

THE INFLUENCE OF BREEDING STATUS AND NEST SITE LOCATION ON MARINE HABITAT USE BY MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS*

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ABSTRACT

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The Marbled Murrelet *Brachyramphus marmoratus* is a threatened seabird that relies on old-growth forest for nesting. We compare marine space use between breeding and non-breeding birds, and how marine home range locations and overlap vary with respect to nesting location and breeding status. We collected very high frequency (VHF) radio-telemetry data in southern British Columbia from Clayoquot Sound (190 birds; 2000–2002) and Desolation Sound (206 birds; 1998–2001). The sites differ strongly in their oceanic exposure and surrounding terrestrial features. Kernel utilization distribution-based estimates showed that breeders and non-breeders had similar overall distributions, but breeders were more spatially aggregated. Pooled home ranges of non-breeders were larger than those of breeders, but the distributions of individual home range sizes did not differ significantly by breeding status. However, compared with non-breeders, breeding murrelets were more likely to share their home range with other breeders. Home range sizes were larger and commuting distances were longer at Desolation Sound than at Clayoquot Sound; the average home range size for individuals was 241 ± 6.7 km² at Clayoquot Sound and 330 ± 8.8 km² at Desolation Sound. Individuals that nested closer together were more likely to share their marine home range in Desolation Sound, but not at Clayoquot Sound. Commuting distance to a nest site was not related to home range size at either site. Our results support the hypothesis that, at a local scale, breeding murrelets congregate at specific foraging areas and are not strongly constrained by commuting distance to nesting locations. Our results also support the concept that home range size may be indicative of the overall habitat quality of an area. We quantify connectivity between terrestrial and marine habitats and highlight important historical foraging locations.

Key words: *Brachyramphus marmoratus*, VHF telemetry, marine home range, utilization distribution, British Columbia, spatial, nesting, breeders, non-breeders

INTRODUCTION

Seabirds are one of the most threatened groups of birds on the planet (Birdlife International 2018, Dias *et al.* 2019). They are susceptible to changes in marine habitat for foraging and terrestrial environments for rearing young (Dias *et al.* 2019). As they spend most of their lives on water, marine spatial planning initiatives such as marine protected areas, recommended shipping routes, and emergency first response areas due to oil spills are imperative for their protection (Canada 2021). The identification of marine Critical Habitat for Marbled Murrelets and other seabirds is required under the Canadian Species at Risk Act (ECCC 2021). Space use metrics, including home ranges (Worton 1989) and hotspot analyses (Hazen

et al. 2013), serve as tools to quantify marine habitat use as a basis to gauge threats. At-sea survey data have often been used to build home ranges and hotspot maps (Smith *et al.* 2014). In this study, hotspot maps reflect marine areas that are frequently used by individuals or groups. Although at-sea surveys are effective for species-level inferences, they are much less effective for quantifying and interpreting intraspecific variation. Consequently, our ability to investigate differences between breeding and non-breeding populations, and differences in individual space use and interactions, is often lacking.

Here we focus on marine habitat use by nesting Marbled Murrelets *Brachyramphus marmoratus* (hereafter, “murrelets” or MAMU), a

North Pacific-nesting alcid, which is listed as Threatened in Canada (ECCC 2021) and the USA (Washington, Oregon, California; Felis *et al.* 2020) primarily due to loss of coastal old-growth forest nesting habitat in most of its range south of Alaska, USA. Murrelet populations are declining in the largest population in the southern part of their range in Washington (4.1%/yr, 2001–2020), but not in Oregon or California (McIver *et al.* 2022). Long-term population declines (3.8%/yr, 2000–2015) are evident in the South Mainland Coast Conservation region of British Columbia (which includes Desolation). This is not the case on the West and North Coast of Vancouver Island (1996–2017, which includes Clayoquot; Drever *et al.* 2021). Population declines in Alaska are evident at some locations (Piatt *et al.* 2007), but not where home range size has been estimated with telemetry, and the species is not currently listed in Alaska under the Endangered Species Act.

In contrast to most seabirds, which make central place foraging trips from a colony, murrelets nest solitarily at low densities, primarily in old-growth forests. Therefore, their central place foraging is from the nest site. At the landscape scale, suitable murrelet nesting and marine foraging areas are clearly spatially related (Meyer *et al.* 2002, Yen *et al.* 2004, Raphael *et al.* 2015). At a finer scale, it is unclear how the foraging locations of breeding birds are influenced by proximity to nesting habitat, or vice versa (Becker & Beissinger 2003, Barrett 2008, Pastran *et al.* 2021). Although shorter commuting distances require less energy and are likely safer to access (i.e., there is less exposure to aerial predators; Hull *et al.* 2001), some murrelets regularly bypass physically suitable habitat and commute up to 145 km from foraging areas, presumably to acquire nest sites that are protected from nest predators (Zharikov *et al.* 2006, Zharikov *et al.* 2007, Hébert & Golightly 2008, Barbaree *et al.* 2015, Lorenz *et al.* 2017). If commuting distance or diet are key considerations for nest selection, we would expect differences in the marine distribution patterns of breeding and non-breeding murrelets, particularly when breeders are feeding chicks. Dichotomy was observed when Hébert & Golightly (2008) found larger home ranges for non-breeders, especially males, for murrelets breeding in northern California. No statistical differences in marine home range size with respect to breeding status or sex was reported from studies in the Strait of Juan de Fuca, Washington (Lorenz *et al.* 2017) or southeast Alaska (Barbaree *et al.* 2015), but in both studies, the mean home range size was larger in non-breeders compared to breeders (differing by 6%–41%, in different samples).

In this paper, we examine marine home range sizes and locations of murrelets that were radio-tracked at two locations in southwestern British Columbia between 1998–2002. We quantify marine home range attributes of breeders and non-breeders with Kernel Density Estimation-based Utilization Distributions (UD) maps (Van Winkle 1975) based on very high frequency (VHF) radio-telemetry datasets and calculate commuting distance for birds from known nest site locations. We quantify spatial overlap between individuals with respect to geographical location and breeding status, compare proximity between nesting locations and spatial overlap, analyze commuting distance in relation to marine home range size, and compare and contrast home range sizes between study sites.

Assuming that nesting locations affected foraging locations and that central place foraging from the nest site constrained home ranges, we expected (1) that breeders would have smaller marine home ranges than non-breeders. As a corollary, we predicted (2)

less spatial overlap between breeders than non-breeders. Assuming that commuting distance is a consideration with respect to foraging and/or nest site locations, we hypothesized (3) that there should be a spatial relationship between home range overlap and the distance between nest sites, such that breeders nesting closer together would also share marine areas more than those nesting further apart. Finally, because the commuting distance to an individual's nest would covary with marine home range size, those nesting farther away would, in theory, have decreased time and energy to forage (Orians & Pearson 1979, Hunt *et al.* 1999). Therefore, we predicted (4) that those nesting farther inland would have smaller marine home ranges than those nesting closer to shore.

METHODS

Study area

We conducted our study in southern British Columbia in two murrelet conservation regions (Mather *et al.* 2010): Clayoquot Sound (Clayoquot; 49°13'N, 126°03'W) in the West and North Vancouver Island Conservation Region, and Desolation Sound (Desolation; 50°05'N, 124°45'W) off the Strait of Georgia, adjacent to the Southern Mainland Coast Conservation Region (Fig. 1).

Clayoquot, on the outer coast of Vancouver Island, is exposed to the open Pacific Ocean and has numerous small islands, inlets, and temperate rainforest watersheds (Burger & Chatwin 2002). In this area, surface currents occur over the continental slope, with upwelling in the spring/summer and downwelling in the fall/winter (Hourston & Thomson 2018). The terrestrial area has been largely undisturbed by forestry, with large patches of old-growth forest present (Zharikov *et al.* 2006).

