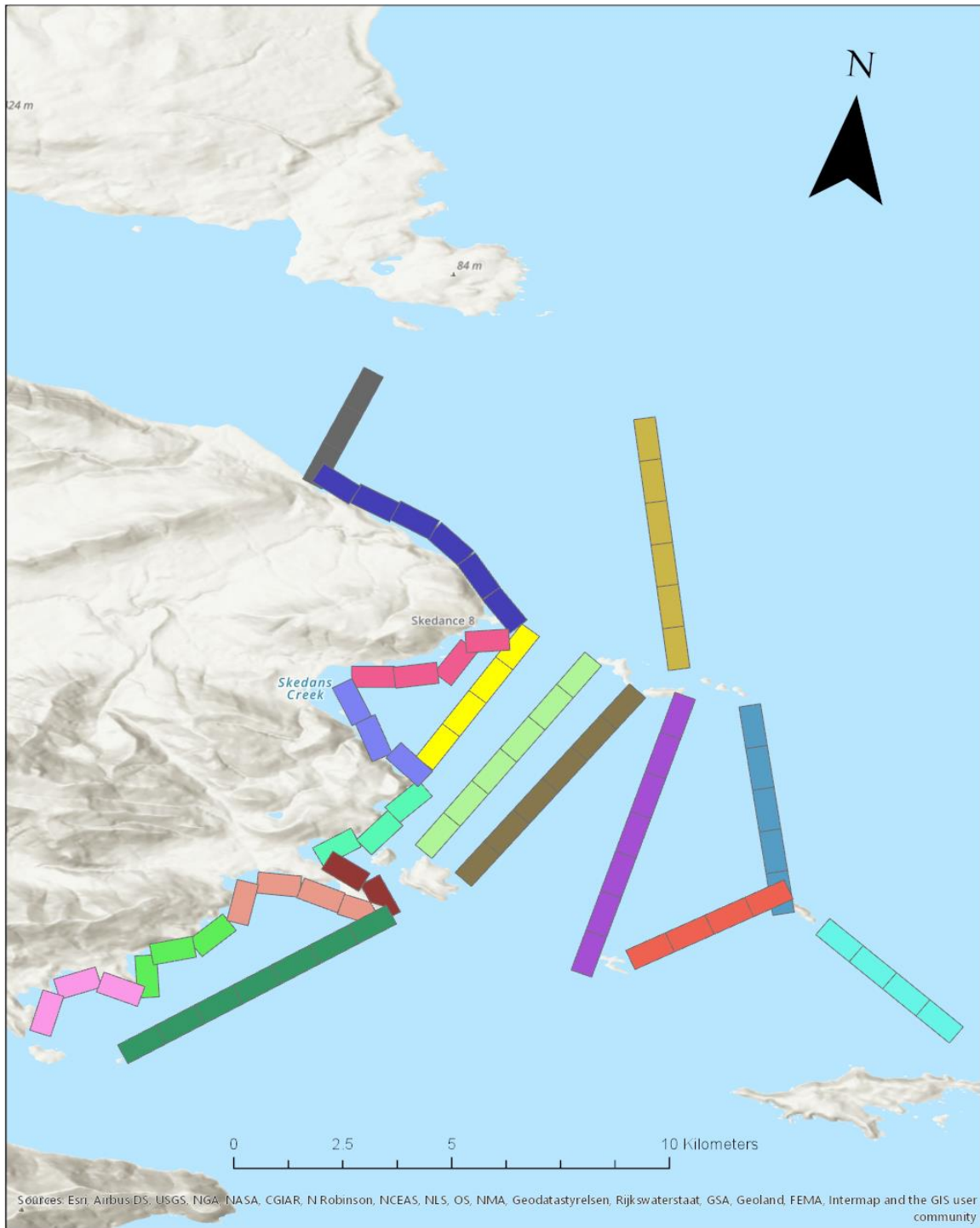


Figure B1 Sea-survey routes in Laskeek Bay, Haida Gwaii, BC. Unique color schemes identify individual transects with transects being cut into 1 km long segments.

