Marine habitat use and movement in response to ocean warming by a threatened forest-nesting seabird

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ABSTRACT

Although anthropogenic climate change has resulted in significant alterations of ocean environments, the degree to which marine organisms can respond behaviorally to climate effects remains poorly understood, especially for species with increased extinction risk. We monitored marine space use and movement of the threatened marbled murrelet (*Brachyramphus marmoratus*) along the central coast of Oregon, USA during the 2017–2019 breeding seasons to quantify marine habitat selection patterns across a range of ocean conditions. We hypothesized that marine locations characterized by upwelling, nearshore areas adjacent to old-growth forest nesting habitat, and protected marine areas would be preferentially selected by tagged birds. Using >4800 locations collected from >180 individuals, we found that murrelets selected areas near small estuaries and with localized upwelling (as characterized by decreased sea-surface temperatures and high salinity), both of which are expected to lead to greater food availability during periods when sea-surface temperatures are elevated and coastal upwelling is reduced (i.e., poor ocean conditions). In addition, we found that individuals did not preferentially select marine areas adjacent to potential old-growth nesting habitat, and that murrelets exhibited limited overlap with protected marine areas regardless of ocean conditions. Unexpectedly, the majority (62%) of tagged individuals moved beyond the boundaries of our 135-km long study area in the year with the poorest ocean conditions (2017), with 15% of birds moving >500 km from their capture location. Our results confirm that marine habitat selection in murrelets becomes decoupled from terrestrial nesting habitat during periods of poor ocean conditions, and that such conditions are associated with low breeding propensity and long-distance movements during the breeding season. In addition to demonstrating murrelets undertake fine- and coarse-scale movements to buffer against poor ocean conditions, our study also emphasizes the importance of considering broad spatial scales in the marine environment when undertaking measures to conserve murrelet populations.

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1. Introduction

Anthropogenic climate change has been impactful on a wide range of ecosystems, including the warming of marine environments that support a high diversity of organisms. Increases in the duration and frequency of marine heatwaves – defined as discrete periods of anomalous warm water events occurring in a particular location (Oliver et al., 2021) – have recently gained attention because they can lead to extensive perturbations to marine ecosystem structure and function (Oliver et al., 2018). For example, a large-scale marine heatwave in the northeast Pacific Ocean during 2014–2016 (Bond et al., 2015) reduced the amount and quality of food resources available to upper trophic predators (von Biela et al., 2019; Arimitsu et al., 2021; Maniscalco, 2023) and ultimately led to extensive reproductive failure and widespread die-offs of seabirds (Frölicher and Laufkötter, 2018; Jones et al., 2018, 2023; Piatt et al., 2020; Woehler and Hobday, 2023) and marine mammals (Gabriele et al., 2022). Lingering effects from that event continued beyond the initial heatwave and resulted in warmer ocean conditions in the Bering and Chukchi Seas (Romano et al., 2020; Kaler and Kuletz, 2022; Jones et al., 2023) and in more southern regions of the Pacific Northwest, leading to unprecedented changes in marine communities (Brodeur et al., 2019; Morgan et al., 2019). The behavioral responses of upper trophic predators to periods when sea-surface temperatures are elevated and coastal upwelling is reduced – including periods of marine heat waves – has become a research priority because such conditions are expected to become longer and more frequent in the future (Oliver et al., 2018; Rivers et al., 2022). Whether upper trophic-level predators can buffer the effects of marine heatwaves by moving to less affected areas, such as protected areas, has had limited study (Bates et al., 2019). Nevertheless, such information is crucial for understanding behavioral responses of marine organisms to marine heatwaves and the resulting poor ocean conditions, as well as determining whether contemporary protected areas serve as refugia during such climatic events.

Seabirds are among the most threatened bird groups because they rely on high-quality nesting habitat and marine foraging areas for successful reproduction (Dias et al., 2019). The marbled murrelet (*Brachyramphus marmoratus*, hereafter murrelet) is a small, seabird in the auk family (Alcidae) found along the western coast of North America that is listed as Threatened under the U.S. Endangered Species Act and is therefore of high conservation concern. Murrelet populations from California to British Columbia have declined from historical levels for several reasons, with loss and fragmentation of old-growth and late-successional forests being a primary cause (Piatt et al., 2007; Nelson, 2020; Drever et al., 2021; Valente et al., 2023). Recovery of murrelet populations is further challenged because murrelets differ from seabirds that nest in colonies close to the ocean and instead use late-successional and old-growth coastal forests for nesting. This "habitat-split strategy" requires murrelets to locate suitable nesting sites, which may be more than 80 km inland, in addition to nearshore areas where they can obtain adequate food for successful nesting (Nelson, 2020). Given the energetic costs of commuting flights (Hull et al., 2001), particularly during the chick-rearing period when adults may make multiple food provisioning trips to the nest each day (Nelson and Hamer, 1995), murrelets are expected to concentrate their foraging activities in coastal areas that are adjacent to their inland nesting sites to reduce energetic costs. During periods of poor ocean conditions, when prey items for chicks (i.e., forage fish; Nelson, 2020) may be less abundant and/or of reduced quality (von Biela et al., 2019; Arimitsu et al., 2021), adjacency of foraging areas to nesting sites may have heightened importance for successful breeding. Ocean conditions can exhibit high inter-annual variation for marine ecosystems within the Northern California Current (Peterson et al., 2014; Morgan et al., 2019), which serves as a stronghold for murrelet populations within the area in which they are listed under the U.S. Endangered Species Act (ESA) along the Pacific Coast (Raphael et al., 2015). Therefore, quantifying the response of murrelets to poor ocean conditions in this region has become a conservation priority for population recovery (Betts et al., 2020).

In this investigation, our primary objective was to quantify marine habitat use and movement of breeding and non-breeding murrelets along the central coast of Oregon, USA using VHF telemetry tagging. Our 3-year investigation was initiated shortly after the 2014–2016 marine heat wave event that took place in the North Pacific (Bond et al., 2015) such that our first year of study covered a period of lingering effects that was characterized by reduced coastal upwelling with gradually improving conditions in subsequent years. To assess habitat use and movement by murrelets, we implemented a step selection function (SSF) framework (Thurfjell et al., 2014) to quantify how spatial and temporal variation of at-sea movements were related to (1) marine biological factors (e.g., chlorophyll *a*, zooplankton) and marine physical properties (e.g., sea-surface temperature, upwelling, salinity) considered important for the species (Becker and Beissinger, 2003; Becker et al., 2007), as well as (2) measures related to terrestrial nesting areas (e.g., distance from coast, extent of available nesting habitat; Ronconi, 2008; Raphael et al., 2015; Lorenz et al., 2016). We predicted that murrelets would be more likely to be found in marine locations with greater upwelling, cooler sea-surface temperatures, and greater concentrations of chlorophyll *a* and zooplankton following previous work with this species (Burger, 1999; Becker and Beissinger, 2003; Ronconi and Burger, 2008). We also predicted that the presence of murrelets would be greater in nearshore areas with a greater proportion of adjacent old-growth forest nesting habitat (e.g., Ronconi, 2008; Raphael et al., 2015; Betts et al., 2020), and that murrelets would be more common near beaches with sandy/gravel shores due to the presence of Pacific sand lance, a prey species often used by murrelets during the breeding season (Lorenz et al., 2016; Fountain et al., 2023).