In contrast to Clayoquot on the “outside,” Desolation is on the “inside,” connected to a semi-enclosed shallow, inland sea—the Strait of Georgia—between Vancouver Island and the mainland (see Thomson 2014, 2021). The Strait of Georgia is connected to the Pacific Ocean at its northern and southern boundaries and has extensive freshwater input from many rivers and streams, including the Fraser River. Desolation is in the northern region, where tidal and wind mixing are the least vigorous. It contains islands, steep-sided valleys, and sheltered waters with fjords. It has been extensively logged, particularly at low elevations, and during the study period it was estimated that ~80% of old-growth forest had been harvested (Zharikov 2016). Desolation experiences heavy seasonal use by recreational boaters due to its accessibility, close proximity to urban areas, and unusually warm waters in summer.

Marine radio-telemetry data

We used at-sea telemetry locations gathered from the Clayoquot (2000–2002) and Desolation sites (1998–2001) by researchers from the Centre for Wildlife Ecology (CWE) and Simon Fraser University (Hull *et al.* 2001, Bradley 2002, Bradley *et al.* 2004, McFarlane Tranquilla *et al.* 2005, Barrett 2008). These locations have now been synthesized and posted on Movebank (Cooke *et al.* 2022a, 2022b). See below for a description of how we distinguished between breeders and non-breeders. Tagging was primarily undertaken to locate a random sample of nest sites used by birds captured on the water, as opposed to locating nest sites via difficult and terrain-biased terrestrial searches (Zharikov *et al.* 2006). Between April and early July, birds were captured at night from small boats using

a “dip-net” technique (Whitworth *et al.* 1997). Captured birds were fitted with radio transmitters with a subcutaneous anchor (Advanced Telemetry Systems, Isanti MN-Model 394 in 1998 and Model 386 in 1999–2002) and released. In addition to locating nests, field crews also obtained geographical location fixes while birds were

at sea. Radio-tagged birds were monitored daily during helicopter flights ranging in altitude from 300–1 500 m, dependent on weather conditions. In addition to flights, researchers conducted scans from land to save on flight time, and from boats when opportunities arose (Hull *et al.* 2001, Barrett 2008). The marine locations of tagged birds

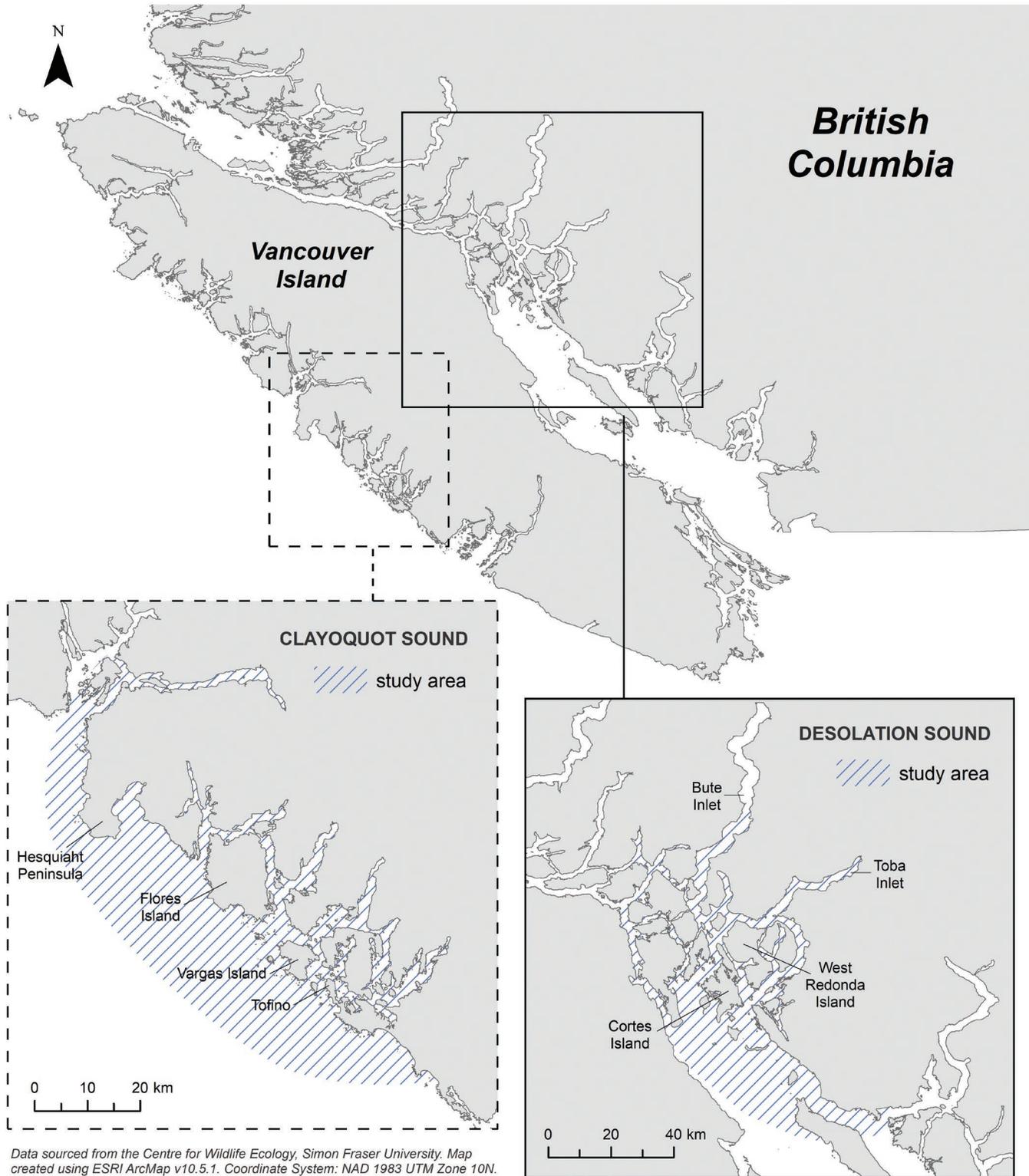


Fig. 1. Map of southern coastal British Columbia, Canada, with two study sites, Clayoquot Sound (Clayoquot) and Desolation Sound (Desolation) marked. Blue shaded area indicates area surveyed for relocations of radio-tagged Marbled Murrelets *Brachyramphus marmoratus*.

were assessed using directional information from radio signals, with a weighted signal strength of 1 (lowest) to 5 (highest), to designate geographical locations. Researchers compared a subset of aerial fixes with those recorded from boat surveys; a procedure that indicated the aerial telemetry-estimated locations were accurate within 500 m (Barrett 2008). Nighttime captures were done in Desolation between 19 April and 17 June, and in Clayoquot between 28 April and 29 June. Five additional birds were caught at Clayoquot in the first week of July 2002.

Nest site locations

Nests of radio-tagged birds were located during separate inland flights (Bradley *et al.* 2004). These flights ranged from 1500–3000 m in altitude, and distance detections in good weather exceeded 10 km. When an inland signal was detected, the location of the signal was fixed to an area $\sim 100 \times 100$ m in size. Where possible, ground-based telemetry was subsequently used to locate the nest tree in which the radio-tagged bird was incubating. However, some nests were inaccessible from the ground because they were located in or adjacent to steep and dangerous terrain or were too distant from suitable helicopter landing locations (Bradley *et al.* 2004). Details and photographs of the nests are available on the Center for Wildlife Ecology website (<http://www.sfu.ca/biology/wildberg/mamuweb/welcome.htm>).