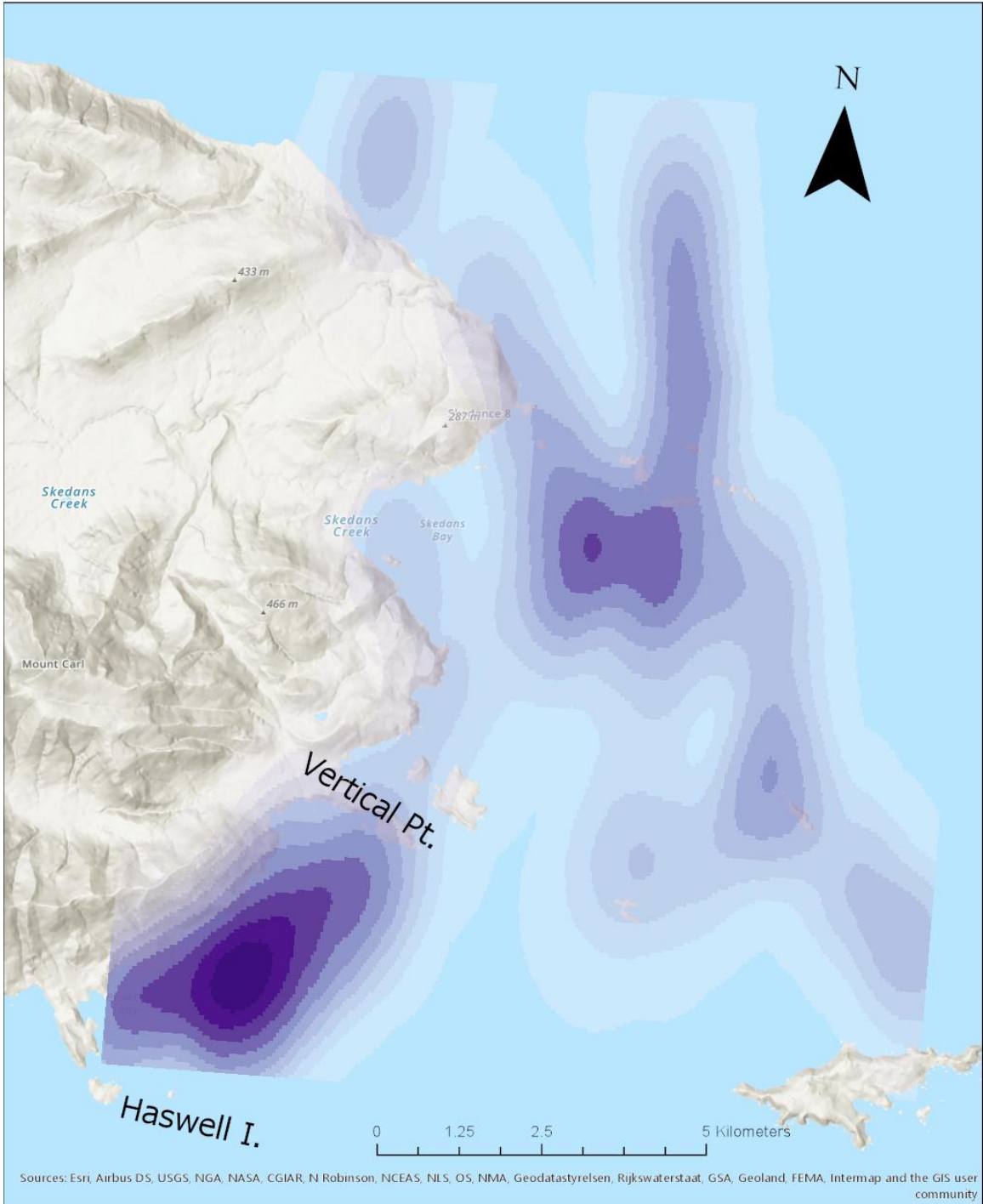


Figure B2 Kernel density map of stratified waters in Laskeek Bay (2018 and 2019), Haida Gwaii, BC. Darker purple indicates a higher density probability of stratified water recordings. Stratified water was determined by taking calculating the temperature difference between 5 and 10 meters depths.

