THE INFLUENCE OF OCEANOGRAPHIC AND TERRESTRIAL ATTRIBUTES ON MARBLED MURRELET (*Brachyramphus marmoratus)* MARINE HABITAT SELECTION DURING THE BREEDING SEASON.

by

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ABSTRACT

We examined how oceanographic and terrestrial features influence marine habitat selection by radio-tagged marbled murrelets (*Brachyramphus marmoratus*), and how selection varies temporally, geographically and with respect to reproductive status. Murrelet marine habitat selection was simultaneously affected by sea surface temperature and nearshore environment characteristics, as well as distance to nest site for breeders, with lesser influence by physical oceanographic features. Marbled murrelets were generally associated with areas characterized by higher relative tidal speeds, greater depths, steeper ocean floor slopes, less freshwater inflow and proximity to sandy beaches, though the strength of these relationships varied. Breeding murrelets were also associated with proximity to nest sites. We observed within-season and between-site variability in murrelet-SST associations, suggesting that murrelets change their foraging tactics as their needs and/or local oceanographic conditions change. We suggest that availability of suitable nesting habitat within proximity of profitable marine foraging areas is critical for recovery of this species.

Keywords: marbled murrelet; habitat selection; marine-terrestrial connection; spatial autoregressive modeling; GIS; conservation biology

DEDICATION

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1 INTRODUCTION

The growth, survival and reproductive success of an animal is dependent on its ability to locate resources in an environment that may be variable in both space and time (Pinaud and Weimerskirch 2002, Robards et al. 2002, Suryan et al. 2002, Aarts et al. 2008). As such, identifying the factors that influence habitat selection (Johnson 1980), understanding how selection differs between animals of different states (e.g., gender, age class, reproductive status), and predicting how habitat selection varies temporally, geographically, and in response to natural or anthropogenic change, is of critical importance for wildlife conservation and resource management (Manly et al. 2002, Louzao et al. 2006, Aarts et al. 2008). Species with lifecycles tied to both marine and terrestrial environments pose an extra challenge for wildlife managers, as reserve design and management strategies need to consider habitat selection both on land and at-sea, as well as linkages that exist between the two ecosystems, including, for example, how the two ecosystems interact to produce good habitat or impose tradeoffs. Seabirds epitomize this juxtaposition between terrestrial and marine systems; however, at-sea studies of seabird habitat selection are relatively rare in comparison to terrestrial studies of breeding habitat (Croll et al. 1998, Ronconi 2008). Moreover, conservation reserves, in general, have typically been aimed at terrestrial environments only (Burger 2002, Carr et al. 2003). Although seabirds nest on land, they spend over 90% of their lives at sea (Ballance et al. 2001), and are dependent on the marine environment for food. Both the reproductive performance (Baird 1990, Pinaud and Weimerskirch 2002) and population dynamics (Jones et al. 2002, Frederiksen et al. 2004) of seabirds have been linked to changes in oceanographic conditions, illustrating the importance of understanding marine habitat selection for seabird conservation.

The marbled murrelet (*Brachyramphus marmoratus*) exemplifies the need to incorporate marine and terrestrial habitat requirements in conservation strategies. Unlike other alcids, marbled murrelets nest solitarily, primarily in old-growth forests, up to 84 km inland (Hamer 1995, Burger 2002). The clutch consists of a single egg, typically laid in a simple depression on the mossy platform of a large conifer (Sealy 1974, Piatt et al. 2007). Marbled murrelets depend on the marine environment for food, taking primarily sand lance (*Ammodytes hexapterus*) and juvenile herring (*Clupea harengus*), as well as euphausiids (e.g., *Euphausia pacifica*, *Thysanoessa spinifera*) (Gaston and Jones 1998). Incubation is biparental; both sexes alternate 24-hr incubation shifts with returning to the ocean to rest and feed. Once the egg has hatched, parents make daily flights from marine foraging areas to their inland nests, sometimes exceeding 100km one way, to deliver a single fish per trip to their chick (Whitworth et al. 2000, Hull et al. 2001).

Numbers of marbled murrelets are believed to be declining throughout most of their range (Burger 1995, Piatt et al. 2007), and they are listed as Threatened in Canada by COSEWIC (Committee on the Status of Endangered Wildlife in Canada), and in Washington, Oregon and California by the USFWS (US Fish and Wildlife Service) (Piatt et al. 2007). While it is has long been assumed that loss and fragmentation of old-growth forests have been and remain the greatest threats to murrelet productivity (e.g., Ralph et al. 1995, Burger 2002, Piatt et al. 2007), there have been no definitive studies determining what factors are most limiting to murrelet populations, and recent work suggests that marine factors may play an important role in determining annual reproductive success (e.g., Becker and Beissinger 2006, Becker et al. 2007, Norris et al. 2007), as well as the distribution of local populations during the breeding season (Piatt et al. 2007). While insufficient nesting habitat may directly limit local murrelet populations, the proximity of nest sites to productive marine areas may also affect the potential quality of nesting habitat, and/or restrict murrelets to closer, but perhaps smaller and less productive marine foraging areas (Hull et al. 2001, Becker and Beissinger 2003). Due to the energetic costs and risks associated with commuting, a breeding murrelet may be faced with a tradeoff between seeking an optimal inland nesting site, characterized by low predation danger, suitable microhabitat features and close proximity to flyways (Ralph et al. 1995), versus remaining within reasonable distance of profitable marine foraging patches. Longer time spent traveling may translate into fewer trips to the nest, fewer prey items provided to the offspring, and thus lower chick growth and survival (Hull et al. 2001), and may involve greater predation risk for the commuting adult (Ralph et al. 1995). Because marbled murrelets only deliver a single fish per trip to the nest, and must rely on high-energy flapping flight to remain airborne, they may be especially sensitive to commuting costs (Hull et al. 2001).

Oceanographic conditions may also limit murrelet populations independently of terrestrial habitat and commuting costs. To survive and reproduce, seabirds must locate profitable foraging sites in an environment where productivity and prey distributions are patchy, and both temporally and spatially dynamic (Hunt et al. 1999, Becker and Beissinger 2003, Weimerskirch et al. 2005, Rey et al. 2007). A reliable prey supply is especially important during the breeding season, when energy demands are highest (Hull et al. 2001). When prey changes in abundance or availability, seabirds may respond by increasing foraging effort (Ronconi 2008), opting not to breed (Peery et al. 2004), abandoning their nest (Gaston and Smith 2001), decreasing their reproductive investment (Erwin and Congdon 2007, Navarro and Gonzalez-Solis 2007) or feeding their chicks lower quality prey items (Pinaud et al. 2005), with the latter two options possibly resulting in slower chick growth, later or poorer condition on fledging, or chick starvation (Baird 1990, Smithers et al. 2003, Pinaud et al. 2005). Variations in the performance of seabird populations, including reduced productivity (Abraham and Sydeman 2004), increased foraging effort (Ronconi 2008), and adult mortality (Jones et al. 2002) have been correlated with shifts in oceanographic conditions, particularly during extreme events such as El Niño (e.g., Gaston and Smith 2001). Recent isotope studies suggest that declines in prey availability have led to shifts in marbled murrelet diet to lower trophic level items than historic populations, and that these shifts may be at least partially responsible for the decline in marbled murrelet productivity (Becker and Beissinger 2006, Becker et al. 2007, Norris et al. 2007). If murrelets are indeed sensitive to marine conditions, then conservation and management strategies need to incorporate both marine and terrestrial requirements; however, most strategies for marbled murrelet recovery are currently aimed at the terrestrial environment (Burger 2000).

In addition to fluctuations in oceanographic conditions and prey availability, anthropogenic threats in marine environments posed by oil spills, by-catch in gill nets, fish farms, coastal urbanization and recreation may have an effect on murrelet populations (Burger 2002, Piatt et al. 2007). Demographic models and marbled murrelet life history show that murrelet populations are sensitive to small increases in adult mortality (Piatt and Naslund 1995), and that population dynamics are most strongly affected by adult survivorship (Beissinger 1995). Because many threats to adults tend to be in the marine environment (Burger 2002), conservation efforts should include marine protected areas and/or regulations governing marine activities in critical murrelet habitat (i.e., areas that are essential for survival, reproduction and population persistence [Murphy and Noon 1991, Hall et al. 1997]).

While huge advances have been made in our understanding of murrelets over the past two decades, patterns of marbled murrelet marine use, particularly in British Columbia, remain a significant information gap. Past research has focused largely on evaluating the effects of terrestrial landscape variables on nest site selection and breeding success (e.g., Nelson and Hamer 1995, Raphael et al. 2002, Zharikov et al. 2006, Malt and Lank 2007). In comparison, fewer studies have examined the physical factors that might explain the spatial and temporal distribution of murrelets at-sea, and serve as good predictors of murrelet marine habitat. Furthermore, we have very little understanding of how terrestrial factors interact with oceanographic processes to produce "good breeding habitat" in coastal British Columbia.

At sea, marine birds typically associate with physical processes that enhance productivity and/or aggregate prey (Hunt et al. 1999, Ballance et al. 2001). Environmental variables such as frontal zones, shelf edges, bathymetry, tidal currents, sea surface temperature and salinity, and river discharge influence primary productivity and prey distribution and abundance in coastal waters (Whitney et al. 2005), and can therefore serve as reliable predictors of profitable foraging habitat (Hunt 1997, Hunt et al. 1998). Marbled murrelet at-sea distributions have been associated with proximity to old-growth forest (Miller et al. 2002, Becker and Beissinger 2003), sandy beaches (Yen et al. 2004*a*, Ronconi 2008) and estuaries (Yen et al. 2004*a*); sea surface temperature (Lougheed 1999, Becker and Beissinger 2003, Yen et al. 2004*a*); stratified water (Piatt and Naslund 1995); water clarity (Day et al. 2003); water depth (Day et al. 2003, Ronconi 2008); and proximity to glacial influence (Day et al. 2003, Yen et al. 2004*a*), though associations vary geographically and by scale. Almost all studies of murrelet marine habitat selection to date utilized survey data, and therefore could not consider reproductive status. Also, only three studies have tracked within-season changes in the factors influencing at-sea habitat selection of marbled murrelets (Lougheed 1999, Speckman et al. 2000, Becker and Beissinger 2003). Given that breeding murrelets are central place foragers, returning to the nest to deliver prey between foraging bouts (Orians and Pearson 1979), one would expect that reproductive status might influence selection of foraging areas, with breeding birds being more constrained in their selection of marine sites than non-breeding birds. Finally, most studies, lacking information on actual nesting location, used distance to contiguous, old-growth forest patches as a proxy for nest site.

The goal of our research was to examine the spatial and temporal patterns of marine habitat selection by breeding and non-breeding marbled murrelets throughout the breeding season, for two environmentally distinct locations in southwestern British Columbia. More specifically, we aimed to 1) compare the relative importance of terrestrial and oceanographic features on marbled murrelet marine habitat selection; 2) examine the effects of sea surface temperature (SST), physical oceanographic features, shoreline characteristics, and distance to nest sites on murrelet marine habitat selection; 3) compare marine habitat selection patterns for breeding and non-breeding marbled murrelets over the breeding season; and 4) examine within-season variation in murrelet-SST associations. This study will assist in developing management strategies for marbled murrelets in British Columbia by examining the factors that influence and predict murrelet marine use at a finer (~1km^2) scale than Yen et al. (2004*a*), and by considering how these factors differ by reproductive status, at two geographically and environmentally distinct areas in British Columbia. This study also is unique in that we consider the effect of distance between known foraging sites and the actual nest sites of breeding birds.