In addition, we quantified murrelet use of nearshore Marine Reserves – defined here as locations within 5.5 km of the shoreline where all extractive activities are prohibited (ODFW, 2022) – as well as adjacent Marine Protected Areas that are less restrictive in the activities they allow. Both protected areas provide sanctuary for commercial fish species and often have higher prey densities than non-protected areas, including juvenile life stages of rockfish (*Sebastes* spp.; Thompson et al., 2017; ODFW, 2022) a group preyed upon by murrelets (Fountain et al., 2023) that may be expected to use protected areas more consistently than other murrelet prey, such as pelagic schooling fish (Brodeur et al., 2005; Rivers et al., 2022). Thus, we expected protected areas would serve as refugia to murrelets and they would spend more time within such areas during poor ocean conditions. Finally, we also report long-distance movements of tagged murrelets during the breeding season, which provides a basis for understanding where murrelets move to during poor conditions and provides insight into how movement of individuals may influence the efficacy of at-sea surveys to quantify populations.

Taken together, our study provided a unique opportunity to examine marine space use and movement of murrelets across a range of ocean conditions – including conditions that curtailed nesting activity – to build on prior work (Ronconi and Burger, 2008; Bertram et al., 2015, 2023) and enhance our understanding of murrelet behavioral responses to poor ocean conditions during the breeding season.

2. Methods

2.1. Study area

Our research occurred during the murrelet breeding season (April-September) in 2017, 2018, and 2019 along the central coast of Oregon, USA, with our core study area covering a ~135 km of coastline from Pacific City, Oregon (N 45°14'13.47", W 123°58'9.35") southward to Florence, Oregon (N 43°58'36.85", W 124°8'23.10"). The coastline and nearshore environment in this area comprises a mix of rocky and sandy shores, cliffs, and outflowing creeks and rivers of varying sizes, with more old-growth forest in the southern portion of our study area (Fig. 1). Regularly conducted surveys indicate that our core study area contains murrelet at-sea population densities that are well above average within the ESA-listed range of the species, with lower-than-average coefficients of variation (Raphael et al., 2015; McIver et al., 2023).

Our study area encompasses three Marine Reserves – Cascade Head, Otter Rock, and Cape Perpetua (ODFW, 2022) – with Cascade Head and Cape Perpetua having areas adjacent to them classified as Marine Protected Areas. Given both Marine Reserves and Marine Protected Areas are locations where resource extraction is prohibited, we combined both in our analyses and refer to them collectively as "protected marine areas" hereafter. Adjacent to the marine portion of our study area is a patchwork of federal, state, and private lands, some of which provide late-successional and old-growth forest habitat that murrelets depend upon for nesting (Nelson, 2020).

To characterize changes to ocean conditions during the course of our study, we obtained daily upwelling indices from the National Oceanic and Atmospheric Administration (NOAA) Fisheries Southwest Fisheries Science Center (https://oceanview.pfeg.noaa.gov/products/upwelling/dnld) for 45°N, 125°W, the closest location to the center of our core study area for which data were available.
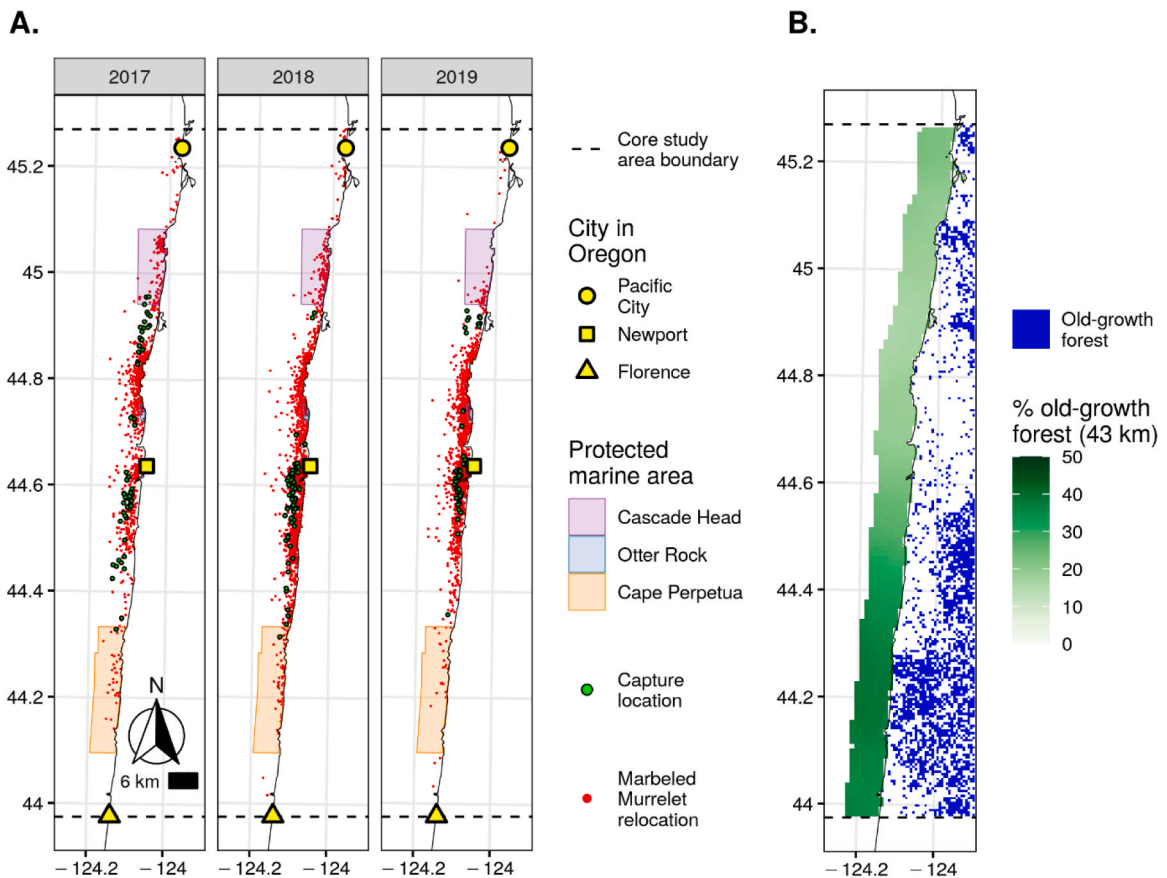

Fig. 1. Maps of the core study area used to study marbled murrelet marine habitat use within the central coast of Oregon, USA extending ~135 km from Pacific City southward to Florence. (A) capture locations (green circles), relocations of VHF-tagged individuals (red circles), and location of three protected marine areas (a combination of Marine Reserves and Marine Protected Areas). (B) illustrates the percentage of land classified as old-growth forest within 43 km of the coast within the core study area.

We used these data to calculate a cumulative upwelling index (CUI), which has been used previously to evaluate the link between murrelet nesting and interannual variation in ocean conditions (Lorenz et al., 2017). To calculate CUI, we took the cumulative sum of the daily upwelling index beginning on the average starting date of physical spring transition from 1969-present for the approximate center of our core study area, (i.e., Day of Year [DOY] = 103; April 13th) and extending to the last day in which aerial telemetry flights were taken during our study (i.e., DOY = 249; September 6th). We calculated CUI separately for each year of study, as well as the 25-year average CUI taken from 1995 to 2019. Similarly, we obtained daily optimum interpolation sea surface temperature (SST) data from NOAA's Environmental Research Division Data Access Program (https://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst21Agg.html) to assess how SST varied across the three years of our study and in comparison to the 25-year average for SST taken from 1995 to 2019.