Data processing and selection

We processed data in R version 4.0.3. The datasets included individual identification numbers, location coordinates, date and time, and the signal strength of all adult murrelets detected on the water. The breeding season each year was defined as the period between first and last breeding classification dates inclusive. To compare home range areas between breeding and non-breeding birds, we restricted our analyses to these time frames. At Clayoquot, the temporal range used was between 01 May and 11 August, and at Desolation we used dates between 25 April and 05 August. To ensure spatial similarity of survey effort, we restricted observations to the areas in Clayoquot and Desolation that were consistently surveyed in all years, based on known helicopter tracks. At Desolation, however, researchers expanded their murrelet capture and search at the beginning of the 2000 field season to include Toba Inlet, which we included in our analysis that year.

We filtered the dataset to exclude point relocations with unknown signal strength or a weak signal strength, which we defined as a value of 1 on the 1–5 signal-strength scale attached to locations in helicopter and boat-based telemetry (Lougheed *et al.* 2002, Bradley 2002). To ensure independence of observations, individuals with multiple same-day relocations were filtered to include only one randomly selected relocation point per day. Both the pooled and individual analyses were limited to data from individuals with ≥ 5 filtered relocation points. Our data filtering resulted in all non-breeders tracked in 1998 and 2001 being omitted at Desolation. Therefore, these years were not included in the comparative analysis between breeding statuses. All available data were used in other analyses. The larger discrepancy between breeding and non-breeding bird numbers in Desolation was a direct result of this filtering process. During the initial study, a more concentrated effort was made to track the breeding birds, so signal strength and number of relocations are generally higher for that group, at that location.

Determining breeding status

We knew the locations and discovery dates of located nests. Locating murrelet nests is notoriously difficult. Therefore, when classifying relocations of individuals as “breeding” and “non-breeding,” we not only utilized confirmed nesting sites, but we also applied a behavioral algorithm developed by Bradley *et al.* (2004) to aid in nest classification. The classification algorithm extracted consecutive 2-d on/off attendance of at-sea patterns associated with murrelets’ 24-hr incubation shifts. We used the first recorded on/off pattern in a given year to indicate when nesting was initiated. Relocations of individuals who displayed this consecutive on/off pattern four or more times were labeled “breeding,” and those individuals who did not display this pattern were labeled “non-breeding.” It is possible that our dataset contained a few early breeders that completed their incubation cycles before capture, especially for the later captures. This is a possible source of error when categorizing breeding versus non-breeding birds. The incubation period for murrelets can range from April to August (Hammer & Nelson 1995, Lougheed *et al.* 2002, McFarlane Tranquilla *et al.* 2005). Because there was a level of uncertainty for those individuals who displayed the on/off pattern fewer than four times—with the possibility of being mislabeled as “non-breeding” after the initial algorithm was applied—individuals labeled as “non-breeders” were cross-checked with the nesting database to reduce the likelihood of identifying an individual as a non-breeder incorrectly.

Foraging distribution, marine home range, distances, and spatial overlap modelling

To describe the spatial area used by a murrelet over time, we used kernel-based utilization distributions (UDs), which are two-dimensional relative frequency distributions for the points of location of an animal over a given time frame (Van Winkle 1975). We used a grid size of 1 km² to calculate the UD. Using the UD values created from filtered relocation points on the water, we built UD maps for pooled datasets of breeders or non-breeders in each year. To explore relationships between nest site locations and marine habitat use, we also built UD maps for each individual breeder with a confirmed nesting site at Clayoquot and Desolation (Appendix 1, available on the website). We saved the UD maps as rasters and projected them onto ArcGIS Pro using a *percent clip* stretch type. Areas with a higher number of relocations are highlighted using this method, and we refer to these areas as “hotspots” for the maps representing individuals and also for pooled data.

UDs are widely used for home range mapping in ecology (Worton 1989, Fieberg & Kochanny 2005). Because we aimed to reduce the fragmentation in the marine home ranges (Kie *et al.* 2010), a bandwidth of 3 km was chosen after a series of visual trials. To minimize over-smoothing, we chose the lowest value that would minimize the fragmentation of the polygons. We used the UD to extract the pooled and individual 95% marine home ranges, recorded in km². This 95% value is frequently used in seabird-related ecological studies to measure the area of active use (Soanes *et al.* 2013). Pooled and individual UD maps were calculated using *KernelUD*, and 95% home range contours were obtained using the *getverticeshr* function, both through the “adehabitatHR” package in R. Finally, we clipped out land areas within the polygons to generate marine home range sizes.

We calculated the commuting distance between marine home ranges and nesting sites, as well as distances between distinct nesting sites. We defined commuting distance as the mean shortest linear distance between relocation points and corresponding nest site (Hull *et al.* 2001). For distances between nesting sites, we calculated the shortest linear distance between all possible combinations of nesting sites that were located within the same year. We calculated the most direct linear flight path from the water to nesting sites. Murrelets often use and fly over water bodies such as inlets to minimize energy costs (Peery *et al.* 2009). We did not have enough information on observed flight paths for all the nesting locations to plot these more complicated routes, and therefore our calculated commuting distances should be considered relative indices of the distances flown by a given bird.

Lastly, we computed the volume of intersection (VI) of utilization distributions to measure spatial overlap (Fieberg & Kochanny 2005) between individual home ranges that occurred in the same year. The VI index provides a single measure of overlap, with 0 indicating no overlap and 1 indicating complete *getverticeshr* overlap. We calculated VI using the *kerneloverlaphr* function in R. This function uses the relocation points of individuals and set bandwidth to calculate the VI value between animals from their full 95% home ranges, including land areas.

Statistical analysis

Modeling was done in R 4.0.3 using the “*glmmTMB*” package (Brooks *et al.* 2017). We modeled variation in home range size based on effects of breeding status and commuting distance, using two generalized linear mixed model (GLMM) sets. The first had 95% marine home range area as the dependent variable and breeding status, study site, and their interaction set as fixed variables, with year as a random variable. The second had 95% marine home range area as the dependent variable with commuting distance, study site, and their interaction set as fixed variables, and year as a random variable. The independent variables for these models (home range size) were numeric (km²) and skewed. After testing a series of distributions using the “*fitdistplus*” package in R, we found a gamma distribution (log-link) to be applicable for both. For the GLMMs, 95% confidence intervals were calculated to infer significance. Predictive plots were then made using the *ggpredict* function from the “*ggeffects*” package in R. Conditional predictive plots show the dependent variable predicted values based on a specified independent variable, with all other variables set to zero (Lüdecke 2018).

We used a GLMM model to explore the effects of breeding status on spatial overlap between individuals (Magle *et al.* 2013). Because our dependent variable was proportional data, the model was run using a beta distribution (logit-linked), with VI values defined as the independent variable and the predictor variables set as breeding status and study site, with year set as a random variable. We included an interaction term between breeding status and site location, to test if the relationship between spatial overlap and breeding status differed between site locations. We used estimates and confidence intervals as a measure of effect sizes and statistical significance. For the 95% confidence intervals, values overlapping zero were deemed insignificant (Das 2019). To explore relationships between proximity of nest sites and marine locations used by birds, we used a GLMM with a beta distribution (log-linked) to model the minimum distance between pairs of nests, study site, and their

interaction as a function of the VI between all pairs of home ranges, with year as a random factor.

RESULTS

Data were available for 96 breeding and 94 non-breeding murrelets at Clayoquot, and 175 breeders and 31 non-breeders at Desolation. The number of relocation points ranged 5–48 per breeder and 6–45 per non-breeder at Clayoquot; and 5–54 per breeder and 6–53 per non-breeder at Desolation. Nest locations were known for 32 of the 96 breeders at Clayoquot, and 99 of the 175 breeders at Desolation.