2 METHODS

2.1 Study Areas

We examined marine habitat selection by marbled murrelets over the breeding season (i.e., May, June and July) at two sites in British Columbia: Clayoquot Sound (2000-2002), on the west coast of Vancouver Island (centre 49°13′N, 126°03′W) and Desolation Sound (1998 -2001), located off the Strait of Georgia, on the southern mainland (centre 50°05′ N, 124°45′ W) (Figure 2.1). While the two study sites share a common topography of long fjords, mountains, glacial valleys and islands, they differ substantially in both oceanographic and terrestrial environments. Clayoquot Sound (CS) is located adjacent to open ocean, and is characterized by exposed marine conditions, strong-offshore winds, and upwellings from the continental shelf (Chatwin and Burger 2002). The terrestrial landscape surrounding CS has relatively few major clearcuts or logging roads (Zharikov et al. 2006), and large, undisturbed areas of old-growth forest remain intact (Chatwin and Burger 2002). In contrast, Desolation Sound (DS) is characterized by sheltered coastal conditions with high freshwater runoff (Thomson 1981). The collision of northerly and southerly tides slightly southwest of DS gives rise to confused tidal patterns and weak tidal currents in the northern Strait of Georgia, and allows for substantial summer warming of the sound (Thomson 1981). The terrestrial landscape in DS is highly altered from 70 years of logging, and loss of original old-growth is estimated at ~80% (F. Huettmann et al., University of Alaska Fairbanks, unpublished data). In 2000-2001, murrelet capture and tracking (see section 2.2 below) at the DS study site was extended to include neighboring Toba Inlet (TOBA), a deep fjord characterized by large summer runoff from glaciers and snowfields, and high turbidity (Pickard and Giovando 1960).

2.2 Marbled murrelet data

We collated at-sea telemetry locations from seven site-years of field data gathered by the Simon Fraser University Marbled Murrelet Research Group (SFUMMRG) under the direction of F. Cooke. Field methods are detailed in Hull et al. 2001 and Bradley et al. 2004. In brief, the SFUMMRG captured marbled murrelets on the water from April to early June (1998–1999 in DS; 2000–2001 in DS-TOBA , 2000–2002 in CS), using small boats and a spotlighting and long-handled fishnet technique (Whitworth et al. 1997). Transmitters were attached using a subcutaneous anchor and epoxy (see Hull et al. 2001, Bradley et al. 2004), and the birds were released and monitored daily by helicopter until either the transmitter failed or fell off, or until the bird died or left the area (Bradley 2002, Bradley et al. 2004). SFUMMRG researchers estimated marine locations using directional information from the radio, weighted by signal strength of 1 (lowest) to 5 (highest), to assign the birds to geographical locations. Detection distance from helicopter flights was a minimum of 5km in good conditions (Bradley et al. 2004), and comparisons of estimated radio locations to those obtained by intensive boat surveys in 1998 indicated that the estimated locations were accurate to within ±500m (E. Krebs, Canadian Wildlife Service, personal communication). This resolution dictated the minimum scale at which subsequent data analyses could take place (see section 2.4 below).

To ensure independence of relocations, we eliminated any same day relocations for a given bird from the dataset by retaining either the relocation with the highest signal strength or, in the event of equal signal strengths, the first detection for that day. We also eliminated all detections with a signal strength of 1, as these relocations could only be interpreted as general marine locations and could not be assumed to have an accuracy of ±500m (R. Bradley, PRBO Conservation Science, personal communication). We classified birds as either "breeding" or "non-breeding" (hereon referred to as "breeding status") based on the presence of consecutive 2-day on/off attendance at sea patterns (OP) associated with 24-hour incubation shifts. Bradley (2002) found that extended consecutive 2-day OPs (≥4) were an accurate indication of incubation behavior in marbled murrelets (probability of detecting OP ≥4 by chance was < 1% and <5% for a 75% and 50% detection probability, respectively). Birds that we could not confidently classify as either non-breeding or breeding (e.g., birds with OPs of 3 or birds that had extended periods of absence between consecutive detections) were removed from subsequent analysis. Despite this filtering, it is possible that birds classified as "non-breeders" may have failed early in incubation, or were marked while chick-rearing. We further classified breeding birds as either "pre-breeding" or "incubating and chick-rearing", with the former category representing detections obtained prior to the start of the on-off pattern. We classified any detections obtained greater than 60 days after initiation of incubation as "post-breeding" (Nelson 1997, Lougheed 1999), and eliminated these detections from the dataset due to an insufficient sample size (i.e., low number of post-breeding detections). We then imported the filtered telemetry data into ArcGIS 9.1 (Environmental Systems Research Institute 2003) and created separate point files for pre-breeding (PREBR), incubating and chick-rearing (INC-CHICK), and nonbreeder (NONBR) birds in each month-year, to distinguish between birds that were commuting and not commuting to a nest. Totals of 68, 75 and 36 breeders and 43, 46 and 101 non-breeders were included in analyses for Desolation, Desolation-Toba and Clayoquot study sites, respectively (Table 2.1).

2.3 Habitat Data

We assembled habitat data for the areas, months and years corresponding to murrelet data collection (Table 2.2). We selected environmental variables based on existing knowledge of murrelet and seabird foraging ecology; however, selection of variables also was constrained by availability of data in digital format for the study areas and years.

Sea surface temperature (SST) patterns may be indicative of areas of enhanced or reduced primary productivity (O'Hara et al. 2006, Becker et al. 2007), and have been associated with seabird, forage fish and zooplankton distributions (e.g., Pakhomov and McQuaid 1996, Rutherford et al. 1999, Yen et al. 2004*a*, Abookire and Piatt 2005, Rey et al. 2007). We obtained SST data as monthly composites from the West Coast Regional Node of the National Oceanic and Atmospheric Administration (NOAA). These composites were created by computing median monthly temperature values from night time images obtained by the Advanced Very High Resolution Radiometer on the NOAA series polar orbiting weather satellites, and have a resolution of ~1km^2/pixel (NOAA 2007). Due to cloud cover, as well as interference between thermal energy from the land and sea surface in narrow channels, the SST grids supplied by NOAA contained numerous "no data" pixels, which needed to be estimated before the data could be used in analyses. Because pixels with SST values were not uniformly spaced throughout the study area, and because contiguous areas of "no data" pixels existed, simple interpolation techniques such as nearest neighbor and inverse distance interpolation (Burrough and McDonnell 1998) could not be applied. Instead, we developed a linear model that predicted SST as a function of geographic, oceanographic and freshwater inflow variables (Table 2.3) that have been shown to be related to SST (Thomson 1981, Nezlin et al. 2004); however, the models did not explain a considerable amount of variability in some SST datasets (Desolation, Toba and surrounding area: r^2 =0.14 to 0.79 for different months-years, mean r^2 = 0.50 ; Clayoquot Sound and neighboring areas r^2= 0.10 to 0.67 for different months-years, mean r^2 = 0.35), and therefore this approach did not account for a substantial amount of uncertainty about the missing values. To incorporate this uncertainty in our analyses, we used multiple imputation to assign SST values to "no data" pixels. Multiple imputation (MI) is a robust statistical technique that accounts for natural variability in the data, and incorporates the uncertainty introduced in the results due to estimation of missing-values (Wayman 2003). In the "regression method" for MI, a linear model is fit based on the relationship between observed values of the incomplete dataset and a set of predictor variables. New parameters are then drawn from the posterior predictive distribution $m > 1$ times (typically 3 – 10) to create m complete datasets. The subsequent analysis is then performed m times using each of the complete datasets, and the results are combined using rules developed by Rubin (1987) for calculating estimates and standard errors that incorporate the missing-data uncertainty. We generated 10 imputations of SST for each month-year of the study period using our linear model in SAS (SAS Institute 2004, PROC MI statement; see Appendix).

We included relative tidal speed, depth and slope variables to examine the direct influence of physical oceanographic features on marbled murrelet distribution, independent of the indirect effects these variables may exert via their influence on SST. Hunt (1995: 222) suggested that tidal processes likely dominate the physical mechanisms that influence prey aggregation in the inlets, sounds and narrows of British Columbia. Bathymetric features interact with tidal currents to concentrate prey (Hunt et al. 1998), and to drive nutrient-rich waters and planktonic organisms to the surface via upwelling events (Thomson 1981, Hunt 1995). Also, both prey and predatory species are often associated with certain depths or depth gradients (i.e., slopes) (Yen et al. 2004*b*, Keiper et al. 2005, Ostrand et al. 2005). We obtained relative tidal speed data from M. Foreman (Institute of Ocean Sciences, Sidney, BC) on a variable resolution triangular grid, constructed from a tidal model of the Eastern North Pacific (Foreman et al., Institute of Ocean Sciences, unpublished data). Grid nodes were smoothed to a 300x 300m raster using ArcGIS 9.1. We obtained bathymetric data as contours from Canadian Hydrographic Service Electronic Charts (1:40 000 to 1:80 000 scale) and interpolated these contours to a raster in ArcGIS 9.1 using the "Topo to Raster" tool. We calculated slope in ArcGIS 9.1 as the steepest incline, in degrees, between neighboring cells of the depth raster.

Freshwater input to nearshore marine areas can affect murrelet foraging opportunities in two ways: freshwater inflow influences the SST, sea surface salinity and nutrient composition of nearby waters, and can therefore enhance primary productivity, plankton concentrations and prey aggregations in these areas (Mackas et al. 1980, Thomson 1981, Abookire et al. 2000); however, turbidity from increased freshwater flow, particularly from glacial sources (Thomson 1981), may limit the ability of murrelets to visually locate prey (Yen et al. 2004*a*). The processes that contribute to the amount and type of freshwater runoff differ both seasonally and geographically. As described in Thomson (1981), rivers flowing into most of Vancouver Island's inlets are fed primarily by rainfall. As a result, freshwater input is highest in the winter-spring rainy season, and is lowest in the summer-fall. In contrast, runoff into larger mainland inlets results primarily from snowmelt, and is thus highest in the snow-melt period, beginning in May. During this time, large amounts of glacial silt are carried into the inlets, resulting in high turbidity and a milky-green coloration. Stream data were obtained as a streamline center network (1:50 000) from the British Columbia Watershed Atlas. As proximity to, number, and magnitude of freshwater input sources may influence nearshore marine habitat, we chose to include two variables describing the influence of freshwater inflow to marine areas: distance to the nearest stream mouth and relative freshwater inflow. The latter variable was calculated as the number of streams, weighted by stream order, within a 3km radius. Because marbled murrelets use stream channels as fly-ways to and from nest sites (Nelson and Peck 1995, Manley 1999), proximity of marine foraging areas to stream mouths may be especially important for breeding birds.

Sand lance (*Ammodytes hexapterus*), a primary prey item in the summer diet of murrelets (Piatt et al. 2007), tend to concentrate in areas with sandy bottoms that are free of mud and silt (Robards and Piatt 1999). As we could not locate a comprehensive dataset of bottom types for our study areas, we included distance to sandy beach as a proxy (Ostrand et al. 2005). We obtained shoreline classification data from the Integrated Land and Management Bureau's Physical and Biophysical Shorezone Mapping System

(1:50 000). We extracted shore zone attributes for our study areas in Microsoft Access (Microsoft Corporation 2002), and then joined these attributes to their associated line vectors in ArcGIS 9.1.

We included mean distance from a given sample plot (see 2.4.3 below) to all nest sites in a given year at a given site as our final habitat variable for breeders only, based on the hypothesis that if proximity to nesting habitat influences breeding marbled murrelet use of marine areas, marine areas in closer proximity to nest sites should be selected. We obtained nest site locations corresponding to radio-tagged birds in the murrelet telemetry data file (described above) from the SFUMMRG as ArcGIS shape files, for each year and study site. Nest locations were initially located by helicopter based telemetry of the radio-tagged murrelets, and later, where logistically possible, confirmed by ground crews (see Hull et al. 2001 and Bradley et al. 2004 for details). Bradley et al. (2004) estimated the spatial accuracy of nest sites to be ± 50-60m.

2.4 Model construction

2.4.1 Overview

Radio-telemetry data constitute a form of "presence-only" data, where observed locations are known, and absolute absence locations are not. A common approach to studying resource selection using radio-telemetry involves modeling used locations, defined by attributes at telemetry relocation points, and "pseudo-absences" or "available resource units", defined by randomly selected locations within the available habitat (Manly et al. 2002, Huettmann and Linke 2003, Alexander et al. 2005, Boyce 2006). Several authors have raised concerns about these approaches, including misclassification of used habitat due to telemetry error (Erickson et al. 2001); pseudo-replication (Aebischer et al. 1993) and biases in estimates of resource selection patterns (Erickson et al. 2001, Thomas and Taylor 2006) due to pooling of relocation points across animals; difficulty in defining "available" habitat (Garshelis 2000); and errors in assessing resource selection arising from classification of sites where animals were not detected as "unused" (Graham et al. 2004) or "available" (Rittenhouse et al. 2008). Moreover, binary classification of sites as used/available or presence/pseudo-absence provides little insight into the differential value of used sites (North and Reynolds 1996, Marzluff et al. 2001, 2004, Millspaugh et al. 2006).