2.2. Murrelet capture and telemetry tagging

We undertook night-time, at-sea murrelet captures from late April until early June each year, departing from Newport, Oregon on nights when conditions were safe for capture procedures. We searched for murrelets within 5 km from shore and up to ~35 km north and ~35 km south of Newport, Oregon, with the direction of travel determined by weather conditions and the locations of recent searches. We used a 4.2 m-long inflatable boat to locate birds by spotlight (Whitworth et al., 1997) and attempted captures with a large dip net, which was supported by a 26 m-long research vessel to which captured birds were taken for processing. Following a brief visual assessment, each bird was banded with a U.S. Geological Survey metal leg band, after which its body mass ($\pm$ 1 g) and culmen length ($\pm$ 0.1 mm) were measured. We then sampled blood from the medial metatarsal vein for DNA sexing. We fitted individuals of sufficient size ($\geq$ 200 g, based on permitting constraints) with a 2.5-g VHF telemetry tag (A4330, Advanced Telemetry Systems, Isanti, MN, US) that was attached to the upper back using a subcutaneous anchor attachment method (Newman et al., 1999). In 2019 only, we fitted n = 7 individuals with a tail-mounted VHF telemetry tag as an alternative attachment method, but this approach was promptly discontinued due to especially poor retention of tags. All birds were released within 1 km of their original capture location site, and total handling time averaged ~ 35 min across years.

2.3. Murrelet relocations

We used a combination of terrestrial- and aerial-based location techniques to relocate radio-tagged birds after the start of capture activities each year. For terrestrial-based tracking, we established 72 fixed telemetry stations that were placed 2–3 km apart across our 135-km long study area, which allowed us to detect individuals from multiple stations in close succession and triangulate their at-sea locations (see below). We visited all fixed stations 6–7 days per week, commencing 30 minutes after sunrise until 11:00 local time; in 2019 only, we conducted additional surveys between 13:00–16:30 to boost sample sizes. At each fixed station, we first conducted an automatic scan for all radio-tagged murrelets using a VHF receiver attached to a 3-element Yagi antenna that was mounted on a tripod and pointed 270° to standardize data collection. The receiver was set to automatically scan for each radio-tagged bird's unique tag frequency in sequence for 8 s before moving to the next tag frequency. Once the initial scan was completed, we manually searched for those individuals that were detected at each station by physically moving the antenna to determine the bearing with the greatest signal strength to the station. Murrelets spend an average of 27 s under the surface when diving (Jodice and Collopy, 1999) so tagged individuals had the potential to be missed with our scanning technique. Therefore, if a tagged bird was detected at a station we also manually searched for it in the adjacent two stations to obtain a more precise location; this approach was implemented in 2019 only.

Nesting murrelets have incubation bouts of approximately 24 h (Nelson, 2020) and the distinct pattern of switching between inland nest sites and nearshore marine areas can be used to establish whether individuals are incubating (Bradley et al., 2004). Therefore, we also conducted aerial telemetry flights to search for those murrelets that went undetected during terrestrial-based telemetry surveys along the coastline. We conducted flights from May–July over the entire coastline of our core study area up to 6 days a week using fixed-wing aircraft outfitted with omni-directional antennae. When a bird's signal was detected from the air, the plane flew in concentric circles to get as close as possible to the signal, at which point a GPS location was taken. As time allowed, we also recorded long-distance movements of murrelets outside of our core study area by undertaking flights that extended as far north as the northern border of Washington and into the Strait of Juan de Fuca, and as far south as Santa Barbara, California. This included n = 5 out-of-state flights (out of a total of 87 flights) in 2017, 4 flights (out of a total of 68) in 2018, and 1 flight (out of a total of 61) in 2019.

2.4. Filtering of location data

Murrelet relocation data were obtained repeatedly across fixed telemetry stations during each terrestrial- based telemetry survey, so we filtered observations from individual birds that were spaced < 15 min apart; we considered these to be duplicate bearings and only retained the first record within each 15-minute window for analysis. We then used complete-linkage hierarchical clustering (Hastie et al., 2009) to merge observations of an individual from different fixed telemetry stations on the same day that were >15 min but <80 min apart into a single group, as previous work in Oregon has shown that murrelets tend to remain in the same ocean area for an average of 77 min (Jodice and Collopy, 1999). This second step resulted in 1–10 bearings per individual taken within the same day. We then used LOAS software (v4.0; Ecological Software Solutions, 2020) to estimate bird locations via biangulation (2 bearings; n = 4030) or triangulation ($\geq$ 3 bearings; n = 7251); single bearings were uninformative and were therefore removed (n = 1851). For biangulation analyses, we used the maximum likelihood estimate with the bearing angle standard deviation and its associated bias, estimated from VHF telemetry tag testing on stationary buoys (Supplementary 1). For triangulation analyses, we used the median

bearing measurement time within each bearing group as the estimate of the location time. For each group of bearings, we then obtained an estimated location and its associated error polygon; because associated error polygons varied from 0 to 275,076 km^2 we applied a third filtering step to remove locations deemed of low accuracy using sensitivity analyses (Supplementary 2) following previous authors (Poole et al., 2004). This third filtering step removed bearing groups whose error polygon > 43.3 km^2 (which corresponded to the 95% quantile of the distribution of the error polygons), leading to n = 27 estimated locations being discarded. Finally, we removed a small number (n = 6) of relocations that were estimated to be >7.3 km offshore because we did not relocate any tagged individuals beyond this distance during aerial surveys and murrelets are typically found using nearshore areas within 3 km from shore (Lorenz et al., 2016; Nelson, 2020).

2.5. At-sea movement modeling

We modeled murrelet movements within our study area using a step-selection function (SSF) approach (Thurfjell et al., 2014). In this framework recorded movements are paired with simulated movements. A "recorded movement" corresponds to a pair of successive point location observations for a specific murrelet that were made up to 14 days apart (Supplementary 3). In contrast, a simulated movement involves starting from an observed point location and generating a new hypothetical second location, as described below. Step selection coefficients, that describe movement preferences, can then be obtained using conditional logistic regression where the dependent variable corresponds to whether a movement is recorded or simulated, and we account for each recorded movement being grouped with a set of simulated movements (Thurfjell et al., 2014). Compared to background sampling-based methods for presence-only modeling of species preferences or distributions, this approach generates pseudo-absence points (simulated movement endpoints) that better account for spatial variation in accessibility (Hazen et al., 2021). For each recorded movement step, we generated 20 hypothetical steps (Gillies et al., 2011; Volpe et al., 2016) using a conditional density estimation approach to account for varying step durations (Supplementary 3). Next, we selected a set of biologically relevant marine and terrestrial/shoreline variables that were available for our study area to evaluate which variables drove at-sea movements (Table 1). We used these measures as proxies for forage fish availability – as forage fish are critical for successful rearing of murrelet young (Nelson, 2020) – because there was no direct measure of forage fish availability for our study area. Because at-sea movements may be influenced by characteristics of adjacent terrestrial and shoreline habitat, we also evaluated how movement was influenced by the extent of old-growth forest, rocky shores, and sand/gravel beaches, and by presence of small river mouths, and large river mouths (Table 1). Where appropriate, we used proportion variables as indicators of proximity (Table 1); for example, if an observation had a large amount of old-growth forest within 43 km, this would be reflected in the corresponding proportion. We included distance offshore and (distance offshore)^2 as predictors for each model; the quadratic term was used to allow for the possibility that murrelets prefer to forage at intermediate offshore distances after accounting for the effects of the other covariates. We also included step length (i.e., geographic distance between observations) as a covariate in all cases because its inclusion can help to reduce bias in the other parameter estimates (Forester et al., 2009). We only considered observed movements that (1) were entirely within the core study area, (2) had covariate

Table 1

Summary of movement model predictor variables. Variables are grouped into "marine" and "terrestrial and shoreline" categories. The resolution column indicates temporal and spatial resolution, where applicable. See Supplementary 5 for details.