Utilization distribution maps

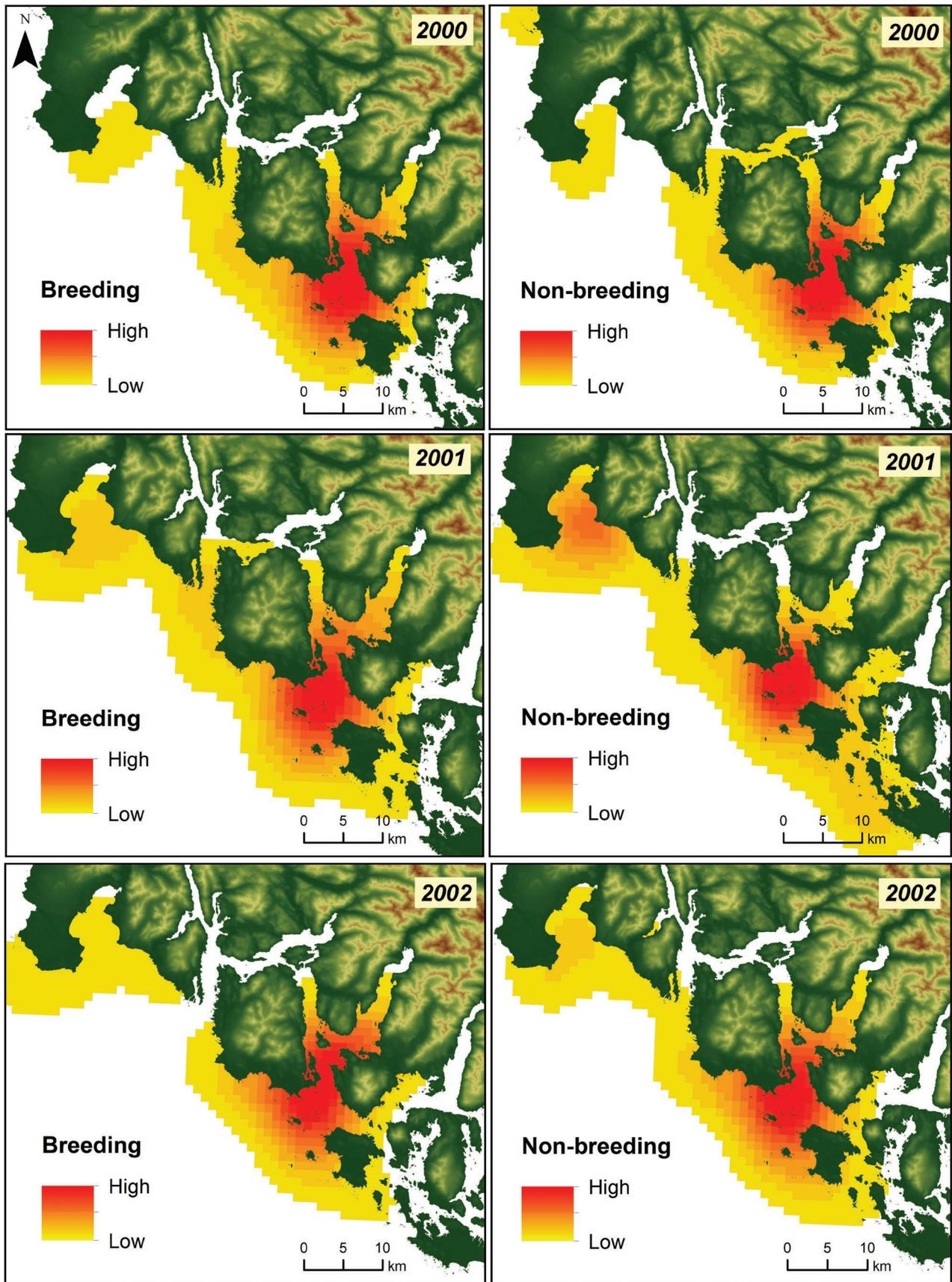
Summary UD maps representing annual frequently-used marine areas (hotspots) generated from relocation data pooled across individuals showed similar general spatial distributions between breeders and non-breeders (Figs. 2, 3). In Clayoquot, the most intense overlay of UDs occurred between Flores and Vargas Islands, focused into the mouth of Herbert Inlet (Fig. 2). In Desolation, usage was highest in the Homfray Channel between East Redonda Island and the mainland (Fig. 3), by both groups in all years (1998–2001). Breeding and non-breeding murrelets were also found in Toba Inlet in 2000 and 2001, when researchers expanded capture effort and relocation search into that inlet. At Clayoquot, non-breeders had an additional hotspot on the waters off the Hesquiaht Peninsula during 2001. Because researchers concentrated their capture effort where they had observed aggregations of murrelets, capture sites largely correspond to intensively utilized home range areas (Figs. 2, 3; Appendix 2, Fig. A2).

Home range sizes and overlap

The average marine home range size over all sites and years was 287 ± 6 km² ($n = 396$). Home ranges were significantly larger at Desolation than at Clayoquot (parameter estimate = 0.65, 95% confidence interval [CI] = 0.51–0.79), in both the pooled analyses (Fig. 4, Table 1) and for individual marine home ranges (Table 3). The number of relocations per individual was not correlated with home range size ($r = 0.12$).

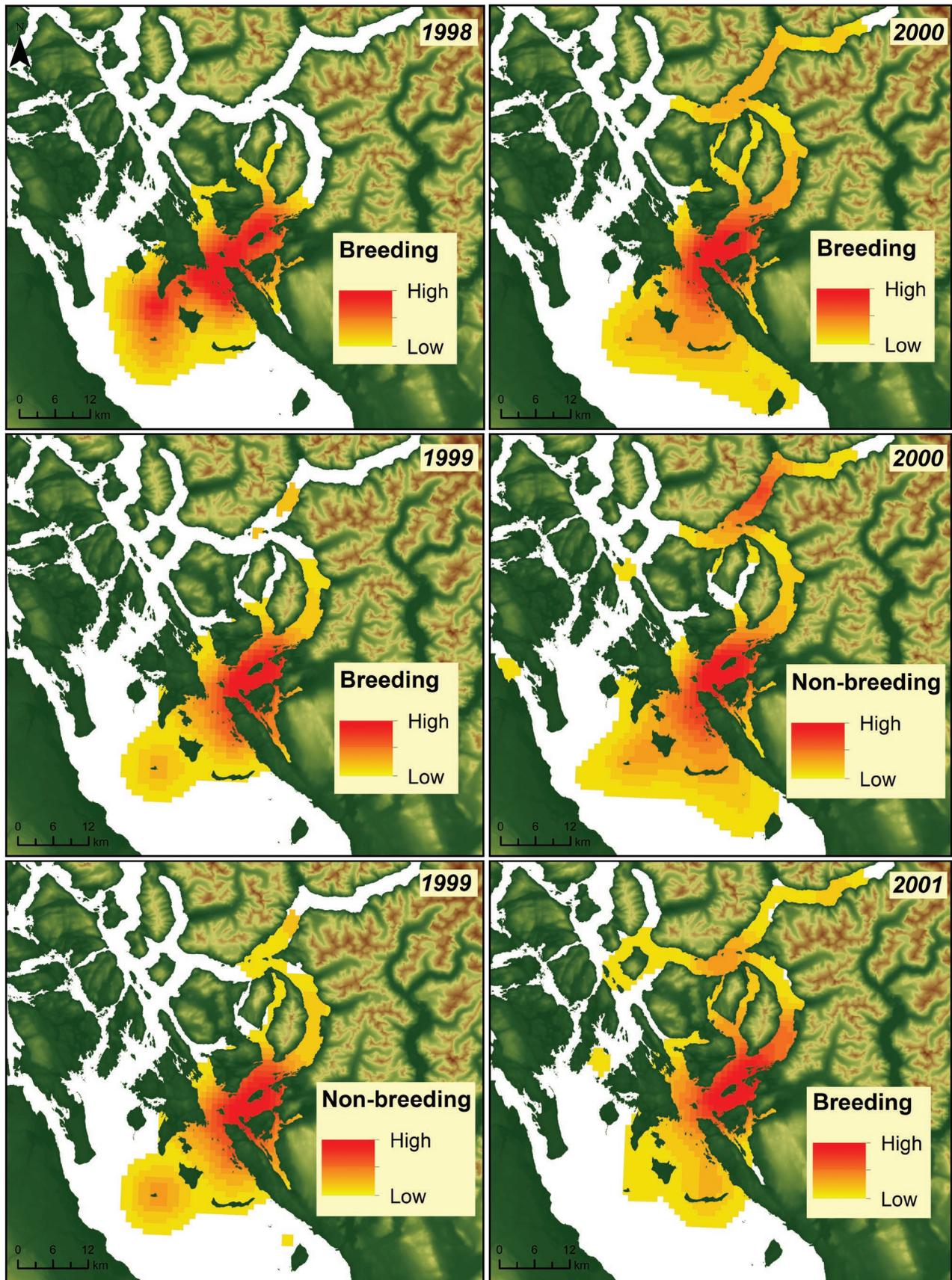
At Clayoquot, non-breeders as a whole had consistently utilized larger home ranges than breeders (Fig. 4, Table 1), although this was not the case at Desolation. Both breeding and non-breeding populations covered larger marine home ranges in 2001 at Clayoquot. However, at Desolation, the 95% marine home range sizes were similar for breeding statuses in both years where comparisons could be made (Fig. 4, Table 1).