Kernel based utilization distributions (UDs) have been used to define animal home ranges for some time, but have only recently been applied to resource selection studies (e.g., Marzluff et al. 2004, Rey et al. 2007). The UD is a probability density function that quantifies an animal or group of animals' relative use of space, over a specific time period, based on point location data (Van Winkle 1975). The height of the UD at any location represents the probability of use at that location relative to other locations within the area covered by the UD (Silverman 1986). The UD for an individual sums to 1, or 100%. We chose to use UDs to quantify marbled murrelet marine use (i.e., our response variable), based on four advantages of the UD method over other approaches to resource selection using radio-telemetry. First, the UD does not require absolute absence data, pseudo-absence data or "available points" (Rittenhouse et al. 2008), as it depicts the probability of an animal occurring at each location as a function of radio-telemetry locations (Marzluff et al. 2001, 2004). Second, error associated with estimation of exact telemetry relocations is reduced, as the UD is a function of all telemetry points (Marzluff et al. 2004). Third, by defining use with a continuous variable (i.e., the probability density distribution) over the animals' range (Millspaugh et al. 2006, Marzluff et al. 2004), the UD provides more information than methods that use simple binary classification systems of used/available or presence/pseudo-absence. Finally, UDs correctly treat the animal or group of animals as the sampling unit (Marzluff et al. 2001, 2004), and circumvents biases arising from an unequal number of telemetry relocations per individual.

Our approach to modeling marbled murrelet marine habitat selection involved 5 steps (Figure 2.2): 1) estimating the UD for each individual murrelet by reproductive status (i.e., PREBR, INC-CHICK or NONBR) in each month-year using a fixed-kernel home range technique; 2) summing the individual UDs for marbled murrelets of the same reproductive status in the same month-year ; 3) measuring the total height of the each of the summed UDs within 1 km^2 sample plots; 4) measuring the habitat values within the same sample plots; and 5) using multiple regression analysis to relate the height of the UDs to habitat attributes.

2.4.2 Estimating the utilization distributions

We used Home Range Tools for ArcGIS (Rogers et al. 2007) to calculate the probability density distributions (i.e., UDs) of individual murrelets, classified by status in a given month-year, using a fixed kernel (Worton 1989, Kernohan et al. 2001) and a least-squares cross validation (LSCV) selected smoothing parameter, as recommended by Gitzen et al. (2006) for clumped distributions. Because telemetry locations were estimated by assigning detections to known geographical locations based on signal strength and direction, numerous points either overlapped or fell within tight clusters, which resulted in failure of LSCV to minimize for several individuals. To correct this problem, we applied a shift to duplicate points and near-duplicate points at a random angle and to a random distance within 50 and 350m, which is within the range of telemetry error (±500m) and should therefore not strongly influence the results of the habitat analyses. Birds of a given status with fewer than three relocations in a given month were eliminated from that month's analyses, as a minimum of three locations is required to create a UD using HRT. For the purposes of this analysis, we were not interested in the size of the foraging ranges, but rather the relative use of marine areas by radio-tagged individuals during the study period. As such, all birds with at least three radiolocations were included in the analyses to maximize the number of individuals included in the study. Furthermore, because only at-sea daytime locations between May and July were used to calculate the utilization distributions, we term these surfaces "summer foraging UDs" rather than "home ranges".

Investigating individual variation in habitat selection was beyond the scope of this study; instead, we were interested in comparing selection between different reproductive statuses. For each study site, we therefore summed the UDs of individual murrelets of the same status in the same month-year to obtain a single UD representing the probability of use by all individuals of a given breeding status within a given month and year (hereon referred to as "MAMU subgroups"), thus treating the subgroups as the categories for analysis.

2.4.3 Sampling the variables

We defined the spatial extent of available resources (i.e., study area) by the area consistently surveyed during helicopter flights (Figure 2.1). We chose to define availability in this manner, as search effort was not uniform throughout the entire 100% UD boundary. Murrelets utilize resources up to 120 km from their nest sites (Hull et al. 2001), and a number of murrelets were found using areas outside the regular survey boundaries on occasional exploratory flights. As such, we believe that the study areas we defined were entirely "available" to all murrelets radio-tagged at each site. Because the survey areas for the Desolation Sound study site differed in 1998-1999 and 2000-2001, however, with the latter years including Toba Inlet, we treated these years separately in all analyses (1998-1999: "DS"; 2000-2001: "DS-TOBA").

We sampled the response variable (height of the UD for a given MAMU subgroup) and habitat variables using a lattice of 1km x 1km plots, which we overlaid on the study area and clipped to include the marine environment only. As a result of the clip, plots that bordered the coast and islands were reduced in size. We later accounted for these differences in sample plot size by normalizing the total height of the UD within each plot by the sample plot size. As we were interested in examining the influence of habitat attributes that act at a local-scale on murrelet marine habitat selection, we chose to use as fine a resolution as possible in selecting our sample plot size. The $1km^2$ sample plot size thus corresponds to the resolution of the telemetry data (±500m), as well as the coarsest habitat data layer (i.e., SST: $1km^2$/pixel). Within each plot, we sampled the following variables using Hawth's analysis tools for ArcGIS (Beyer 2004): total height of the UD for each MAMU subgroup, divided by the number of birds summed in that subgroup (UD-MAMU-SG); average SST, tidal velocity, depth and distance to nest sites; maximum slope; minimum distance to a sandy shoreline and stream mouth; and average number of streams within a 3km radius, weighted by stream order. We measured distance as the Euclidean distance from the center of the sample plot to the feature of interest.

2.4.4 Statistical analysis

We used an information theoretic approach and multi-model inference (Burnham and Anderson 2002) to compare competing models in the candidate set and interpret results. We assembled habitat attributes into one of four groups based on hypotheses about the factors that may influence marbled murrelet marine habitat selection (see Table 2.2); variables in habitat groupings were always included or excluded in candidate models together, reducing the size of the candidate model set and explicitly addressing the hypotheses of interest. We chose to include both linear and quadratic forms of the SST variable group in our candidate set based on a priori hypotheses about potential relationships between murrelet habitat selection and SST (Table 2.2). We arranged MAMU subgroups into nine "MAMU groups" according to study site (CS, DS and DS-TOBA) and status (PREBR, INC-CHICK or NONBR). We included a month and month-SST interaction term in the SST and SST^2 variable groups to examine monthly changes in murrelet response to SSTs over the season, and because monthly differences in the spatial distribution of SSTs were evident from a priori analyses. We considered all additive combinations of the variable groups in our candidate model set as we were interested in: 1) considering the effects of SST, physical oceanographic processes, nearshore characteristics and proximity to nesting habitat on murrelet marine use individually; 2) contrasting the relative importance of each of these variable groups on murrelet marine use; 3) considering additive combinations of these variable groups on murrelet marine use; and 4) using model averaging to calculate the habitat selection function (HSF - Aarts et al. 2008) for each MAMU group. The response variable (UD-MAMU-SG) was log-transformed to meet assumptions of normality and homoscedasticity for regression analyses following examination of the residuals (Rawlings 1988). We calculated the variance inflation factor (VIF) for all habitat variables and found that multicollinearity was not a factor, as individual VIF values were < 10 (Rawlings 1988). Because kernel home range methods (Marzluff et al. 2004), interpolation of habitat variables (Anselin 2002), and natural spatial clumping of resources (Legendre 1993) may induce spatial autocorrelation in measures of resource use, we first fit ordinary least squares (OLS) regression models, and tested for spatial dependence of the residuals using Moran's I analysis in R (R Development Core Team 2008, spdep package). Spatial autocorrelation is problematic in statistical analyses as it invalidates the assumption of independence of errors (Legendre 1993, Dormann et al. 2007). Since Moran's I demonstrated positive spatial autocorrelation of the residuals of the OLS regressions, we used a spatial error autoregressive (SAR) model in R (spdep) to account for spatial dependence of errors. The spatial error model is defined as follows (Fortin and Dale 2005: 230):

$$Y = \alpha + X\beta + \lambda W(Y - X\beta) + \varepsilon$$

where Y is the vector of observations of the response variable; α is the constant term (intercept); X is the matrix of independent (predictor) variables; β is the vector of regression coefficients; λ is the spatial autocorrelation coefficient; W is an $n \times n$ matrix describing the local neighborhood around each 1 km^2 sample plot; and ε is the vector of randomly distributed, independent errors. The spatial autocorrelation component is therefore a neighborhood matrix applied to the difference between observed and expected values (i.e., residual variation) given the predictor variables (Miller et al. 2007). We defined the neighborhood weights matrix (W) by first order (Rook's case) contiguity, as simple contiguity-based neighborhood measures have been found to be more successful than complex distance based methods (Dennis et al. 2002). We constructed the spatial weights matrices in Geoda 0.9.5i (Anselin 2003), and then imported the weight matrices into R for use in the SAR models.

For each MAMU group (e.g., DS PREBR, DS NONBR…etc.), we performed our regression analysis 10 times, once using each of the 10 imputed SST datasets, generating 10 sets of regression estimates for each of the candidate models. We used multiple imputation combining rules, as outlined in Rubin (1987), to synthesize model coefficients and standard errors into a single set of regression estimates for each of the candidate models. We calculated the arithmetic average of the log-likelihoods across the 10 sets to obtain a single log-likelihood value for each candidate model.

For each model, we used the averaged log-likelihood to calculate Akaike's Information Criterion (AIC_c) and contrasted this value to AIC_c of the best model (ΔAIC_c). We also calculated the relative weight of evidence for each model ("Akaike weight", w_i), which can be interpreted as the probability that model i is the best model for the observed data, given the candidate set of models (Burnham and Anderson 2002). We estimated the relative importance of each variable group in predicting the probability density of each MAMU group by summing the w_is over all models in which each variable group appeared. Finally, to reduce model selection bias and uncertainty, we used model averaging (Burnham and Anderson 2002) to calculate the HSF for each MAMU group.

2.5 Figures and tables

Figure 2.1 Map of the Desolation Sound (DS), Desolation Sound/Toba Inlet (DS-TOBA) and Clayoquot Sound (CS) study areas in southwestern British Columbia. Shaded and hatched areas depict core areas surveyed for radio-tagged marbled murrelets.