Variable	Description/motivation	Resolution	Reference	Models*
Biologically Effective Upwelling Transport Index (BEUTI)	May be associated with food availability	Daily; 1° latitude (spline interpolation)	Jacox et al. (2018)	MF
Zooplankton concentration (millimole nitrogen / m^3)	Estimates derived from the LiveOcean computer simulation model	Daily; irregular grid (500–1500 m)	Fatland et al. (2016)	MF, MR, C, CY, CB, CNB
Chlorophyll concentration (mg/m^3)	Potential indicator of marine productivity	Monthly; 4 km	NASA (2020)	MF
Salinity (PSU)	Estimates derived from the LiveOcean computer simulation model	Daily; irregular grid (500–1500 m)	Fatland et al. (2016)	MF, MR, C, CY, CB, CNB
Sea-surface temperature (SST) anomaly (°C)	Indicator of deviations from normal ocean temperatures	Daily; 0.01°	JPL MUR MEaSUREs Project (2015)	MF, MR, C, CY, CB, CNB
Old-growth forest	Proportion of land within 43 km that was classified as old-growth forest	Static; 30-m (old-growth raster)	Ohmann and Gregory (2002)	TF, TR, C, CY, CB, CNB, OG, OGL, OGS
Rocky shores	Proportion of rocky shoreline within 43 km; potential forage fish habitat	Static; N/A	NOAA (2017)	TF
Sand/gravel beaches	Proportion of sand/gravel beach shoreline within 43 km; potential forage fish habitat	Static; N/A	NOAA (2017)	TF, TR, C, CY, CB, CNB
Small river mouths	River mouths w/in 43 km with long-term average discharge rate < 10 m^3/s	Static; N/A	Lehner and Grill (2013)	TF, TR, C, CY, CB, CNB
Large river mouths	River mouths w/in 43 km with long-term average discharge rate $\geq$ 10 m^3/s	Static; N/A	Lehner and Grill (2013)	TF, TR, C, CY, CB, CNB

*Models include: Marine Full (MF), Terrestrial Full (TF), Marine Reduced (MR), Terrestrial Reduced (TR), Combined (C), Combined by Year (CY), Combined breeders (CB), Combined Non-breeders (CNB), Old-growth (OG), Old-growth and latitude (OGL), Old-growth sensitivity (OGS).

data available at the start and end, and (3) were made over a period of at most 14 days (Supplementary 3); thus, the total sample size was lower than that of the full dataset.

To fit our models, we used a Poisson response generalized linear mixed modeling approach with random intercepts for each stratum (group consisting of 1 actual and 20 simulated movement steps), and the stratum-level random effect variance set to 10^6 (Muff et al., 2019; Supplementary 3). For each predictor variable, we also included random slopes that differed among individual murrelets, allowing for individual-specific variation. For the combined model, we visualized the estimated effect sizes by plotting the relative probability of movement steps as a function of each covariate, both at the population level and for each individual (Avgar et al., 2017). Positive parameter estimates associated with predictor variables indicate that murrelets tended to move in the direction of higher values of those variables; conversely, negative estimates indicated movements tending toward lower values.

2.6. Home range analysis and use of protected marine areas

We used the Permissible Home Range Estimation (PHRE) algorithm method (Tarjan and Tinker, 2016) to estimate marine home ranges for each bird located within our core study area. In this algorithm, kernel density estimation (KDE) is performed in a transformed space where the dimensions are log-transformed distances offshore and position along the coastline. Compared to ordinary spatial kernel density estimates, the resulting back-transformed kernel density estimates better reflect the contours of the coastline, which is important because murrelets are typically found within 3 km of shore (Lorenz et al., 2016; Nelson, 2020). We used UTM zone 10 N northing (y coordinate) and (log)distance offshore as our transformed variables for PHRE, and we fit the KDE models in the transformed space using the 'np' R package (Hayfield and Racine, 2008) with bandwidths estimated using maximum likelihood-based cross validation. We then predicted the probability density function for each bird at 100 m resolution and used it to calculate 50%, 75%, 90%, and 95% home range sizes, with 50% home range considered to be an individual's core area. To estimate marine home range size, we conducted bootstrapping analyses to determine the minimum number of locations needed to accurately estimate individual home ranges. The median sample size at which the home range size coefficient of variation stabilized was 39 relocations (Supplementary 4); consequently, we restricted our home range analysis to the n = 35 murrelets for which we had at least 39 relocations. For each home range, we also calculated the percentage overlap with the protected marine areas located within our core
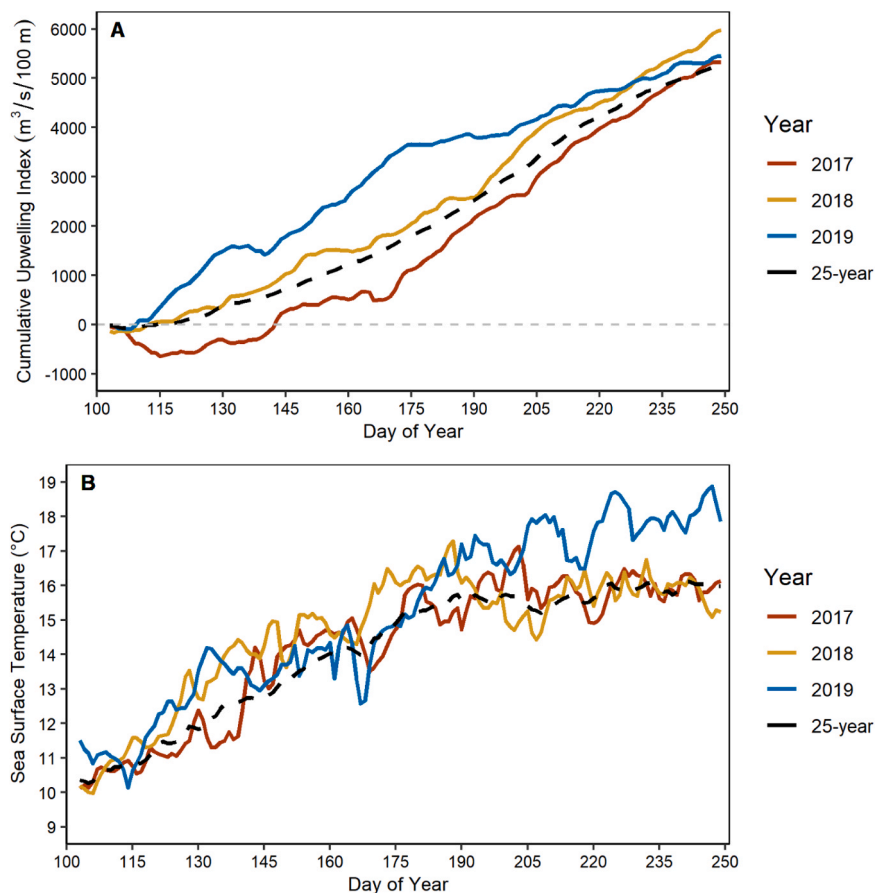

Fig. 2. Annual variation in (A) Cumulative Upwelling Index (CUI) and (B) Sea Surface Temperature (SST) across the three years of this study (2017–2019; solid colored lines) as well as the 25-year average (1995–2019; dashed black line).

study area. In addition to the individual-specific home range sizes, we also summed all the home ranges at each probability level using raster addition to identify at-sea areas that experienced high use by murrelets.

To investigate drivers of home range size we constructed general linear models where sex (2 levels: female, male), breeding stage (2 levels: breeding, non-breeding), and year (3 levels: 2017, 2018, 2019) were fitted as fixed effects to the models using a normal distribution and a logit function in the 'glm' R package. Finally, within the core study area, we statistically tested for variation in protected marine area use among years. We did this by fitting a generalized linear mixed model using the 'glmmTMB' R package (Brooks et al., 2017) with a binary response indicating whether each observation occurred within a protected marine area, with year as a categorical fixed effect, and bird identity as a random effect.