Non-breeders, on average, had larger home ranges than breeders (Table 2); however, overall, there was no significant difference in marine home range size between individual breeders and non-breeders (parameter estimate = 0.09, 95% CI = -0.01 to 0.20; Table 3). At Clayoquot, spatial overlap among individuals was significantly greater compared to Desolation (parameter estimate for VI = -0.80, 95% CI = -0.88 to -0.72; Table 3). Overall, breeders (predicted VI = 0.35) had significantly greater (parameter estimate = -0.35, 95% CI = -0.42 to -0.28; Table 3) spatial overlap than non-breeders (predicted VI = 0.27). This difference held when we restricted the breeders in the analysis to those with confirmed nesting locations (Appendix 2, Table A1).



Data source: Centre for Wildlife Ecology, Simon Fraser University. Map created using ESRI ArcMap v10.5.1. Coordinate System: NAD 1983 UTM Zone 10N.

Fig. 2. Comparisons of kernel-based utilization distribution maps of Clayoquot Sound, British Columbia, Canada, for breeding and non-breeding populations of Marbled Murrelets *Brachyramphus marmoratus*.



Data source: Centre for Wildlife Ecology, Simon Fraser University. Map created using ESRI ArcMap v10.5.1. Coordinate System: NAD 1983 UTM Zone 10N.

Fig. 3. Kernel-based utilization distribution maps of Desolation Sound, British Columbia, Canada, for breeding populations of Marbled Murrelets *Brachyramphus marmoratus* in 1998–2001, as well as non-breeding populations in 1999–2000.

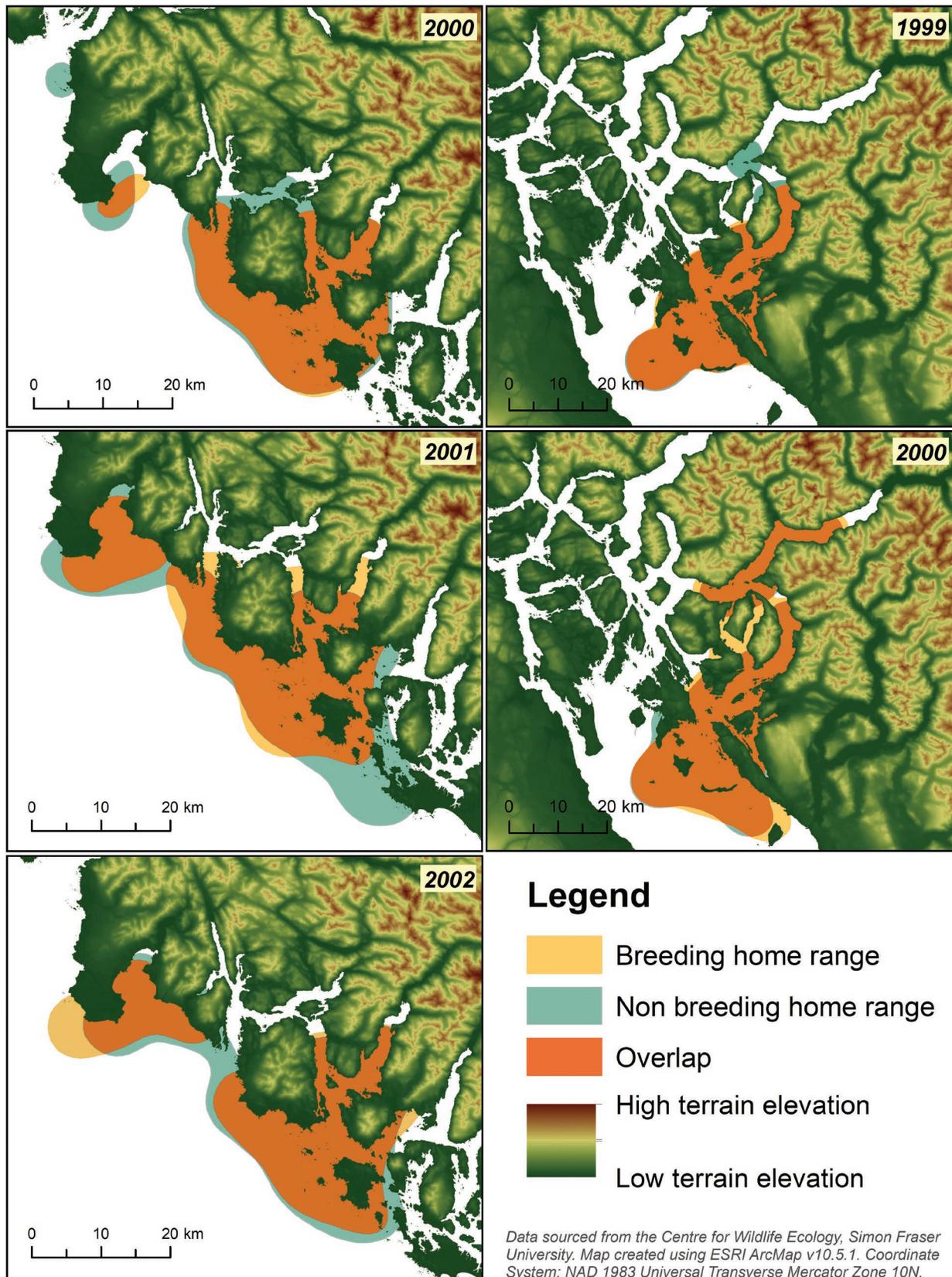


Fig. 4. Marine home range overlap in British Columbia, Canada, for breeding and non-breeding populations of Marbled Murrelets *Brachyramphus marmoratus*. Left panels show Clayoquot Sound (Clayoquot) data in 2000–2002, and right panels show Desolation Sound (Desolation) in 1999–2000. Clayoquot had 24 breeders and 46 non-breeders in 2000, 38 breeders and 21 non-breeders in 2001, and 34 breeders and 27 non-breeders in 2002. Desolation had 68 breeders and 21 non-breeders in 1999, and 63 breeders and 10 non-breeders in 2000. No comparisons were made in 1998 and 2001 in Desolation Sound due to a lack of non-breeding individuals.