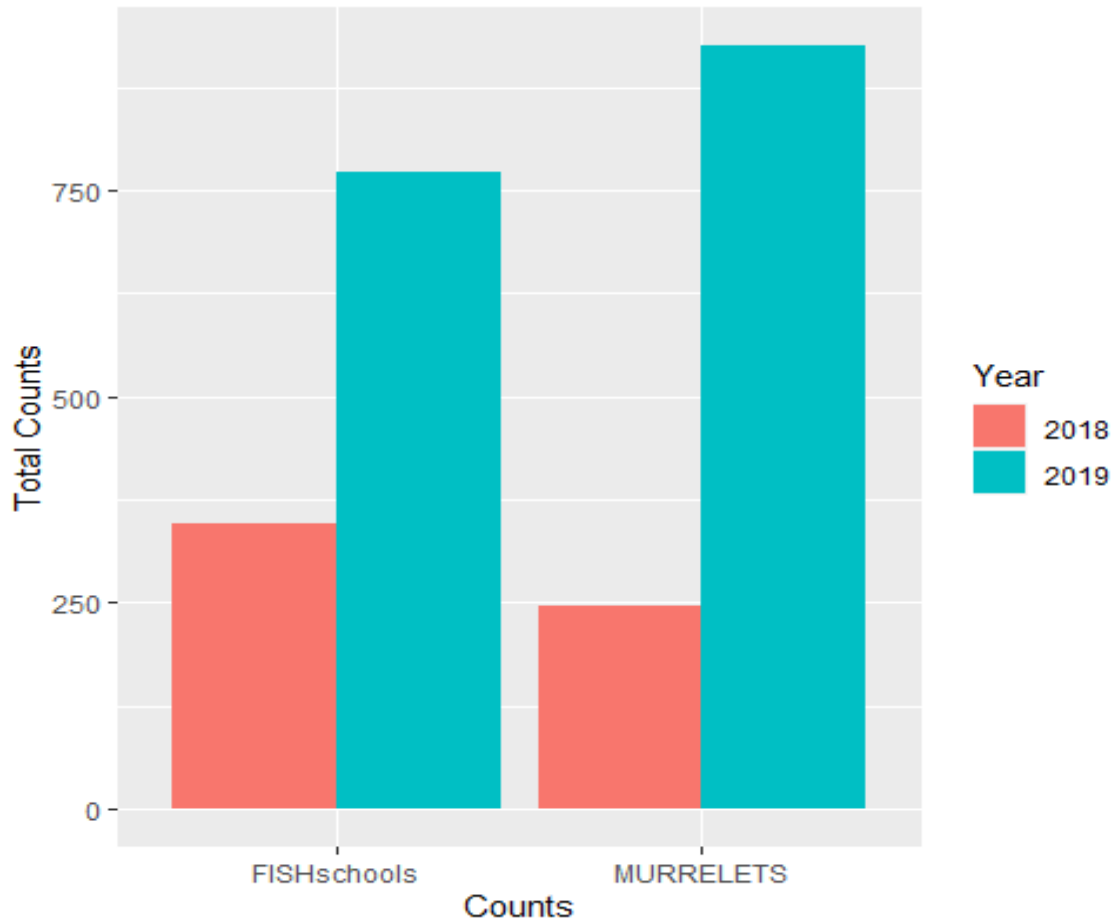


Figure B3 Total counts from sea-surveys in Laskeek Bay of fish schools and murrelets (*Brachyramphus marmoratus*) in Laskeek Bay, Haida Gwaii, BC. Counts are tallied for 2018 and 2019.