3. Results

Ocean conditions were variable across years, with the lowest CUI values occurring in 2017; these values were consistently below the 25-year mean across the season (Fig. 2A); SST values were more variable for 2017 with broad overlap of the 25-year mean across the season (Fig. 2B). We captured 234 individual murrelets, of which 188 (84 males, 103 females, and 1 bird of unknown sex) were large enough to receive a radio-tag; 61 individuals were tagged in 2017, 76 were tagged in 2018, and 52 were tagged in 2019, including one individual tagged in 2019 that was a recapture from 2017. Overall, we spent >5500 h searching for individuals from terrestrial-based telemetry surveys and >720 h searching for individuals using aerial telemetry. After filtering data, we obtained 4893 relocations at sea from 186 tagged murrelets (83 males, 102 females, 1 unknown sex), with each individual detected an average of 53.8 days (SD = 30.2, range: 1–117 days). The vast majority of relocated murrelets (89%) were detected within 2 km of shore (median ± SD: 839 ± 921 m), with the remaining 11% detected up to 7.3 km from shore. The median water depth in which tagged murrelets were relocated was 11.0 m (SD = 11.0, range: 0–270 m). No radio-tagged murrelets nested in 2017, whereas 8 tagged individuals were recorded at 7 nests in 2018 and 4 tagged individuals were recorded at 4 nests in 2019. Breeding propensity – measured as the number of tagged birds that nested/the number of tagged birds – was 0%, 10.5%, and 7.6% during the 2017, 2018, and 2019 breeding seasons, respectively.

3.1. At-sea movements

Using data from 173 individuals and 3535 at-sea movements, we found that the combined
movement model with terrestrial/shoreline and marine predictor variables performed best, followed by the terrestrial/shoreline model after variable selection (Δ AIC = 34.6; Table 2, Table S5.1). In the top combined movement model, murrelets tended to select movement steps that were away from warm ocean temperatures (i.e., high sea-surface temperature values; β = −0.365; SE: 0.285). The presence of zooplankton, extent of nearby old-growth forest, sand/gravel beaches, and proximity to large river mouths were all negatively associated with murrelet step choices (Table 2, Fig. 3). We also found that murrelets tended to move towards gradients in salinity, and toward small river mouths (Table 2).

Contrary to our predictions, extent of old-growth forest had a consistent significant negative effect across all models; however, there was variability in the estimated magnitude, ranging from −0.194 (95% CI: [−0.400, −0.012]) in the middle 50% old-growth forest model to −1.665 (−1.926, −1.404) in the non-breeders model (Table S5.1). In the latter case, among-bird variability for this variable was also high (estimated standard deviation: 0.932). As expected, step length tended to be positively associated with step duration for low- to moderate-movement step durations (Supplementary 3). Correlations among predictor variables were generally low, except between the number of small and large river mouths within 43 km (r = 0.89; Figure S5.1). The combined movement model with terrestrial/shoreline and marine predictor variables performed best, followed by the terrestrial/shoreline model after variable selection (Δ AIC = 34.6; Table 2, Table S5.1). In contrast, both the old-growth forest and marine models performed substantially worse with respect to AIC (Table S5.1). All predictors in the combined model were statistically significant (p < 0.001), which was expected

Table 2

Marbled murrelet step selection function model results for the combined model. Both marine and terrestrial/shoreline variables were included after stepwise selection. For each variable, positive parameter values indicate that murrelets tend to move toward locations with greater values of that variable. The "Estimate," "SE," "p-value," "Lower," and "Upper" columns correspond to the population-level step selection coefficients, and the σ_{bird} column shows the corresponding random slope standard deviation estimate, with higher values indicating greater among-bird variability. "Lower" and "Upper" columns show 95% confidence interval lower and upper endpoints. See Table S5.1 for additional model results.

| Term	Estimate	SE	p-value	Lower	Upper	σ_{bird}
Old-growth forest	-1.195	0.098	< 0.001	-1.388	-1.003	0.482
Sand/gravel beaches	-0.261	0.064	< 0.001	-0.386	-0.135	0.464
Zooplankton	-0.267	0.089	0.003	-0.442	-0.091	0.28
Large river mouths	-0.22	0.079	0.005	-0.375	-0.065	0.41
Salinity	0.436	0.09	< 0.001	0.261	0.612	0.461
Small rivers mouths	0.675	0.069	< 0.001	0.54	0.809	0.001
SST anomaly	-0.557	0.279	0.046	-1.104	-0.01	0.001
Distance offshore	-0.905	0.123	< 0.001	-1.146	-0.664	0
Distance offshore squared	-1.281	0.229	< 0.001	-1.731	-0.831	0.594
Step length	0.896	0.03	< 0.001	0.837	0.955	0.228
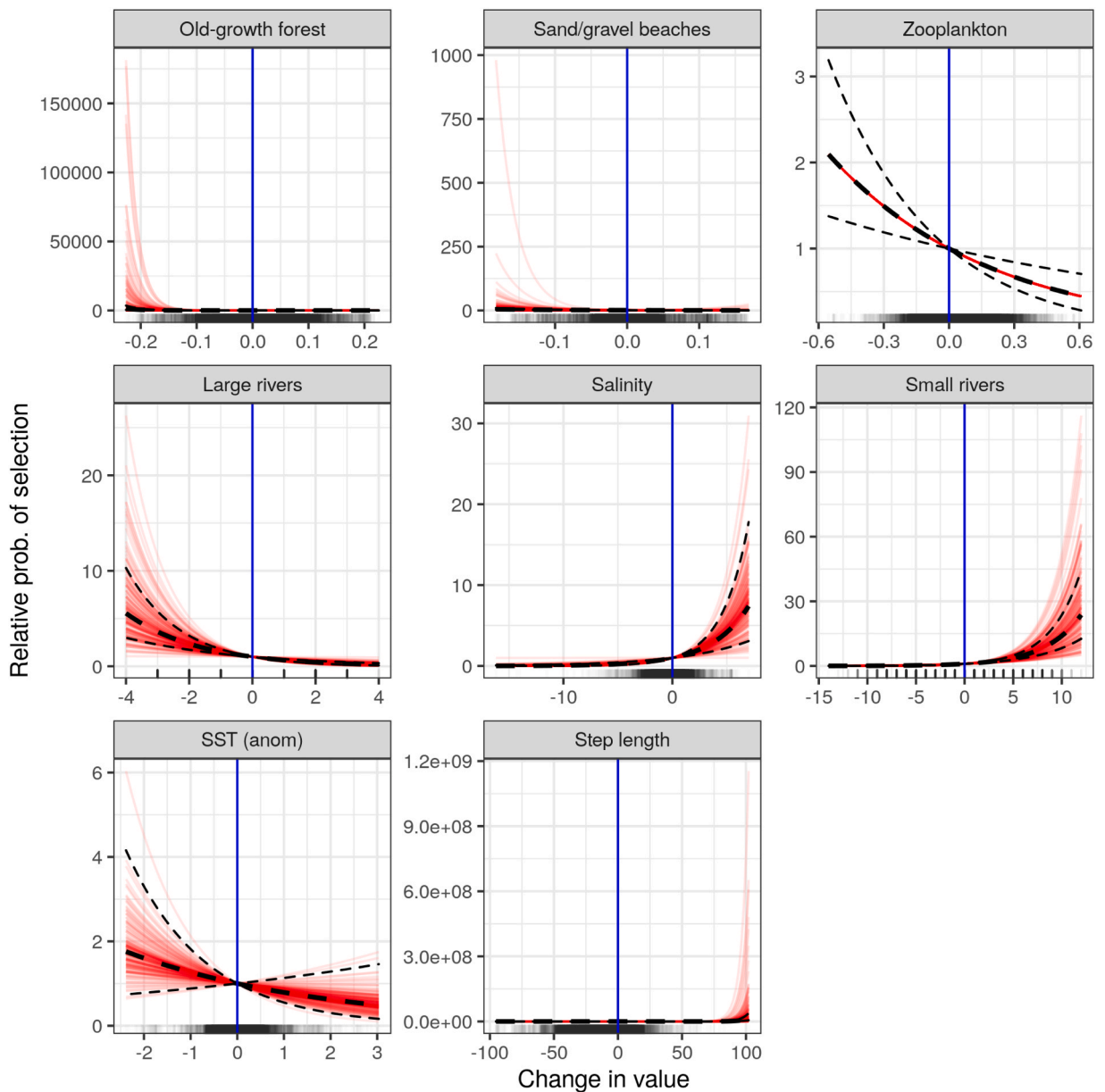
Fig. 3. Relative probabilities of selection for the combined movement model covariates used to assess marbled murrelet habitat selection, in order of having the greatest effect on movement to least effect (left to right, then top to bottom), followed by step length. Plots illustrate the relative probability of movement as a function of the change in one predictor variable when the other predictors are held constant. The thick black dashed line shows the overall estimated relationship, the thin black dashed lines show the associated 95% confidence interval lower and upper limits, and the thin red lines show estimates for individual birds. As an example, the overall relationship for zooplankton has a relative probability of approximately 0.5 at a 0.6 change in value; this indicates that, on average, marbled murrelets were half as likely to make a movement step associated with a 0.6 increase in zooplankton concentration than to make a movement step associated with no change in zooplankton concentration.