Marine use with respect to nest sites

At both sites, the birds concentrated their marine usage at specific individual hotspots, as noted previously, differing little with respect to nest site location (Fig. 5). At Desolation, however, birds nesting in the Toba watershed utilized Toba, or both Toba Inlet and the Homfray Channel hotspot, whereas no birds nesting elsewhere made extensive use of Toba (Fig. 5, Appendix 2, Fig. A2). Commuting distances were longer at Desolation (mean = 34.8 km, standard deviation [SD] = 14.0 km) compared to Clayoquot (mean = 20.1 km, SD = 12.5 km; $t = 5.6$, $df = 58.2$, $P < 0.001$), including comparisons

restricted to 2000 and 2001, when data were available from both study sites (Appendix 2, Table A2). Commuting distance was not significantly related to 95% marine home range size (Table 4). The relationship of the distance between pairs of nest sites and spatial overlap of the home ranges used by the nesting birds (Fig. 6) showed somewhat different relationships by site (Table 4). At Desolation, pairs of birds nesting closer shared more marine habitat than those nesting farther apart, which was not the case in Clayoquot, where the opposite trend was observed; site had a significant interactive effect on how distance between nest sites was related to the overlap (VI) between individuals (Table 4). Maps showing individual nest locations, marine home ranges, and hotspots are provided in Appendix 1.

TABLE 1
Yearly 95% marine home ranges (km²) of pooled breeding and pooled non-breeding Marbled Murrelets *Brachyramphus marmoratus* in Clayoquot Sound and Desolation Sound, British Columbia, Canada

Year	Clayoquot Sound		Desolation Sound	
	Breeding	Non-breeding	Breeding	Non-breeding
1998	–	–	442	–
1999	–	–	449	488
2000	–	–	732	708
2001	342	413	589	–
2002	481	600	–	–

DISCUSSION

We used historic VHF tracking data to quantify breeding season marine habitat use by murrelets at two important, but very different, areas within two murrelet conservation regions of southern British Columbia. We modelled marine habitat use as marine home ranges and spatial overlap, and we visualized frequently used marine areas (hotspots) with UD maps. At Clayoquot, the water between Flores and Vargas islands was a hotspot each year, suggesting it provided superior forage fish availability and/or safety (Pastran *et al.* 2021). Unfortunately, forage fish populations are not monitored in the region. The area has shallow water (Range 1–40 m depth) compared to the fjords nearby that ranged 1–200 m in depth, and it is known to support Pacific Sand Lance *Ammodytes hexapterus*, a common

TABLE 2
Means and ranges of yearly individual 95% marine home ranges (km²) for breeding and non-breeding Marbled Murrelets *Brachyramphus marmoratus* in Clayoquot Sound and Desolation Sound, British Columbia, Canada

Year	Clayoquot Sound						Desolation Sound					
	Breeding			Non-breeding			Breeding			Non-breeding		
	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>
1998	–	–	–	–	–	–	270	142–377	15	–	–	–
1999	–	–	–	–	–	–	256	151–426	27	255	105–419	21
2000	193	108–347	24	229	98–578	46	395	133–710	63	412	252–572	10
2001	259	103–560	38	270	129–415	21	326	155–585	29	–	–	–
2002	238	124–564	34	256	152–426	27	–	–	–	–	–	–

TABLE 3
Parameter estimates for models predicting marine home range size and spatial overlap (Volume of Intersection) of Marbled Murrelets *Brachyramphus marmoratus* based on breeding status and study site (Clayoquot or Desolation Sound, British Columbia, Canada), with year set to a random variable

Dependent variable	Predictors	Estimate	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	<i>P</i> value
Marine home range size	Intercept	5.34	0.10	5.13	5.55	<0.001
	Status[non-breeding]	0.09	0.05	-0.01	0.20	0.08
	Site[Desolation]	0.65	0.07	0.51	0.79	<0.001
	Status[non-breeding]*Site[Desolation]	-0.17	0.09	-0.35	0.00	0.05
Spatial overlap (Volume of Intersection)	Intercept	0.17	0.19	-0.20	0.55	0.37
	Status[non-breeding]	-0.35	0.03	-0.42	-0.28	<0.001
	Site[Desolation]	-0.80	0.04	-0.88	-0.72	<0.001
	Status[non-breeding]*Site[Desolation]	0.01	0.06	-0.12	0.13	0.93