Appendix C.

Supplementary Material for Chapter 4



Figure C1 Kite Stand with attached fibreglass extendable pole, researcher unpacking kite to attach to stand.



Figure C2 Depiction of Bald eagle deterrent kite (left) and Peregrine falcon deterrent kite (right).
Source: Margo Supplies

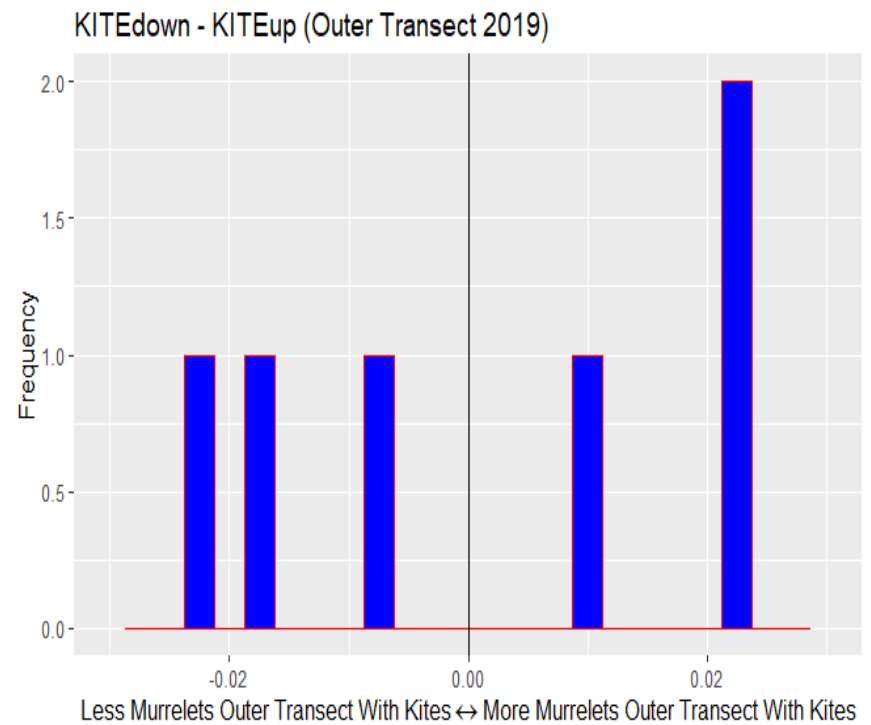
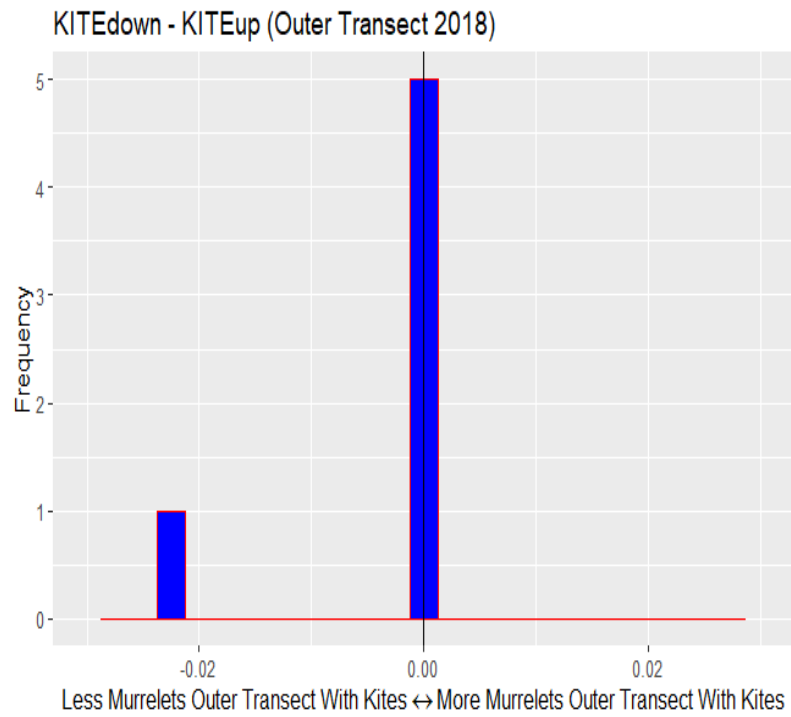