because these variables were selected using stepwise variable selection with the marine and

terrestrial/shoreline models and parameter estimates tended to be consistent across years (Table S5.2). The standard deviations of individual-specific random slopes were frequently high, indicating large variability among individual murrelets in movement patterns (Fig. 3, Supplementary 5). However, the random effect SDs for distance offshore were typically small.

3.2. Marine home ranges and use of protected marine areas

We obtained 1891 locations (range: 39–91 locations per individual) from the 35 individuals for whom we were able to calculate

marine home ranges; these individuals comprised n = 22 females and n = 13 males, and n = 6 breeders vs. n = 29 non-breeders (Table 3). We detected no strong differences in home range size based on sex, breeding status, or year of study; this was true for models using the 95% home range (sex: $\chi^2 = -12.6$, df = 34, p= 0.67; breeding status: $\chi^2 = 30.8$, df = 34, p= 0.42; year: $\chi^2 = 20.6$, df = 34, p= 0.32) as well as the 50% home range (sex: $\chi^2 = -0.14$, df = 34, p = 0.55; breeding status: $\chi^2 = 0.07$, df = 34, p = 0.82; year: $\chi^2 = 2.1$, df = 34, p= 0.19). Similarly, neither sex nor proportion of home range located within protected marine areas were significant predictors of home range size (p > 0.1). Although murrelets had overlapping home ranges throughout much of the core study area (Fig. 4), only 12.1% of murrelet relocations (n = 552) occurred within the boundaries of protected marine areas. In addition, we did not observe variation in protected marine area use across the three years of study, with no evidence that the extent of relocations occurring within protected marine areas differed between the year of poor ocean conditions with the other years we examined (2017 vs. 2018: p = 0.64; 2017 vs. 2019: p = 0.80).

3.3. Long-distance movements

The vast majority (93.3%) of relocations of tagged birds (n = 4563) occurred within our core study area, where our relocation efforts were concentrated. Aerial telemetry flights undertaken beyond our study area provided an additional 330 locations, with tagged individuals detected outside of the core study area in each year (Fig. 5). Murrelets tagged in our study ranged north to the northwestern coast of Washington and south to San Francisco Bay, California; of note, we did not detect any individuals in the Strait of Juan de Fuca in Washington. Overall, 62% of radio-tagged individuals moved out of the core study area at some point during the 2017 breeding season, whereas fewer individuals left in 2018 (24%) and 2019 (17%). Fifteen radio-tagged individuals were relocated >500 km from their capture location, with more tagged murrelets traveling this distance in 2017 (14.8%) relative to 2018 (5.3%) or 2019 (3.8%). The greatest distance traveled by a tagged individual occurred in 2017 when 2 individuals moved ~750 km from their original capture location. In contrast, the greatest distance travelled by a breeding individual was ~61 km. Our search effort beyond the boundaries of our core study area differed across years, with 60 aerial telemetry flights taken in 2017, 18 taken in 2018, and 6 taken in 2019.

4. Discussion

During three years of intensive monitoring using radio-tagging, we found that the breeding propensity of murrelets was low and a substantial number of tagged individuals moved out of our 135-km long coastal study area. Those murrelets that did remain within the core study area selected movement steps that took them closer to areas of cooler sea-surface temperatures, greater salinity, and the mouths of small rivers. Cooler sea-surface temperatures and greater salinity characterize upwelling zones and frontal boundaries (Bakun, 1996; Emmett et al., 2006) that are often rich in prey species, and such areas are used by murrelets while foraging (Becker and Beissinger, 2003); the mouths of small rivers can likewise experience enhanced prey availability through the frontal boundaries they create (Pastran et al., 2021). In contrast, we found that murrelets tended to select movement paths that took them away from areas of potential nesting habitat (old-growth forest). Although prior studies have found that murrelet at-sea distributions are often adjacent to breeding habitat (Zharikov et al., 2006; Raphael et al., 2015; Drever et al., 2021), this result is perhaps not surprising in our study given the low nesting propensity of murrelets during our study. Indeed, our findings parallel previous work that found that the link between terrestrial nesting habitat and marine foraging areas changed with ocean conditions such that murrelets distributed themselves close to nesting habitat only when upwelling and local prey availability were high (Becker and Beissinger, 2003; Peery et al., 2004). This decoupling is an important consideration for understanding where murrelets spend time on the ocean relative to good ocean conditions, with relevance to the efficacy of at-sea surveys used to quantify population trends (Raphael et al., 2015).

We found no support for the hypothesis that murrelets altered their use of protected marine areas across years with differing ocean

Table 3

Marbled murrelet home range summary statistics. Home range sizes were estimated using the permissible home range estimation algorithm. Sex is indicated as male (M) or female (F) and the column labeled 'n' reports statistics (i.e., mean, median, and range) for the numbers of relocations used to estimate murrelet home ranges. The rows 'Range' show the minimum and maximum values for each category. Home range sizes and percentages of home ranges within protected marine areas (a combination of marine reserves and marine protected areas) are expressed in the columns as 50%, 75%, 90%, and 95% probability levels, with 50% home range considered to be the core use area. Proportion of home range in protected marine areas was relatively similar across all four probability levels. Detailed home range data for each of the 35 birds used in our analysis can be found in Supplementary 4.