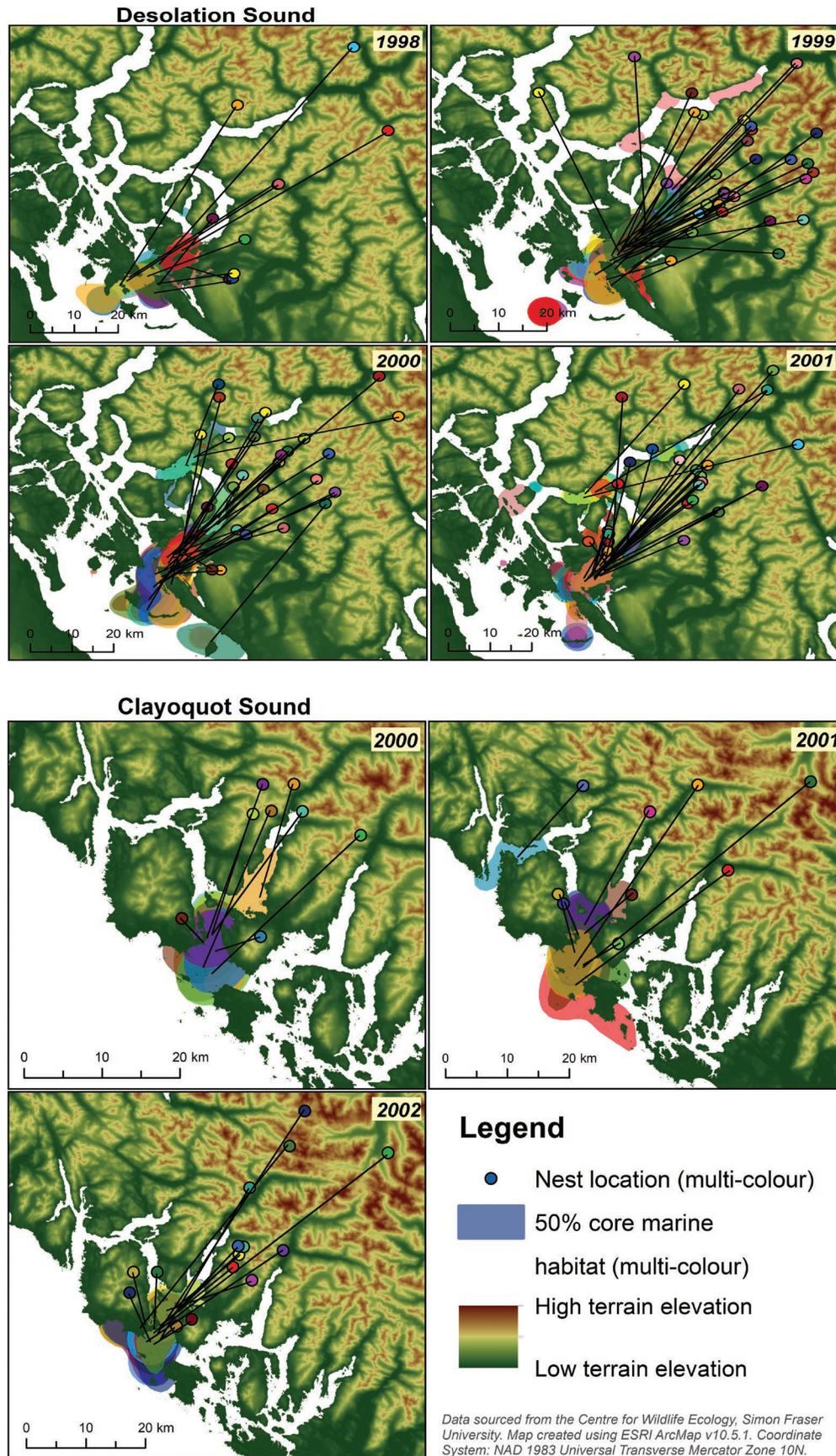


Fig. 5. Shortest distance from nest site to centroid of the core marine habitat (50%) in Desolation Sound (1998–2001) and Clayoquot Sound (2000–2002), British Columbia, Canada. If the core area consisted of multiple polygons, the largest polygon area centroid was used to visualize distance.

TABLE 4

Parameter estimates for models predicting breeding Marbled Murrelets' *Brachyramphus marmoratus* marine home range size as a function of nest-site to foraging areas commuting distances (km) and site; and for home range spatial overlap (Volume of Intersection) between pairs of birds as a function of distances between pairs of nest sites, as well as study sites, both with year as a random variable

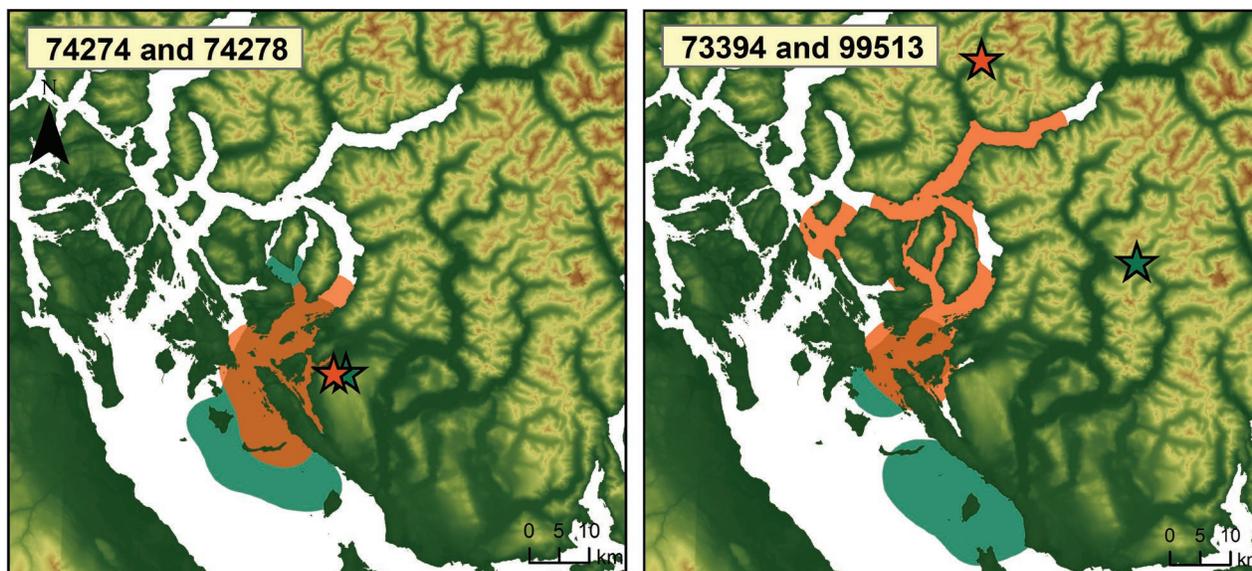
Dependent variable	Predictors	Estimate	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	P value
Marine home range size	Intercept	5.09	1.30	4.84	5.35	<0.001
	Commuting Distance	8.15 ⁻⁰⁶	4.66 ⁻⁰⁶	-9.76 ⁻⁰⁷	1.73 ⁻⁰⁵	0.26
	Site[Desolation]	5.69 ⁻⁰¹	1.50 ⁻⁰¹	2.74 ⁻⁰¹	8.64 ⁻⁰¹	<0.001
	Commuting distance*Site[Desolation]	-5.00 ⁻⁰⁶	5.19 ⁻⁰⁶	-1.52 ⁻⁰⁵	5.18 ⁻⁰⁶	0.388
Spatial overlap (Volume of Intersection)	Intercept	-0.85	0.34	-1.50	-0.19	0.01
	Distance between nests	0.04	0.08	-0.11	0.18	0.62
	Site[Desolation]	1.13	0.17	0.79	1.46	<0.001
	Distance between nests*Site[Desolation]	-0.17	0.08	-0.32	0.02	0.03

murrelet prey species (Robards *et al.* 1999). Within the murrelet marine hotspot location, subtidal sand wave habitat (see Robinson *et al.* 2021) where sand lance bury themselves has been confirmed in Russell Channel between Vargas and Flores islands (DFB unpubl. data). An independent study using at-sea counts also confirmed hot spots of murrelets during breeding between Vargas and Flores islands in 2007 and 2008 (Muirhead 2010). Off Flores Island, murrelets were also observed foraging on epibenthic zooplankton such as mysids. It is noteworthy that ocean temperatures at Desolation are more variable than Clayoquot, being about 1 °C colder in winter but, on average, 4.3 °C warmer (and increasing) in summer (1935–2016, Iwabuchi 2019, see also Amos *et al.* 2014).

In 2001, birds in Clayoquot had larger home ranges than during 2000 and 2002, with the waters south of the Hesquiaht Peninsula

also being a hotspot for non-breeding murrelets. Murrelets in the California Current Ecosystem off Oregon were observed to shift distribution with changes in upwelling intensity or water temperature (Becker & Beissinger 2003). Clayoquot is also in the California Current Ecosystem and is therefore exposed to open ocean and directly influenced by changes in coastal productivity related to the duration and intensity of upwelling-favourable (northwesterly) winds (Xi *et al.* 2019). During our study in 2000, 2001, and 2002, spring transitions (onset of upwelling) were early and upwelling magnitude (March to November) was average to large (Hourston & Thomson 2018).

In the Desolation region, murrelets were primarily recorded within and close to Desolation Sound itself. The waters where murrelets were concentrated are characterized by a mixture of shallow



Data source: Centre for Wildlife Ecology, Simon Fraser University. Map created using ESRI ArcMap v10.5.1. Coordinate System: NAD 1983 UTM Zone 10N.

Fig. 6. Examples of two sets of nesting Marbled Murrelets *Brachyramphus marmoratus* in the year 2000 with their corresponding 95% marine home range in Desolation Sound, British Columbia, Canada. The orange color is associated with birds 74274 and 73394, and the green color is associated with birds 74248 and 99513. Other individual nesting locations and home ranges are available in Appendix 1.

areas and deep trenches that provide habitats for several species of forage fish (Mackas *et al.* 2010). Pacific Sand Lance burying habitat has been identified near the sound (Robinson *et al.* 2020), and sand lance have been directly observed being held by breeding murrelets (fish-holding behavior) in nearby Inlets (Mahon *et al.* 1992, Loughheed *et al.* 2002). Juveniles of Pacific Herring *Clupea pallasii*, salmon (Salmonidae), and Northern Anchovy *Engraulis mordax* have also been recorded in murrelets' diets in Desolation (Janssen *et al.* 2009). During our study in 1998 and 2001, juvenile herring were among those most abundant on record, and levels were average in 1999 and 2000 in the Strait of Georgia (Boldt *et al.* 2018). Diet reconstruction from breast feather isotopes using samples from 1999, 2000, 2006, and 2007 were consistent with increasing dependence on krill (Euphausiacea) versus forage fish during the pre-breeding period (Janssen *et al.* 2009).