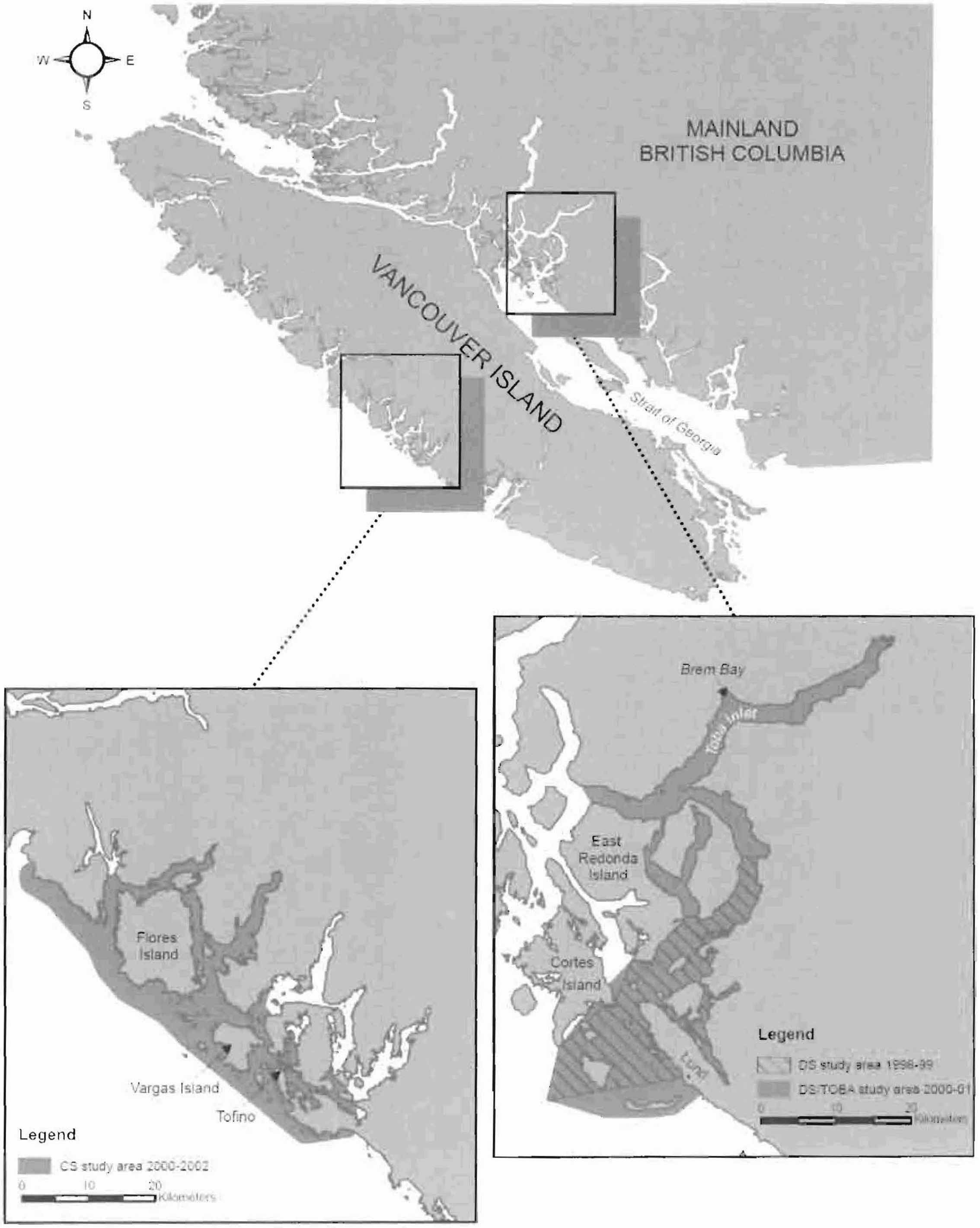


Table 2.1 Number of radio-tagged individuals (n) and average number of relocations per individual (p) included in the analysis of marbled murrelet habitat selection by reproductive status in each month of study, at three sites in southwestern British Columbia. PREBR = pre-breeding birds, INC-CHICK = incubating and chick-rearing birds, and NONBR = non-breeders.

Study Site		**Reproductive Status**					
		PREBR		INC-CHICK		NONBR	
	Month	n	p	n	p	n	p
Desolation							
	May	30	10.0	10	6.5	12	14.3
	June	7	7.9	41	10.7	31	15.3
	July	–	–	42	8.7	27	11.6
Desolation-Toba							
	May	54	13.3	29	7.2	41	13.5
	June	13	9.8	62	10.4	42	18.4
	July	–	–	34	7.1	31	9.9
Clayoquot							
	May	20	9.4	7	7.6	49	8.0
	June	13	10.7	26	9.8	93	19.4
	July	–	–	25	8.6	52	7.0

Table 2.2 Predictor variables included in regression analyses of marbled murrelet marine habitat selection in southwestern British Columbia, 1998 – 2002. Habitat variables were grouped into four suites based on a priori hypotheses about the distribution of marbled murrelets at-sea. Both linear and quadratic forms of the SST variable group were included in the candidate set of models.

Habitat variable	**Description (unit)**	**Variable group (associated hypothesis)**
SST	Sea surface temperature (°C)	SST[a] and SST^2[b]
TIDVEL	Relative tidal speed (m/s)	Oceanography (O)
DEPTH	Ocean depth (m)	Oceanography (O)
SLOPE	Maximum slope between neighbouring depth cells (degrees)	Oceanography (O)
SAND	Distance to sandy shore (m)	Nearshore environment (SH)
STREAMD	Distance to nearest stream outflow point (m)	Nearshore environment (SH)
STREAMF	Number of streams within 3km radius, weighted by stream order	Nearshore environment (SH)
NESTD	Average distance of foraging site to all nest sites (m)	Nesting habitat (N)

[a] The linear SST variable group, defined as follows: SST + SSTxMONTH + MONTH

[b] The quadratic SST variable group, defined as follows: SST^2 + SST^2xMONTH + SST + SSTxMONTH + MONTH

Table 2.3 Predictor variables used for the imputation of missing sea surface temperature values. Data sources are provided, as well as associated hypotheses used in variable selection.

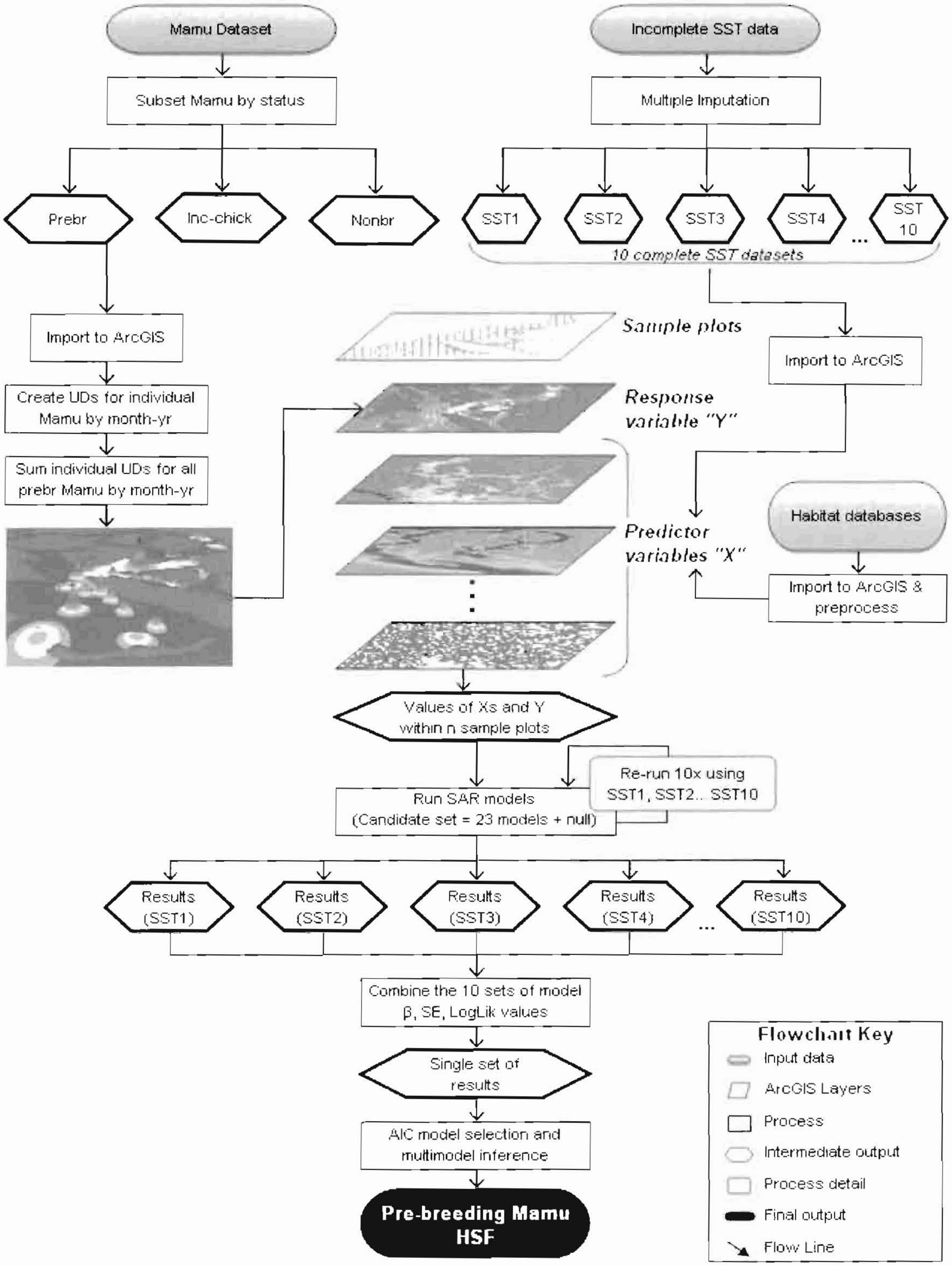
Variable	Data source	Rationale
Geographic		
X		SSTs differ by spatial location; SST dynamics differ in inlets, straits and open ocean and between nearshore areas and open water.
Y		
Land within 5km radius (km^2)	ILMB[a]	
Distance to coast (km)	ILMB	
Oceanographic		
Relative tidal velocity (m/s)	Foreman et al. (unpublished data)	SSTs are influenced by tidal mixing and upwelling; shallow areas may be more prone to warming than deeper waters.
Depth (m)	CHS[b]	
Freshwater input		
Distance to stream (km)	BCWSA[c]	Freshwater inflow, particularly from glacial sources may result in cooler SSTs directly via input and indirectly via mixing of the surface layer.
Relative freshwater flow	BCWSA	

[a] Integrated Land and Management Bureau, BC watershed basemap.

[b] Canadian Hydrographic Service, Electronic contour charts.

[c] British Columbia Watershed Atlas.

Figure 2.2 Flowchart outlining our approach to building a habitat selection function (HSF) of pre-breeding (PREBR), incubating and chick-rearing (INC-CHICK) and non-breeding (NONBR) marbled murrelets (MAMU) at-sea. The flowchart uses PREBR murrelets as an example. The processes outlined were repeated for INC-CHICK and NONBR birds at each of the three study sites (Desolation, Desolation-Toba and Clayoquot; see Figure 2.1). SST= sea surface temperature; UD = utilization distribution; SAR = spatial autoregressive model.



3 RESULTS

3.1 Model selection

The most parsimonious model of marbled murrelet at-sea probability density differed among study sites and reproductive statuses (Table 3.1). However, in general, marbled murrelet marine habitat selection was simultaneously affected by SST and nearshore environment characteristics, as well as distance to nest site for breeders, with lesser influence by physical oceanographic features. Top models explained between 30 and 71% of the variation (Negelkerke r^2) in murrelet at-sea probability densities (Table 3.1). All top models had Akaike weights (w_i) of <0.95, suggesting that interpretation of a confidence set of models would be more appropriate than drawing inference from a single best model (Burnham and Anderson 2002).

All models contained within the 95% confidence set (Σw_i is just > 0.95 – Burnham and Anderson 2002) for all murrelet groups at all sites included the SST^2 variable group. Models that excluded SST^2 had AIC_c difference values (Δ_i) of 25 or more, suggesting that these models were very poor for explaining variation in the response variable. Excluding SST entirely from the models (i.e., linear and quadratic forms) resulted in Δ_i values of 140 or more. Clearly, SST has an important effect on marbled murrelet habitat selection, irrespective of reproductive status and study site.

Distance to nest site appeared in the top model for 5 of the 6 breeding murrelet groups, and was included in all models comprising the confidence set for pre-breeding and incubating/chick-rearing birds at both Desolation (DS) and Clayoquot Sound (CS). Support for distance to nest site was less consistent at Desolation-Toba (DS-TOBA), as only half of the models contained in the confidence sets of breeding birds included this variable group. However, distance to nest appeared in the top 2 of 4 confidence-set models for incubating/chick-rearing birds, but in the bottom 2 of 4 confidence-set models for pre-breeding birds at this site, suggesting that distance to nest site still had an important influence on marine habitat selection by incubating and chick-rearing birds, but only played a minor role in habitat selection for pre-breeding birds at this site.

Nearshore environment characteristics were included in the majority ($\geq 67\%$) of models comprising the 95% confidence set for all murrelet groups at all sites, and were included in top models in almost all cases, with the exception of pre-breeding birds at CS. In contrast, barring non-breeders at CS, oceanographic features were absent from at least half of models included in the confidence sets of all murrelet groups at all sites, and only appeared in the top model for 2 of the 9 murrelet groups (DS-TOBA PREBR and CS NONBR), one of which (DS-TOBA PREBR) had a high degree of model uncertainty (w_i = 0.359).