| Values	Sex	n	Home range size (km²)				Home range protected marine areas (%)			
			50%	75%	90%	95%	50%	75%	90%	95%
Mean	F&M	54.03	27.9	60.4	107.6	141.7	9.9%	8.2%	9.1%	9.9%
Median	F&M	48.0	20.7	49.9	87.5	117.9	5.1%	5.1%	4.9%	5.1%
Range	F&M	39–91	6.3–75.3	14.4 – 150.1	24.5–271.3	31.4–375.5	0–84.2%	0–75.2%	0–66.3%	0–63.5%
Mean	F	53.82	29.9	64.9	113.3	148.0	12.1%	10.0%	10.6%	11.3%
Median	F	48.5	22.01	52.21	88.99	118.97	9.0%	5.5%	4.9%	5.4%
Range	F	39–91	6.3–75.3	14.4–150.1	24.5–271.3	32.4–375.5	0%	0%	0.1%	0.4%
Mean	M	54.38	24.5	52.8	98.1	130.9	6.1%	5.3%	6.5%	7.3%
Median	M	48	18.9	43.7	74.8	93.5	1.7%	4.9%	5.0%	4.5%
Range	M	40–91	6.9–52.6	16.3–106.3	29.6–192.6	37.8–255.7	0–30.4%	0–14.0%	0–20.2%	0–23.6%
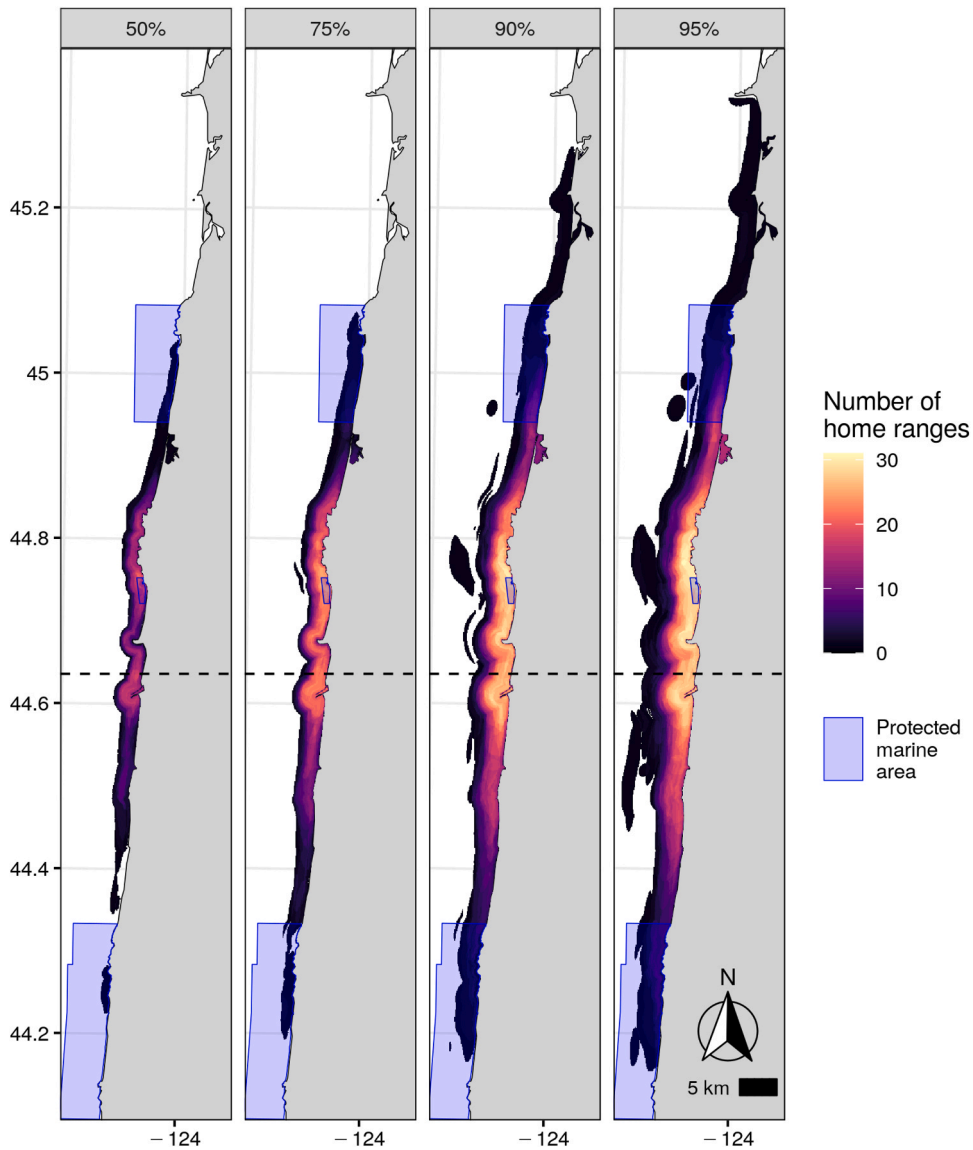
Fig. 4. Marbled murrelet home range density across the study area in relation to three protected marine areas (light blue), showing extensive home range overlap throughout the core study area. Panels show the number of home ranges based on the 50%, 75%, 90%, and 95% home ranges of the n = 35 marbled murrelets used in our analysis. The central location of our core study area (Newport, Oregon) is shown with a dashed black line.

conditions, as only ~12% of murrelet relocations overlapped with protected marine areas. There are at least three non-mutually exclusive explanations as to why tagged individuals made limited use of protected marine areas during our study. First, protected marine areas may have lacked the types of food resources sought by murrelets – such as pelagic schooling fish – that can be important diet items during the breeding season (Fountain et al., 2023). Such species are typically characterized by patchy distributions (Brodeur et al., 2005) and can occur outside of the nearshore environments where murrelets forage (Nelson, 2020), and therefore may have been missing from protected areas. More broadly, the large exodus of murrelets from our core study area is consistent with the idea that forage fish moved further offshore than where murrelets typically occur, beyond the boundaries of our study area, or both. A second potential explanation is that murrelet prey items may have occurred within protected marine areas but their use by murrelets was not energetically profitable, particularly for breeding birds with increased energetic needs. This could have been a function of reduction in forage fish quality during warmer ocean conditions (Brodeur et al., 2019; von Biela et al., 2019) and/or the relatively small footprint of protected marine areas within our study area. Finally, protected marine areas can provide larger predatory fish with protection from harvest, and competition from these upper-trophic predators may have reduced the density of forage fish prey that murrelets seek within protected marine areas. We hypothesize that all of these drivers may have worked together and led to most murrelets avoiding protected marine areas in our study.