The capture locations at both sites (Appendix 2, Fig. A2) closely match the locations of foraging hotspots. As a practical matter, birds were captured by field workers where large numbers of birds were available within range of field camps. In 2000 and 2001, birds nesting around Toba were more likely to have been initially captured and have home ranges partially or completely in Toba than birds not nesting in that drainage (Appendix 2, Fig. A2). In contrast, no birds captured in Desolation proper had primary home ranges in Toba. Nest sites and high use areas would likely have shown greater variation had there been more widespread capture effort throughout the study areas.

Breeding and non-breeding murrelets had similar overall marine habitat distributions at both Clayoquot and Desolation sounds. Breeders, however, had somewhat more concentrated distributions than non-breeders, with home ranges that were smaller on average and had greater overlap with one another. In northern California, Hébert and Golightly (2008) used radio-tagged birds to look at differences between breeders and non-breeder ranges, following the birds up to 160 km along the shoreline. They found that non-breeders had substantially larger home ranges than breeders, particularly males. In Alaska and the Strait of Juan de Fuca, non-breeding birds also generally had larger home ranges than breeders (Barbaree *et al.* 2015, Lorenz *et al.* 2017).

In contrast to these previous findings and our first prediction, we did not find significant differences in marine home range sizes. Our findings indicate that although populations of non-breeders were somewhat more dispersed, the distributions of individual foraging effort did not strongly differ between the two groups, contrary to what we had predicted. A parsimonious biological explanation for our findings is that the foraging ranges of breeders were not strongly constrained by their nest site locations, which is consistent with the commuting distance analyses discussed below. However, methodological differences may affect the interpretation of our results. We clipped radio fixes within a consistently monitored range to make valid comparisons. At both locations, our study took place along ~100 km of shoreline. Therefore, we may not have captured the full range of variation in movements. This is exemplified by fortuitous recordings of birds leaving the Clayoquot study region to fly over Vancouver Island to the Strait of Georgia, closer to Desolation. Researchers flying overhead detected two breeding and one non-breeding individual originally tagged in Clayoquot (Appendix 2, Fig. A1). In contrast, in the two years when both sites were intensively monitored, we did not detect any movement between sites. Additionally, we relied on a 24 hr on/off

pattern on marine waters to categorize breeders and non-breeders. The vast majority of the birds we used were captured in early May, but a few birds were caught in later June and early July. Incubation time for murrelets can range from early April to early August (Hamer & Nelson 1995). Therefore, it is possible that a small subset of the birds that were caught had already completed their incubation cycle; these birds would not display the on/off pattern and would consequently be mislabeled non-breeders.

Our results contribute to a growing body of literature supporting the notion that marine home range size for individual murrelets varies regionally. For our study, the average marine home range size (for Desolation and Clayoquot) was 287 km². This is roughly twice the size of the mean range size (127 km²) calculated at Port Snettisham, Alaska (Barbaree *et al.* 2015) and from Prince William Sound, Alaska (143 km², Kuletz 2005). It is, however, less than one-third the size of the mean home range size (938 km²) calculated for northwest Washington state (Lorenz *et al.* 2017) and about half the size (505 km²) estimated in waters off northern California (Hébert & Golightly 2008). Contributing to the variation in home range sizes may be differences in foraging conditions between regions, with birds inhabiting waters containing scarcer prey potentially traveling over a wider range to forage.

A north to south pattern in home range size is plausible, but discrepancies in methodology between tracking studies (e.g., minimum convex polygon vs. kernel density ranges) or differences in the bandwidths chosen for estimating kernel density ranges also contribute to this variation. Using similar methods, notable differences were observed between commuting distance and home range sizes for our study sites. Birds commuted farther to their nesting sites at Desolation (35.04 km) than at Clayoquot (19.78 km). This observation, plus less spatial overlap between individuals and larger average home ranges in Desolation (330 km² versus 241 km² at Clayoquot) shows that birds in Desolation moved greater distances to and within their marine environment. There was, however, no relationship between commuting distance and marine home range sizes, as we had initially predicted. Assuming that smaller home ranges reflect more concentrated or reliable prey (Whitworth *et al.* 2000, Adams *et al.* 2004) or potentially fewer murrelets competing, we suggest that better foraging conditions exist at Clayoquot than in Desolation. Movements by birds nesting in the Toba Inlet watershed to Desolation, but not vice versa, indicate better foraging in Desolation than in the more glacial-outflow-influenced inlet. Previous analyses (Barrett 2008) of the data gathered in our radio-tracking study found that cooler sea-surface temperatures were strong predictors of marine habitat utilization in June at Desolation. Future studies could compare current marine productivity and food web composition between regions and between sites, given two decades of strong indications of ocean warming, and explore connections between prey availability and ocean temperature.

There are numerous reports that breeding season distributions of murrelets correspond with distributions of terrestrial nesting habitat on a broad geographic (Meyer *et al.* 2002, Yen *et al.* 2004, Raphael *et al.* 2015) and local scale (Becker & Beissinger 2003, Barrett 2008, Raphael *et al.* 2015, Pastran *et al.* 2021), but few studies directly link nesting locations to marine habitat choice (Barbaree *et al.* 2015, Lorenz *et al.* 2017). Birds nesting in Desolation did not forage in Clayoquot or vice versa (but see above), but rather chose to forage at regional hotspots closer to their nesting sites. Initially, we predicted that there would be less spatial overlap between

breeders, and those nesting closer together would also share marine areas. Contrary to these predictions, breeders at both locations had strong patterns of commuting from their nest sites to a central foraging location, a behavior also observed from birds tagged at Prince William Sound, Alaska (Kuletz 2005). At Desolation, however, home range locations differed somewhat between birds nesting in Desolation versus Toba inlet, and as predicted, overlap of home ranges was less for nests located further apart, probably reflecting this partial spatial segregation. No such relationship was found at Clayoquot. The lack of a relationship between commuting distance and home range size in general, which we had expected to find, and limited differences in overlap, indicates that at this geographic scale, the costs of commuting did not offset foraging benefits; alternatively, the benefit of travelling further from foraging sites to safe nest sites may offset commuting costs.

Based on our results, we also suggest that breeders, even those who are not breeding pairs, may prefer to forage in close proximity to one another, indicated by individual breeders having significantly greater overlap with other breeders than non-breeders. This could be evidence of more efficient catch per effort through group feeding (Mahon *et al.* 1992). Recent evidence indicates that murrelets may be more social than previously believed and that they may communicate with one another when searching for potential nesting sites (Valente *et al.* 2021). Therefore, the strong centralized distribution of breeding populations could reflect both foraging and social benefits derived from close proximity to conspecifics. Our study shows that breeders and non-breeders have similar marine distributions, with specific focal areas of high use, especially by breeding birds. These historical telemetry datasets offer unique regional insights and facilitated quantification of the spatial extent of important marine and terrestrial habitats, which are *both* needed for conservation efforts (Betts *et al.* 2020). The partitioning of terrestrial versus marine impacts on survival and reproduction remains a challenge for this unusual forest nesting seabird.

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