3.2 Relative importance of variable groups

The relative importance (RI) of the variable groups was assessed by summing the Akaike weights across all models in the candidate set in which the variable group appeared (Burham and Anderson 2002). SST^2 was consistently the most important variable group, receiving a maximum RI value of 1.0 across all murrelet groups at all sites (Figure 3.1). Distance to nest site was equally important for breeders at DS and CS, with RI values of 0.99 to 1.0; however, nest site was slightly less important at DS-TOBA, where RI values were 0.32 for pre-breeding birds and 0.86 for incubating and chick-rearing birds. Nearshore environment characteristics were generally important, receiving RI values ≥0.83 for all murrelet groups with the exception of pre-breeding birds at CS, for which habitat selection was dominated by SST^2 and distance to nest site, and nearshore environment played a minor role (RI = 0.148). Physical oceanographic features were the least important variable group for 8 of the 9 murrelet groups, receiving on average 5 and 3.5 times less support than SST^2 and nearshore environment characteristics, respectively. Oceanographic features showed greatest evidence of importance for CS non-breeders (RI=0.748), but only out-ranked another variable group at DS-TOBA, where physical oceanographic features were slightly more important than distance to nest site in predicting marine habitat selection of pre-breeding birds. The linear form of the SST variable group received essentially no support, confirming that the response to SST was quadratic for all murrelet groups at all sites.

3.3 Variable effects

3.3.1 Nearshore environment, oceanographic features and distance to nest sites

Model averaged coefficients indicated that marbled murrelets were generally associated with areas characterized by higher relative tidal speeds, greater depth, steeper ocean floor slopes, less freshwater inflow and closer proximity to sandy beaches. However, the large unconditional standard errors for some of these variables relative to their coefficients (Table 3.2) suggested that considerable uncertainty existed as to their true relationship with habitat selection for some murrelet groups, particularly for the physical oceanographic variables. Breeding birds usually selected areas closer to nest sites, though there were exceptions. Below, we describe the effects of the non-SST habitat variables on murrelet marine habitat selection at each study site, considering only those features for which the magnitude of the parameter estimate was greater than the magnitude of its unconditional standard error (i.e., $|\beta/SE| > 1.0$). We considered coefficients that were smaller than the standard error to have an uncertain effect.

At the DS study site, marbled murrelets of all reproductive statuses concentrated their at-sea activities in areas with less freshwater inflow, and in closer proximity to stream mouths. Breeders further selected areas that were closer to sandy beaches and nest sites, and incubating and chick-rearing, but not pre-breeding birds, were associated with areas of steeper ocean-floor slopes and greater depths.

Similar to DS, all murrelets at DS-TOBA selected areas that were closer to sand, and that had less freshwater inflow; however, only incubating/chick-rearing birds were associated with proximity to nest. Both incubating/chick-rearing and non-breeding birds selected areas further from streams, while pre-breeding birds selected areas closer to streams. Murrelets of all statuses at this site were associated with areas of deeper water, and only pre-breeding birds were further associated with areas characterized by greater ocean floor slopes.

Incubating/chick-rearing and non-breeding birds at CS showed greater use of areas that had less freshwater flow, and that were further from stream mouths. Non-breeders were additionally associated with proximity to sand, greater relative tidal velocities, greater depths and steeper ocean floor slopes. While incubating and chick-rearing birds selected areas in closer proximity to nest sites, pre-breeding birds were more likely to be located in areas further from nest sites. Pre-breeding birds at this site showed no association with any of the shoreline or oceanographic variables.

3.3.2 Sea surface temperature

Although model selection and variable importance metrics showed that SST was strongly related to marbled murrelet habitat selection, model averaged coefficients indicated that this relationship differed temporally, and among study sites and reproductive statuses (Figure 3.2). At DS (1998–1999), the relationship between breeding murrelets and May SST was bowl shaped, with lower relative probability of use in waters between 11 and 13°C, and selection for waters with SSTs at each extreme. In the same month, non-breeders selected waters with temperatures below ~11°C; this coincided with the lower peak for breeders. Murrelets of all statuses selected areas with cooler SSTs in June (relative probability of use < 0.20 beyond 12.2°C), and concentrated their activities in waters between 13 and 16.5°C (relative probability of use > 0.90) in July, with non-breeders selecting cooler temperatures than breeders.

At DS-TOBA (2000-2001), results of the regression analysis suggested a general pattern of murrelet probability densities that peaked at particular SSTs. Peak SST ranges within each murrelet group generally increased over the season, with highest relative probability densities (>0.90) occurring at temperatures between ~ 10.3 to 12.6°C in May, 13.6 to 16.4°C in June and 14.1 to 16.5°C in July. Non-breeders selected slightly warmer temperatures than incubating/chick-rearing birds in both May and July; however, the highest peak range we observed was for pre-breeding birds in June. The large SE:β ratio for pre-breeding murrelets in May, and incubating and chick-rearing birds in June, suggested considerable uncertainty as to the effect of temperature on habitat selection by these murrelet groups during these months.

At CS, the patterns of selection in relation to SST were generally consistent across murrelet groups: the relative probability of use for all murrelet groups in May exhibited a dome shaped response that peaked in areas with SSTs between 10 and 12°C, with non-breeders again selecting slightly warmer temperatures than breeders. Similar to the DS study site, all murrelet groups at CS showed selection for cooler temperatures in June, with relative probability of use dropping to 0.20 or less beyond 9.8°C. In contrast to June, the relationship between July SST and incubating/chick-rearing murrelet probability densities exhibited a very steep positive slope around beginning at ~ 11 °C. The effect of July SST was uncertain for non-breeders at this site (SE> β).

3.4 Figures and tables

Table 3.1 AIC$_c$ ranking of models describing marine habitat selection by marbled murrelets in summer at three study sites (DS = Desolation Sound; DS/TOBA = Desolation Sound and Toba Inlet; CS = Clayoquot Sound) in southwestern British Columbia. The number of parameters (k), AIC$_c$ differences (Δi), Akaike weights (w_i) and Negelkerke's r-squared (r^2) for models that comprise the 95% confidence set (i.e., Σw_i is just ≥ 0.95) for each group of murrelets are shown. The years of data collection are indicated following the study site acronym.

Pre-breeding					Incubating and chick-rearing					Non-breeders				
Models	**k**	**Δi**	**w_i**	**r^2**	**Models**	**k**	**Δi**	**w_i**	**r^2**	**Models**	**k**	**Δi**	**w_i**	**r^2**
DS: 98-99					**DS: 98-99**					**DS: 98-99**				
SST^2 + SH + N	12	0.000	0.685	0.71	SST^2 + SH + N	15	0.000	0.527	0.55	SST^2 + SH	14	0.000	0.721	0.37
SST^2 + O + SH + N	15	1.909	0.264	0.71	SST^2 + O + SH + N	18	0.339	0.445	0.55	SST^2	11	3.079	0.155	0.37
SST^2 + N	9	5.510	0.044	0.70						SST^2 + O + SH	17	3.816	0.107	0.37
DS/TOBA: 00-01					**DS/TOBA: 00-01**					**DS/TOBA: 00-01**				
SST^2 + O + SH	14	0.000	0.359	0.30	SST^2 + SH + N	15	0.000	0.622	0.48	SST^2 + SH	14	0.000	0.710	0.56
SST^2 + SH	11	0.421	0.291	0.30	SST^2 + O + SH + N	18	1.950	0.234	0.48	SST^2 + O + SH	17	1.793	0.290	0.56
SST^2 + O + SH + N	15	1.253	0.192	0.30	SST^2 + SH	14	3.900	0.088	0.48					
SST^2 + SH + N	12	2.206	0.119	0.30	SST^2 + O + SH	17	4.835	0.055	0.48					
CS: 00-02					**CS: 00-02**					**CS: 00-02**				
SST^2 + N	9	0.000	0.793	0.54	SST^2 + SH + N	15	0.000	0.865	0.35	SST^2 + O + SH	17	0.000	0.682	0.45
SST^2 + SH + N	12	3.535	0.135	0.54	SST^2 + O + SH + N	18	3.764	0.132	0.35	SST^2 + SH	14	2.074	0.242	0.45
SST^2 + O+ N	12	5.196	0.059	0.54						SST^2 + O	14	4.682	0.066	0.45

[a] Models include the following variable groups: Sea surface temperature in quadratic form (SST^2); Nearshore environment characteristics (SH); Physical oceanographic features (O); and distance to nest sites (N).

Figure 3.1 Relative importance of variable groups included in the regression analysis of marbled murrelet marine habitat selection in southwestern British Columbia, 1998 – 2002. SST = sea surface temperature; SST2 = SST in quadratic form; O = physical oceanographic features; SH = nearshore environment characteristics; and N = distance to nest site.