Breeding propensity was lowest and movement out of the core study area was highest in 2017, when none of the 61 tagged
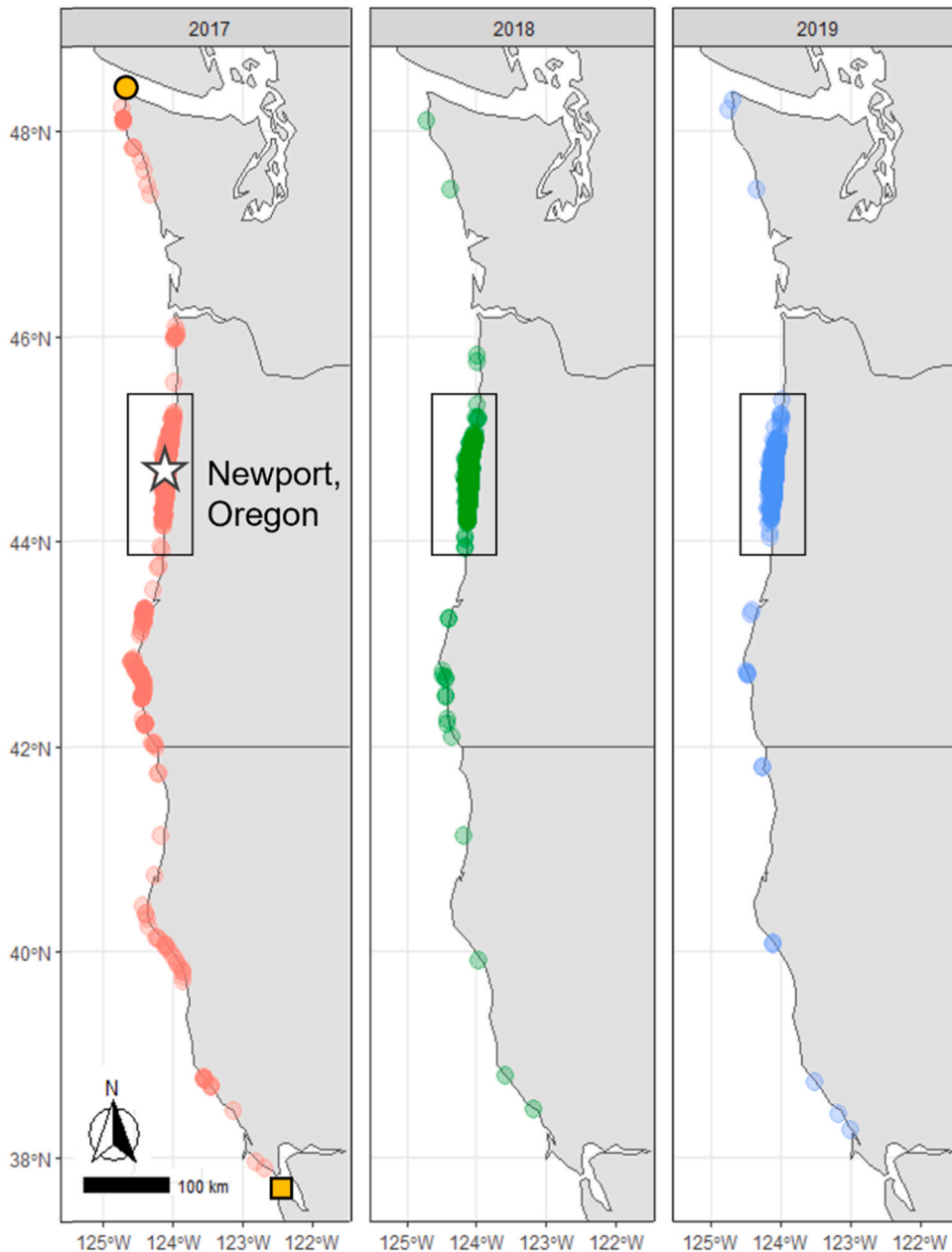
Fig. 5. Long-distance movements by radio-tagged marbled murrelets outside of the 135-km long core study area (black rectangles) during the 2017 (n=61 individuals), 2018 (n=76 individuals), and 2019 breeding seasons (n=52 individuals). The greatest proporition of tagged murrelets moving outsdie of the core study occurred in 2017 when ocean conditions were poorest and no tagged individuals nested. Searches for individuals undertaking long-distance movements took place northward to the northern border of Washington (orange circle) and into the Strait of Juan de Fuca, and southward to Santa Barbara, California with tagged individuals only being detected as far south as San Francisco, California (orange square). The white star shows Newport, Oregon, which is located close to the center of our core study area.

individuals nested and the majority of individuals left our core study area; fifteen individuals moved >500 km from their capture location. Murrelets can move large distances between foraging areas and nesting sites during the breeding season (Whitworth et al., 2000; Lorenz et al., 2017) and they can make extensive movements in the post-breeding period as well. (Bertram et al., 2015, 2023). However, there is limited evidence for long-distance movements (>250 km) within the marine environment during the breeding season like that observed in our study (Hebert and Golightly, 2008). Our observations suggest that murrelets undertake such movements to buffer against anomalous environmental conditions in their marine environment. This idea is bolstered by additional research undertaken in our study area in 2021 during a period of improved ocean conditions that found murrelets had substantially higher breeding propensity (i.e., 36.7% of 49 radio-tagged individuals) that was accompanied by very limited movement of tagged

individuals out of our core study area (Rivers et al., unpub. data). That murrelets avoided poor ocean conditions by making short-term movements to other regions in our study is consistent with a relatively large increase in the number of individuals detected at-sea in California during 2017 relative to the density of individuals recorded on surveys in that area conducted before (2013) and after (2021) our study (McIver et al., 2023). Such increases are likely due to short-term movements from more northernly regions, and do not appear to be driven by increases in breeding output in California given the relatively small numbers of murrelets in that region (McIver et al., 2023) and the low levels of recruitment that characterize murrelet populations (Beissinger, 1995; Peery et al., 2004; Nelson, 2020).

Our study found that murrelets had reduced breeding propensity during poor ocean conditions, which parallels a robust study using 20 years of survey data that found occupied sites had increased vacancy rates during poor ocean conditions (Betts et al., 2020). Our findings also concur with prior investigations that found ocean conditions can have a strong influence on whether murrelets occupy inland nest sites (Burger, 1999; Ronconi and Burger, 2008). Overall, the proportion of radio-tagged birds that nested during the course of our study (0.06) was substantially lower than that of several previous large-scale tagging studies conducted throughout the murrelet's range in British Columbia, Canada (Bradley et al. [2004]: 0.65), Washington, USA (Lorenz et al. [2017]: 0.13), and California, USA (Peery et al. [2004]: 0.31) even though we used the same capture (Whitworth et al., 1997) and tagging procedures (Newman et al., 1999) as prior studies. Although differences in the location and timing of prior tagging studies introduces additional variation, such strong differences suggest that at least one – and perhaps multiple – environmental factors in our study differed substantially from prior investigations. We hypothesize that the environmental conditions that characterize our study area (i.e., open ocean conditions where murrelets are exposed to basin-scale perturbations to the marine environment) contributed to the marked reduction in nesting activity and concurrent increase in large-scale movements during our study, which took place shortly after the widespread marine heat wave of 2014–2016. This idea is based on studies in other parts of the murrelet's range that have found lower breeding activity by murrelets that foraged on the open ocean, relative to those inhabiting protected bays and inlets (Bradley et al., 2004; Lorenz et al., 2017). Additionally, oceans conditions during our study were worse relative to historic conditions in our study area (Harvey et al., 2020; Weber et al., 2021); thus, the low nesting propensity of tagged birds in our study appears to be explained by both generally poor ocean conditions and the open ocean environment that murrelets encounter in the central coast of Oregon.

Despite the limited breeding activity we observed, our study area has long been considered a murrelet population stronghold within its ESA-listed range considering the relatively high abundance and low coefficient of variation of at-sea abundance estimates (Raphael et al., 2015; McIver et al., 2023). Thus, the low breeding propensity we observed should not be indicative of this area being poor for murrelet conservation; instead, it should serve as a reminder that even areas that serve as strongholds for imperiled species can, and do, experience strong negative impacts to populations that are driven by climate change. On the one hand, murrelets may be able to undertake behaviors that buffer against poor ocean conditions and allow them access to food resources that support successful reproduction (Strong and Duarte, 2023). However, marine heatwaves are increasing in both their frequency and intensity (Laufkotter et al., 2020), some of which will continue to negative impact populations of murrelets and other upper trophic predator within marine environments (Piatt et al., 2020; Soledad Lemos et al., 2020; Rivers et al., 2022; Jones et al., 2023; Woehler and Hobday, 2023). Whether such ongoing changes will increase the likelihood that contemporary protected marine areas are used by upper trophic predators is unclear, and ultimately may require the establishment of new protected marine areas for effective conservation measures of threatened taxa with the continued expansion of climate change (Bruno et al., 2018; Wilson et al., 2020).

CRediT authorship contribution statement

Rivers James: Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Betts Matthew:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization. **Roby Daniel:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Nelson Kim:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Adrean Lindsay:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Data curation. **Bailey Guerrero Jennifer:** Writing – review & editing, Writing – original draft, Investigation. **Wolf Christopher:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Garcia-Heras Marie-Sophie:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02857.

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