Figure C4 The difference in the proportion of murrelets (*Brachyramphus marmoratus*) that were situated along the outer transect when kites were flying (KITE_{up}) from when they were not (KITE_{down}) between paired treatment trials, separated by year. Positive values indicate more murrelets along the outer transect when kites were flying.

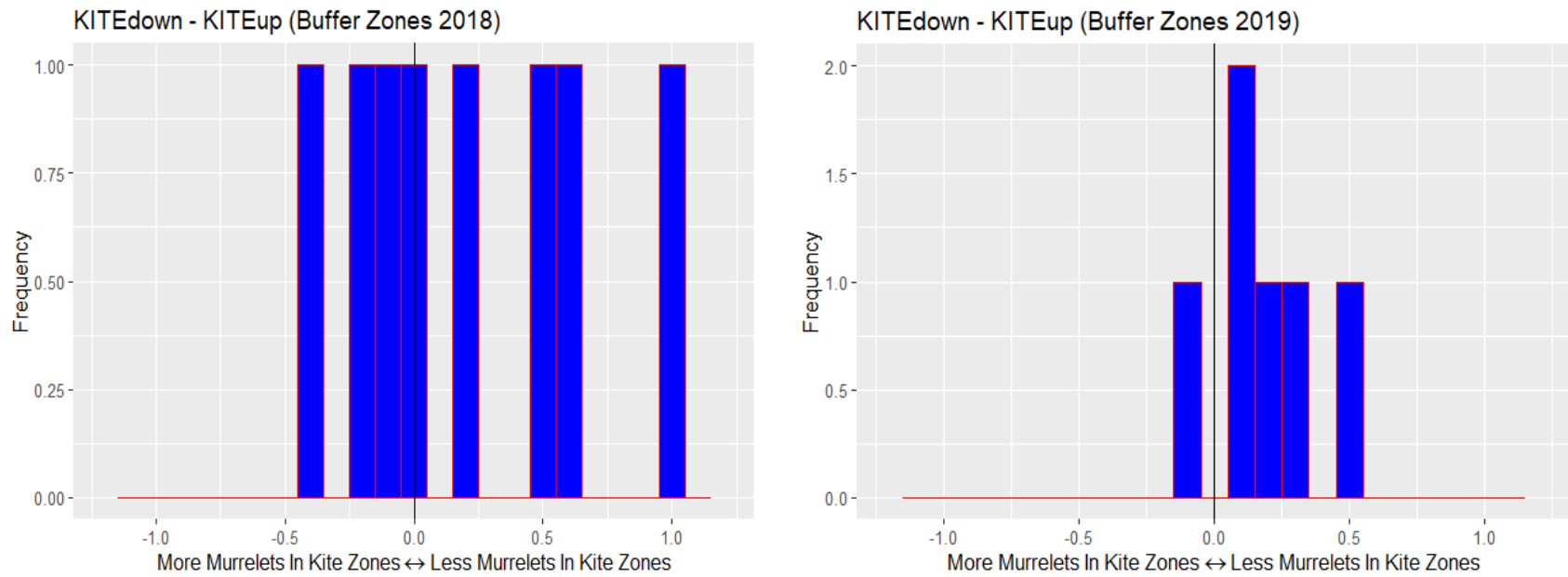


Figure C5 The difference in the proportion of murrelets (*Brachyramphus marmoratus*) that were situated within kite buffer zones when kites were flying (KITE_{up}) from when they were not (KITE_{down}) between paired treatment trials, split by year. More positive values indicate fewer murrelets in buffer areas when kites were flying.