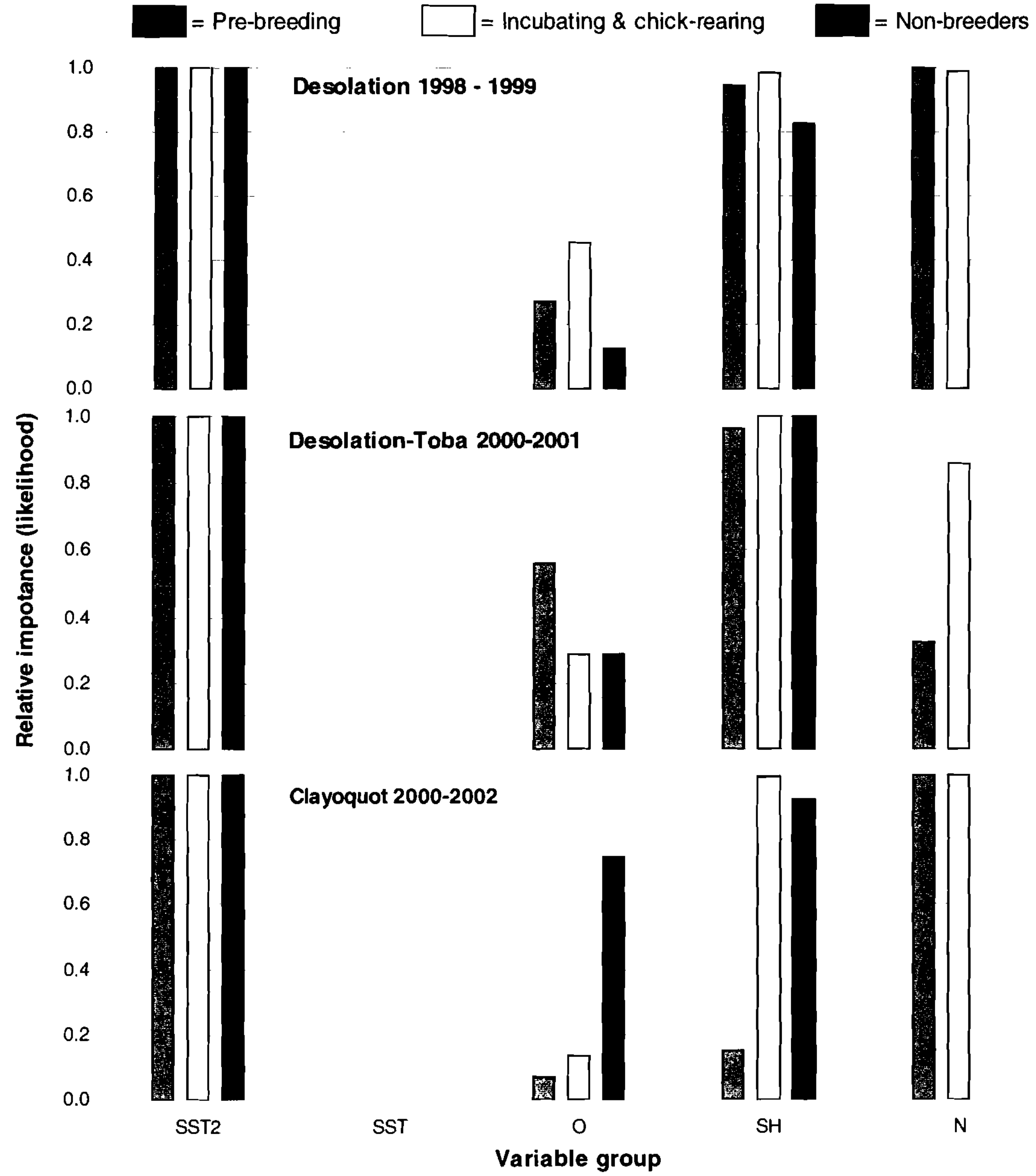
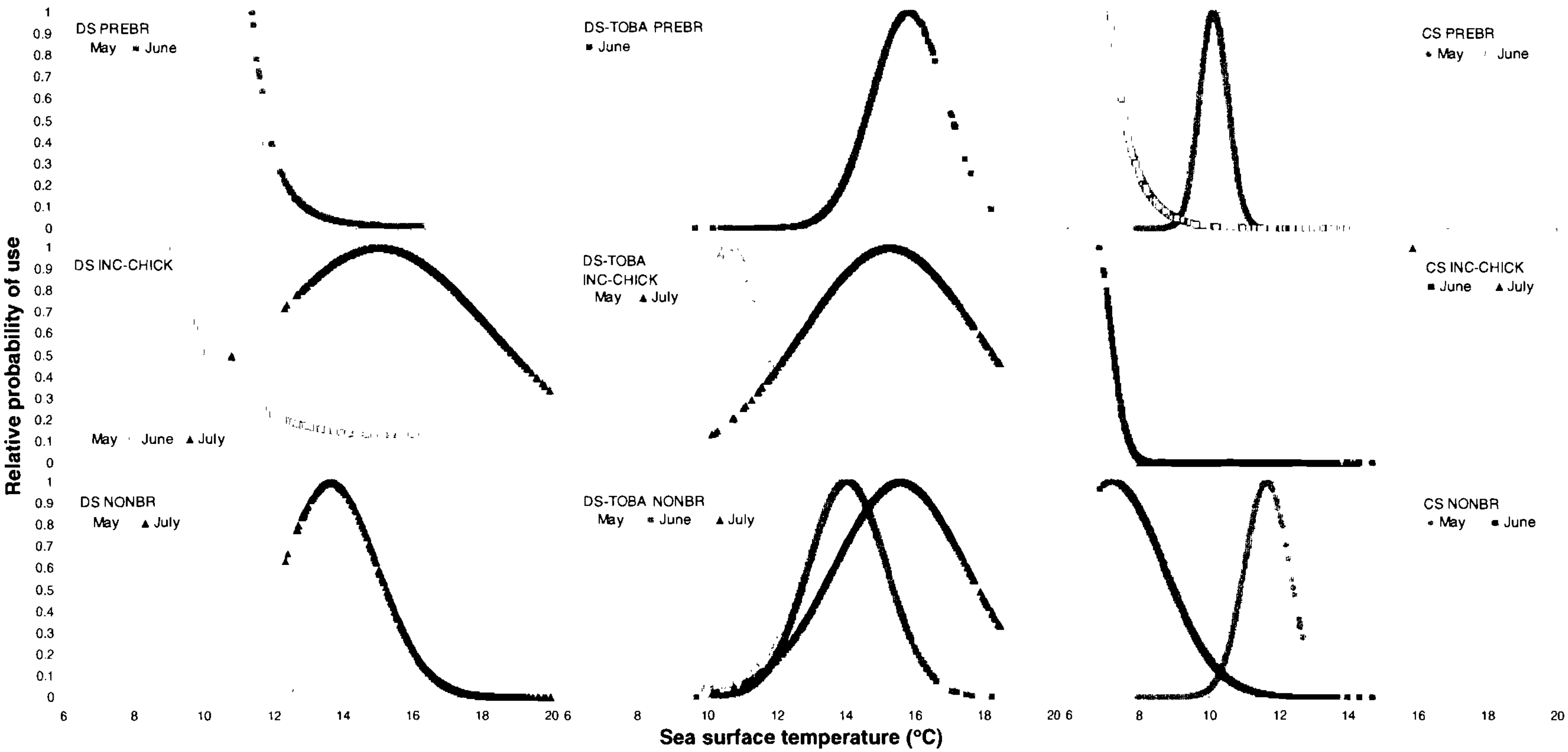


Table 3.2 Regression coefficients (β) and their unconditional standard errors (SE) from model averaged habitat selection functions describing marbled murrelets at-sea in southwestern British Columbia. Bolded βs are greater in magnitude than their respective SE, and shaded βs do not cross zero within their 95% confidence interval. See Table 2.2 for definitions of variable abbreviations and measurement units.

	Desolation: 98-99		Desolation-Toba: 00-01		Clayoquot: 00-02	
Predictor Variable	**β**	**SE**	**β**	**SE**	**β**	**SE**
Pre-breeding						
MAY	**27.5**	18.3	23.2	43.6	**-374.2**	29.6
SSTxMAY	**-3.77**	2.88	-4.75	7.87	**63.6**	6.25
SST^2xMAY	**0.157**	0.114	0.216	0.355	**-3.12**	0.334
JUNE	**53.1**	7.63	**-111.7**	22.6	**-35.0**	10.6
SSTxJUNE	**-5.71**	1.08	**13.9**	3.30	**-2.27**	1.93
SST^2xJUNE	**0.170**	0.040	**-0.436**	0.121	0.037	0.092
TIDVEL	-0.870	0.926	0.497	2.66	0.197	0.391
DEPTH (x100)	0.026	0.030	**0.124**	0.088	0.018	0.081
SLOPE	0.001	0.002	**0.007**	0.006	0.001	0.002
SAND (x1000)	**-0.138**	0.098	**-0.202**	0.080	-0.048	0.084
STREAMF	**-0.175**	0.069	**-0.135**	0.097	0.011	0.023
STREAMD (x1000)	**-0.304**	0.125	**-0.358**	0.150	-0.075	0.095
NESTD (x1000)	**-0.210**	0.039	0.008	0.015	**1.55**	0.059
Incubating & chick-rearing						
MAY	**26.9**	17.2	**-69.8**	58.7	-1352.0	1397.4
SSTxMAY	**-4.33**	2.66	**12.7**	11.2	315.7	318.2
SST^2xMAY	**0.178**	0.103	**-0.592**	0.526	-16.5	18.1
JUNE	**13.7**	6.48	6.09	7.53	**63.8**	59.9
SSTxJUNE	**-1.58**	0.944	-0.787	1.07	**35.3**	12.3
SST^2xJUNE	**0.051**	0.035	0.021	0.040	**-2.59**	0.620
JULY	**-10.6**	4.01	**-18.2**	7.17	**513.1**	66.9
SSTxJULY	**1.46**	0.500	**2.33**	0.900	**-72.6**	12.5
SST^2xJULY	**-0.045**	0.016	**-0.077**	0.030	**3.81**	0.569
TIDVEL	0.155	0.634	0.421	0.779	1.18	2.64
DEPTH (x100)	**0.038**	0.031	**0.033**	0.029	0.800	0.905
SLOPE	**0.002**	0.002	0.001	0.001	-0.006	0.014
SAND (x1000)	**-0.127**	0.061	**-0.398**	0.068	1.03	1.78
STREAMF	**-0.149**	0.043	**-0.119**	0.065	**-1.03**	0.520
STREAMD (x1000)	**-0.168**	0.077	**0.203**	0.118	**5.82**	1.77
NESTD (x1000)	**-0.083**	0.022	**-0.048**	0.031	**-8.11**	0.231
Non-breeders						
MAY	**46.5**	40.9	30.2	30.4	**-167.2**	23.9
SSTxMAY	**-7.06**	6.44	**-7.08**	5.64	**28.1**	4.80
SST^2xMAY	0.253	0.253	**0.367**	0.261	**-1.20**	0.240
JUNE	2.40	19.3	**-82.5**	17.9	**-22.6**	9.49
SSTxJUNE	-0.382	2.84	**11.0**	2.61	**3.39**	1.95
SST^2xJUNE	0.007	0.104	**-0.391**	0.095	**-0.232**	0.099
JULY	**-51.5**	14.0	**-35.1**	9.05	-10.3	11.7
SSTxJULY	**7.27**	1.77	**4.16**	1.22	1.36	2.15
SST^2xJULY	**-0.266**	0.056	**-0.134**	0.041	-0.073	0.098
TIDVEL	0.290	0.566	0.658	1.14	**2.64**	2.10
DEPTH (x100)	0.004	0.020	**0.047**	0.042	**0.578**	0.547
SLOPE	0.002	0.002	0.001	0.002	**0.021**	0.013
SAND (x1000)	-0.005	0.127	**-0.406**	0.104	**-0.450**	0.212
STREAMF	**-0.275**	0.102	-0.039	0.093	**-0.145**	0.068
STREAMD (x1000)	**-0.296**	0.153	**0.272**	0.159	**0.280**	0.237

Figure 3.2 The relative probability of marbled murrelet marine habitat selection in southwestern British Columbia, as a function of sea surface temperature. Graphs are organized by study site (DS = Desolation Sound; DS-Toba = Desolation Sound and Toba Inlet; CS = Clayoquot Sound) and reproductive status (PREBR = pre-breeding; INC-CHICK = incubating and chick-rearing; NONBR = non-breeders). All other covariates were held constant at their mean values when generating lines. Only effects with coefficients greater than their corresponding standard errors are depicted. Solid points represent effects where the 95% confidence interval for the estimate did not cross zero.



4 DISCUSSION

Conservation efforts for the endangered marbled murrelet have largely focused on terrestrial breeding habitat; however, recent studies have suggested that the marine environment is also important in determining the distribution of marbled murrelets, and may be limiting marbled murrelet populations both through interactions with, and independently of, terrestrial habitat (e.g., Meyer et al. 2002, Becker et al. 2007, Norris et al. 2007). As it is generally assumed that animals select habitat so as to maximize survival and reproduction (Block and Brennan 1993, Boyce and McDonald 1999, Manly et al. 2002) patterns of habitat selection likely provide a good indication of habitat quality (i.e., the ability of an area to satisfy these life requirements), and can thus help identify areas of critical habitat (Ronconi 2008). Our results clearly support the role of both marine and terrestrial factors in defining critical murrelet marine habitat, as top habitat selection models across all murrelet groups included components of both ecosystems. Sea surface temperatures (SSTs) were consistently the most important predictor of murrelet marine habitat selection, receiving a maximum relative importance rating of 1.0 across all murrelet groups at all sites. Nearshore environment features were generally important, and appeared in top models for all but one murrelet group. The importance of both SST and nearshore environment most likely reflect associations with prey abundance and availability, as discussed below. Proximity to nest site was also important for breeders, but was more important at Clayoquot (CS) and Desolation (DS) than at Desolation-Toba (DS-TOBA). Birds nesting in Toba commuted further to foraging grounds than birds nesting in DS or CS, largely avoiding Toba Inlet in favor of DS, most likely because of increased turbidity in Toba Inlet due to high glacial runoff (E. Krebs Canadian Wildlife Service, unpublished data, see 4.1.1 and 4.1.2 below). Oceanographic features were generally less important than SST, nearshore environment, and distance to nest site in predicting murrelet at-sea probability densities.

Although this is the first study to describe and compare the relative importance of SST, nearshore environment characteristics, physical oceanographic features and distance to nest site, our results generally support findings of previous studies that examined some of these variables. In California, Becker and Beissinger (2003) found that murrelet marine habitat selection was related primarily to SSTs and distance to nest habitat at a meso-scale, and to SSTs and prey availability at a fine-scale, and that depth was generally less important in explaining variability in murrelet distributions at both scales. However, nearshore features (e.g., substrate, freshwater inflow, distance to streams), tidal speeds, and seafloor slope were not investigated in this study. In Prince William Sound, Alaska, Day et al. (2003) found that the distribution of marbled murrelets was more strongly influenced by SST and shoreline substrate than by water depth. More recently, Ronconi (2008) investigated murrelet at-sea distributions off southwestern Vancouver Island, and found that murrelet habitat selection at a fine-scale was predicted primarily by distance to sandy beaches and sandy substrate, and secondarily by SST in one of three years; depth and slope, though included in the analysis, were not identified as main predictors of habitat selection at a fine-scale. Day et al. (2003) and Ronconi (2008) did not include distance to nest habitat, tidal speeds, or freshwater inflow in their fine-scale analyses. While our results support the findings of these studies, we provide additional insight by describing and comparing the relative importance of all four habitat variable groups on marbled murrelet marine habitat selection in a single-study, at a fine-scale, for two environmentally distinct locations, and across three reproductive statuses.

4.1 Variable effects

4.1.1 Nearshore environment characteristics

Marbled murrelets at all three study sites showed selection for areas close to sandy beaches and with relatively less freshwater inflow. Selection for areas characterized by sandy substrates and/or proximity to sandy beaches is well supported by previous studies of marbled murrelet marine distributions in British Columbia, both at fine (Ronconi 2008) and coarse (Yen et al. 2004*a*) scales, and most likely reflects selection for areas favored by sand lance, *Ammodytes hexapterus*. Sand lance, a primary prey item of marbled murrelets in British Columbia (Burkett 1995, Gaston and Jones 1998), alternate between lying buried in sandy substrate at night, and feeding pelagically in schools during the day (Haynes et al. 2007).

Freshwater runoff on British Columbia's mainland is highest from May to July and originates primarily in glaciers and snowfields, resulting in large amounts of silt being carried into mainland inlets during these months (Pickard 1961, Thomson 1981). Selection for areas with lower glacial influence is consistent with findings of both Yen et al. (2004*a*) and Day et al. (2003) who suggested that the increased turbidity resulting from glacial inflow may limit marbled murrelets' ability to visually locate prey. This mechanism may help to explain the negative relationship that we observed between marbled murrelet probability densities and areas of high-runoff at DS and DS-TOBA; however, we also observed a negative relationship at the CS site, where runoff is predominantly fed by rainwater and peaks from October to June (Pickard 1963). This observation suggests that an additional or alternate mechanism may be driving marbled murrelet selection for areas characterized by lower runoff. High freshwater runoff, particularly in the spring, promotes warming of the surface layers, and enhances vertical stratification with restricted vertical mixing of nutrients (Kaiser and Forbes 1992, Piatt and Springer 2003). This in turn can result in lower marine productivity, and thus reduced prey availability (Kaiser and Forbes 1992, Lougheed 1999). Also, sand lance are most active between temperatures of 10 and 15°C (Winslade 1974), and may vacate warmer areas to move to deeper and/or cooler waters (Kaiser et al. 1991). Sand lance also prefer more saline waters (Abookire and Piatt 2005), and may therefore be unavailable to murrelets in areas where early spring runoff has created warm, reduced-salinity surface layers.

Unlike relative freshwater inflow and distance to sandy beach, the relationship between murrelet at-sea probability densities and distance to stream mouths was inconsistent between study sites. While murrelets at DS chose areas closer to stream mouths, birds at CS chose areas further from streams mouths. At DS-TOBA, the response varied between birds of different reproductive statuses. Although the reason for these differences is uncertain, it may result from a different balance between opposing selection for nesting in areas closer to flyways, but further from freshwater inflow. As such, we suggest that future studies utilize distance to nest site (or nest habitat) and relative freshwater inflow to independently consider these influences.

4.1.2 Physical oceanographic features

Several studies have reported that murrelets are most abundant in shallow waters, typically less than 60m in depth (Piatt et al. 2007). In contrast, the results of this study suggest either no association with depth, or weak selection for deeper waters, with strongest effects at DS-TOBA. Several factors may be responsible for this disparity. First, within deep-water fjords, underwater shelves and sills, mouths of inlets and bays, island passes and bends in the channel can create local upwellings, currents and eddies, which can serve to concentrate prey (Hunt 1995, Kuletz 2005). In Prince William Sound, Alaska, murrelets that foraged within a deep-water fjord were associated with these types of bathymetric and topographical features (Kuletz 2005). This was generally the case for murrelets at DS-TOBA as well, as foraging activities in the deep Toba fjord were concentrated primarily at the mouth of Toba inlet (E. Krebs, unpublished data). Likewise, birds that were associated with deeper waters at DS and CS also were associated with steeper ocean floor slopes (Table 3.2). Second, Ostrand et al. (2004) found that while marbled murrelets forage in shallower areas when high-energy prey are abundant, murrelets are less selective for depth when prey availability is low. Lastly, a recent behavioral analysis of sand lance revealed segregation of age classes by depth, with young of the year selecting deeper waters than 1+ year sand lance (Haynes et al. 2007). Although marbled murrelets target 1+ year sand lance to feed to their chicks, they predominantly feed on young sand lance themselves. Haynes et al. (2007) suggest that murrelets foraging in areas near sandy beaches (as murrelets in our study did) may target deeper waters when foraging for themselves. These findings suggest that depth may not be a reliable predictor of marbled murrelet marine habitat, as associations with depth are influenced by other factors including bathymetric characteristics, prey availability and foraging activity (i.e., chick or self).

The relationship between tidal velocity and murrelet marine distribution is inconsistent in the literature. For example, while Yen et al. (2004*a*) found no associations between tidal speeds and murrelet densities at a coarse-scale in British Columbia, Kaiser et al. (1991) found that murrelets tended to aggregate in strong currents during the latter half of the breeding season in southwestern DS. While our findings are consistent with those of Yen et al. (2004*a*), we acknowledge that our use of median tidal speed values for the season may have prevented us from identifying associations that we might have otherwise detected if our variable for tidal speed had varied temporally. Likewise, future studies may want to consider including not only a measure of the magnitude of tidal speed at a given location, but also variability of speed, as areas with consistently high (or low) tidal speeds may be more important than areas with maximum (or minimum) tidal speeds, owing to predictability.

4.1.3 Sea surface temperature

Previous studies of marbled murrelet-SST associations have shown few consistencies. Although several studies suggest that murrelets associate with cooler SSTs (e.g., Burger 2000, Yen et al. 2004*a*, Ronconi 2008), other studies have reported selection for warmer waters (e.g., Day et al. 2003), or the absence of a trend (e.g., Kaiser et al. 1991). However, in general, past studies have either ignored temporal variation, or considered interannual or seasonal variation only, thus pooling data across months, years and/or reproductive statuses. This pooling could result in masked trends or invalid conclusions if murrelets reverse affinities either over time or between reproductive states (Lougheed 1999, O'Hara et al. 2006, Abraham 2008). We documented both short-term and between-site variation in marbled murrelet-SST associations, and this variation may be the reason for the observed disparities among previous studies. Although we observed selection for cooler temperatures in some months, at some sites (e.g., all reproductive statuses in June in CS), associations with SST in other months were either dome-shaped, suggesting an optimal range of SSTs (e.g., all statuses in July in DS-TOBA), bowl-shaped, with selection for temperatures at each extreme (e.g., DS PREBR and DS INC-CHICK), or lacking entirely (e.g., DS NONBR in June). Other studies that considered short-term temporal variation in murrelet-SST associations also reported variability in SST affinities: Becker and Beissinger (2003) found that the strength of marbled murrelet SST affinities in California varied at the scale of days to weeks, and was dependent on upwelling intensity. Speckman et al. (2000) found that murrelet abundance in southeastern Alaska was negatively correlated with SST in some months and years, but positively correlated in other months and years. In British Columbia, a fine-scale boat-based study of murrelet-SST associations by reproductive status found that while both incubating and chick-rearing birds generally selected cooler temperatures, the relationship was reversed for incubators in one of three years (Lougheed 1999). Seasonal and short-term variation and reversal of SST affinities have also been observed for other seabird species, and likely reflect responses to spatiotemporal differences in prey availability, abundance or quality (O'Hara et al. 2006, Abraham and Sydeman 2006, Abraham 2008). Under this hypothesis, the murrelet-SST associations observed in this study could indicate the favorable SST-range of prey targeted in each month, at each site.

Murrelets are opportunistic feeders (Burkett 1995), and may switch prey as prey availability, abundance or quality changes daily, seasonally or annually (Becker et al. 2007, Ronconi 2008). For example, in central California waters, when krill were more abundant in cool water years, marbled murrelets fed at a lower trophic level prior to breeding than post-breeding; however, in warmer years, when krill were less available, pre and post breeding diets were similar (Becker et al. 2007). Prey switching in response to prey abundance, availability and quality has also been observed for other alcids: Cassin's auklets (*Ptychoramphus aleuticus*) feed predominantly on *Euphausia pacifica* prior to the spring transition to upwelling in California, presumably because these are the most available prey at this time. Following the spring transition, the auklets switch to more energetically favorable juvenile fish, until June, when the fish grow too large for consumption. At this time, the birds switch to *Thysanoessa spinifera*, which are larger and slightly more energy-dense than *E. pacifica* (Ainley et al. 1996*a*, Abraham 2008). Similarly, common murres feed predominantly on euphausiids in early spring, when these crustaceans are most abundant and available due to daytime surface swarming associated with reproductive behavior, but switch to juvenile rockfish in May, when these fish attain an appropriate size for consumption (Ainley et al. 1996*b*). These studies suggest that the diet of opportunistic feeders like murres, auklets and murrelets vary as a function of prey availability, quality and abundance. Furthermore, both euphausiids and forage fish species are known to associate with particular SSTs (Pakhomov and McQuaid 1996, Ware and McFarlane 1995, Abookire and Piatt 2005). Euphausiids, for example, are generally found in areas with relatively cool SSTs (Ware and McFarlane 1995), while sand lance, as mentioned above, are most active between 10 and 15°C (Winslade 1974), a range that coincides with several of the peaks we observed (Figure

3.2). It is thus likely that the strong affinities but temporal variability we observed in marbled murrelet-SST relationships reflects variation in target prey species over the course of the season.

Seabirds-habitat associations also may vary in response to reproductive demands and constraints (e.g., Lougheed 1999, Hyrenbach et al. 2002, Abraham and Sydeman 2006). Optimal foraging theory predicts that birds should forage so as to maximize net energy gain (MacArthur and Pianka 1966); thus, reproduction may constrain incubating and chick-rearing murrelets to different foraging sites than non-breeding birds due to the costs and predation risk imposed by commuting between nest sites and foraging areas, and/or impose increased energetic demands that may alter foraging strategies (Abraham and Sydeman 2006, Vilchis et al. 2006). Also, while adult murrelets consume euphausiids and fish, they only feed their chicks fish, and tend to target larger fish for their chicks than for themselves (Burkett 1995, Kuletz 2005). This provisioning requirement also could lead to changes in habitat selection patterns. However, if changes in murrelet-SST associations were due to the demands or constraints associated with reproduction, the variability that we observed in SST affinities should be greatest between different reproductive groups. This was not the case, as we observed greater variability in murrelet-SST relationships between months at the same study site, and between similar months at different study sites, than between birds of different reproductive statuses at the same site, for which curves were quite similar in any given month (Figure 3.2). Thus, the SST variability observed in this study likely reflects the response of murrelets to temporal changes in prey abundance, availability or quality, rather than constraints or demands imposed by reproduction. Ongoing research in DS supports this hypothesis; isotope analysis has revealed that murrelets at this site feed predominantly on euphausiids in early spring, but by mid-May, euphausiids were almost entirely absent from the diet (M. Janssen, University of Guelph, unpublished data). This pattern was observed for all birds irrespective of breeding status, suggesting that murrelets are more likely taking advantage of high euphausiid abundance, and potentially the availability of daytime surface swarms, early in the season, and switching to fish prey as euphausiid abundance declines with increasing water temperatures (McFarlane et al. 1997). Note however, that we are not suggesting that breeding murrelets do not alter their foraging strategies while breeding. In contrast, it is likely that breeding murrelets, while targeting similar habitat as non-breeders, increase foraging effort to offset costs of commuting to these habitats (Ronconi 2008, E. Krebs, Canadian Wildlife Service, unpublished data). Also, because we subset birds based on their link to a nest site (i.e., searching for nest [PREBR], commuting to a nest [INC-CHICK, or no nest [NONBR]), incubating and chick-rearing birds were grouped together and thus we may not have detected shifts associated with the change in reproductive demands from incubating to chick-rearing (see Lougheed 1999).

4.1.4 Distance to nest sites

With the exception of pre-breeding birds at CS, marine habitat selection by breeding murrelets was negatively correlated with distance to nest site, suggesting that murrelets are either 1) selecting marine areas that are within close proximity of their nesting sites, or 2) choosing nesting sites that are in close proximity of high-quality foraging areas, or balancing both factors. If selection of foraging areas is strongly influenced by commuting distance from a selected nest site, with shorter distances favored (1), we should have observed some dissimilarity in the marine habitat associations of breeding and non-breeding birds. Likewise, if commuting distance does not influence murrelet marine or nesting habitat selection, than we should not have detected any relationship between murrelet at-sea distributions and distance to nest site. In contrast, we observed both a strong negative association between distance to nest site and murrelet at-sea probability densities, and similar habitat and SST associations between breeding and non-breeding birds, suggesting the latter mechanism (2): that proximity of nests to favorable marine foraging areas influences the value and selection of a nest site. Future studies that investigate the spatial overlap between breeding and non-breeding murrelet foraging ranges would help to test this hypothesis.

4.2 Model performance and study limitations

Ecological modeling studies generally recommend that the predictive power of a model be evaluated using an independent data set (Fielding and Bell 1997, Guisan and Zimmerman 2000). This was not possible for our study due the absence of a fine-scale independent set with which to test the effectiveness of the habitat selection functions. In addition, the limited sample size once data had been subset into murrelet groups by month prevented us from further subsetting the data into a calibration (or training) set and an evaluative (or testing) set, as other authors have done (e.g., Becker and Beissinger 2003, Nielson et al. 2004). Collection of an independent set in the future would allow stronger assessment of the predictive ability of our models. Nonetheless, top model fits (r^2) ranged between 0.30 to 0.71 (mean=0.48), suggesting that while the models explained a substantial amount of variation in murrelet habitat selection for some murrelet groups in some months, there are certainly additional variables influencing murrelet at-sea distributions at a fine-scale, which we did not include in our models. In selecting explanatory variables to model murrelet at-sea habitat selection, we focused on abiotic factors that likely influence foraging opportunities, via their affect on either prey abundance, distribution or quality (e.g., SST, sandy beaches, depth, freshwater inflow), or access to foraging sites (e.g., constraint of nest distance). Direct measures of prey abundance would likely reduce the amount of unexplained variation; however, surveys to determine prey distributions are typically expensive and logistically challenging, and therefore difficult to obtain. Likewise, other factors, such as predators (Lougheed 1999, Peery et al. 2006), competition (Burkett 1995, Ronconi 2008) and presence of conspecifics (Fauchald et al. 2000) can also influence habitat selection at-sea, and management strategies should consider the results of this study in combination with studies that have examined these additional factors.

Habitat models have become useful tools for assessing a species' needs; however, accuracy and precision of these models depends not only on the strength of the relationships between the response and predictor variables, but also on the quality of the input data. Accuracy of location estimates remains a major limitation in radio-telemetry studies (Erickson et al. 2001). Our use of fixed kernel utilization distributions (UDs) helped to mitigate some of this error by quantifying the relative use of habitat by a radio-tagged murrelet as a function of all telemetry points obtained for that individual, in contrast to representing use by a single point (Marzluff et al. 2001). Use of UDs also avoided problems associated with assuming that points where animals were not detected were "unused" (Marzluff et al. 2001, Rittenhouse et al. 2008). However, we acknowledge that the transformation of point locations to UDs can also introduce uncertainty into analyses, particularly for individuals with low sample sizes (Marzluff et al. 2004, Millspaugh et al. 2006). In contrast to the response variable, predictor variables were derived from GIS layers and were not measured in-situ. Selection and accuracy of the habitat variables was therefore constrained by the availability and quality of digital data layers for our study areas and years. Spatial uncertainty also can be introduced into variables that are interpolated to grids from point data (i.e., the depth and tidal velocity layers; Barry and Elith 2006); however, given the very fine-resolution and spatial coverage of our input data layers (see Methods), we are confident that any error introduced via interpolation of these layers is minimal. As well, our use of a multiple imputation technique in developing the SST variable allowed us to account for the uncertainty in SST estimates in our final habitat selection models.

While the focus of this study was to examine marbled murrelet marine habitat selection at a relatively fine-scale (i.e., within the summer foraging range), a number of researchers suggest that habitat selection is a nested-hierarchal process, whereby foragers first locate large-scale features likely to be associated with prey patches, and then use finer-scale features to locate habitats within these areas where prey are likely to be aggregated (e.g., Johnson 1980, Fauchald et al. 2000, Weimerskirch 2007). Perception of environment and foraging decisions are thus scale-dependent (Pinaud and Weimerskirch 2005), and patterns of selection and variable effects that exist at one scale may not be observed, or may differ, at another (Burger 2002, Meyer et al. 2002). As such, we suggest that the results of our analysis be considered within the context of findings at coarser scales to accurately identify areas that are critical to murrelets.

4.3 Management implications and recommendations

Marbled murrelets selected marine habitat based on a combination of features from both terrestrial and marine environments, suggesting that management of murrelet populations should include strategies that not only target both ecosystems, but that integrate them. Both SST and distance to nest site variable groups dominated habitat selection by breeding murrelets, suggesting that availability of suitable nesting habitat within proximity of profitable marine foraging areas is critical for this species. While this has been assumed to be true, our data confirm it formally for the first time and provide some quantification as to the relative importance of these variables. This finding has important implications for murrelet conservation: marbled murrelets, like other long-lived seabirds, are fixed investors, and may reduce parental investment or forgo breeding if their own survival is jeopardized (Navarro and Gonzalez-Solis 2007). As such, decreases in availability of suitable nest sites in proximity to productive marine foraging areas, and/or declines in foraging conditions or access to foraging sites, could result in murrelets opting not to breed or making fewer provisioning trips to the nest, which could affect chick survival. As such, designation of critical areas for murrelets must simultaneously consider both marine and terrestrial habitats, as failure to do so may be detrimental for conservation of this species.

Given the obvious importance of access to profitable marine areas for both breeding and non-breeding murrelets, conservation will require the maintenance and perhaps restoration of marine habitat quality (Norris et al. 2007), particularly in areas where prey resources are scarce or declining, or where anthropogenic activities overlap with critical foraging areas. Due to the reduction and fragmentation of old-growth forest habitat, conservation efforts for the marbled murrelet have mainly targeted the terrestrial nesting environment; however, marine factors including oil spills, coastal development, bycatch and disturbance from vessels and pleasure craft are all recognized, though largely understudied, threats to murrelet populations (Burger 2002, Piatt et al. 2007). Knowledge of the magnitude of anthropogenic impacts at-sea on murrelet demographics is incredibly limited; future studies should therefore focus on quantifying marine threats so that appropriate strategies to mitigate these impacts can be applied. Both DS and CS are popular boating destinations during the summer season, and because murrelets exhibit negative relationships to boat traffic (Kaiser et al. 1991, Speckman et al. 2004, Bellefleur et al. 2007), boating tourism may negatively impact the ability of marbled murrelets' to feed in these areas during the breeding season, and thus deserves attention in management strategies.

While basin-wide studies such as Yen et al.'s (2004*a*) are useful for understanding large-scale trends in murrelet marine habitat selection, our study suggests that strong fine-scale habitat associations also exist, which should be used to define critical areas at a local-scale. Desirable murrelet marine habitat at our study sites generally consisted of areas that were close to sandy beaches, that received less freshwater inflow, and, for breeders, that was in close proximity to nesting habitat. Robust relationships such as these, which are consistently detected across geographical areas, can help guide protected area strategies; however, while simple "rules of thumb" are feasibly attractive, local-scale differences need to be considered for management to be successful. The range and combination of habitat conditions to which murrelets are exposed varies throughout their range, and as such, the combination of variables to which murrelets respond also will vary between geographical areas, as the SST-murrelet relationships in this study clearly indicate. While this study has taken an important step towards resolving uncertainty about marbled murrelet marine habitat selection, future habitat selection studies in different regions will further aid in defining murrelet marine habitat suitability, so that appropriate reserves can be sited.

In addition to spatial variability, our study provides evidence for short-term temporal variation in habitat selection. Marine environments are highly dynamic; prey abundance and availability change over relatively short time periods (Suryan et al. 2002, Weimerskirch 2007) and, as suggested by the temporal variability we observed in murrelet-SST associations, murrelets may respond to these changes by adjusting their foraging tactics. Although the direction of the murrelet-SST relationships was highly variable, SST was an important predictor of desirable murrelet marine areas across all groups and study sites. As SST is often closely correlated with the abundance and distribution of prey species (Baird 1990), this suggests that murrelets are closely associated with prey availability and abundance. A better understanding of the mechanism that is driving the observed variability in SST affinities may help us to understand how murrelets might respond to oceanographic variation and changes in prey distributions, which in turn can help guide protection strategies. This will require further studies that investigate murrelet foraging behavior in response to prey availability, composition and abiotic indicators such as SST. Policies aimed at conserving critical marine areas for marbled murrelets may also require unique strategies that accommodate these temporal shifts, such as spatiotemporal closures of critical marine areas, or dynamic marine-zone boundaries (Hyrenbach et al. 2000, Louzao et al. 2006).

APPENDIX – MULTIPLE IMPUTATION TECHNIQUE FOR MISSING DATA

Multiple imputation (MI) is a simulation technique used for "filling in" missing data values, while accounting for the uncertainty due to estimation of these missing values in subsequent analyses (Rubin 1987, Schafer and Olsen 1998). MI is therefore advantageous over single imputation techniques that ignore this uncertainty, and thus lead to underestimated variance estimates and higher rates of Type 1 error (Schafer and Olsen 1998). Also, unlike bootstrapping, multiple imputation achieves a high level of efficiency with only a small number of imputations, typically between 3 to 10 (Schafer 1999, Schafer and Olsen 1998).

Multiple imputation is a three step process: In the first step, missing values are "filled in" $m>1$ times with estimated values. Next, each of the m datasets are analyzed separately, as if there were no missing values. Finally, the results of the m analyses are combined using rules developed by Rubin (1987), which account for the uncertainty associated with the imputation, to produce one overall set of estimates (Horton and Lipsitz 2001). These steps, simplified from Horton and Lipsitz (2001) and Schafer (1999) and placed in the context of a single incomplete SST dataset (e.g., July 1998), are detailed below.

One approach to the imputation step (first step above) is the regression method. Using this method, a linear model:

$$SST_{obs} = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \ldots.. \beta_iX_i$$

was fit using observed values of the incomplete SST dataset (SST_{obs}) and a set of covariates (X_1, $X_2 \ldots X_i$) as outlined in Table 2.3. Based on the fitted regression model, new parameters (β^*) were drawn (i.e., simulated) from the posterior predictive distribution of the parameters m=10 times, and missing values (SST_{miss}) were replaced by:

$$SST_{miss} = \beta^*_0 + \beta^*_1X_1 + \beta^*_2X_2 + \beta^*_3X_3 + \ldots \beta^*_iX_i + \sigma^*\varepsilon$$

where σ^* is the estimate of variance from the model and ε is a simulated normal random variate. To ensure that the imputed SST values were consistent with seasonal sea surface temperatures at each of our study sites, we set maximum and minimum values for the estimates (i.e., bounded prior). Once the m imputed datasets were created, the statistical analysis was conducted separately for each dataset as if there were no missing data (step 2). In our case, the spatial autoregressive (SAR) models were run m=10 times, once using each of the 10 imputed SST datasets. This yielded 10 different sets of estimates for each of the habitat selection models in the candidate set. The estimated coefficients and standard errors from each of these 10 sets were then combined using rules developed by Rubin (1987), to obtain a single set of estimates. Specifically, the overall regression coefficients ($\overline{Q}$) are calculated as the arithmetic average of the m estimated coefficients (Q_i):

$$\overline{Q} = \frac{1}{m}\sum_{i=1}^{m} Q_i$$

The total variance of $\overline{Q}$ consists of two components: the within-imputation variance ($\overline{U}$), which is the arithmetic average of the m individual variance estimates (U_i):

$$\overline{U} = \frac{1}{m}\sum_{i=1}^{m} U_i$$

and the between-imputation variance B, which is the variance of the estimated coefficients:

$$B = \frac{1}{m-1}\sum_{i=1}^{m} (Q_i - \overline{Q})^2$$

The total variance (T) is then calculated as:

$$T = \overline{U} + (1 + \frac{1}{m})B.$$

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