



Habitat associations of marbled murrelets during the nesting season in nearshore waters along the Washington to California coast



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ABSTRACT

The marbled murrelet (*Brachyramphus marmoratus*) is a seabird in the family Alcidae that forages in nearshore waters of the Pacific Northwest, and nests in adjacent older-forest conifers within 80 km offshore. The species is of conservation concern due to habitat loss and declining numbers, and is listed as Threatened in British Columbia, Canada and in the United States portion of its range south of Canada. Recent monitoring in the United States indicated that murrelet numbers continued to decline there, especially in the waters of Washington State. To better understand this decline, and to inform conservation planning for the species, we evaluated how terrestrial and marine factors influence the distribution and abundance of the murrelet in coastal waters, including whether at-sea hotspots of murrelet abundance exist. Murrelet at-sea abundance and distribution were determined by surveys conducted annually from 2000 to 2012 in coastal waters from the United States–Canada border south to San Francisco Bay. We summarized mean and variance of murrelet density at the scale of 5-km segments of coastal waters throughout this area. We used a boosted regression tree analysis to investigate the contributions of a suite of marine and terrestrial attributes to at-sea murrelet abundance in each segment. We observed several regional hotspots of higher murrelet abundance at sea. Terrestrial attributes made the strongest contribution, especially the amount and cohesiveness of suitable nesting habitat in proximity to each segment, whereas marine attributes explained less of the spatial and temporal variations in murrelet abundance. At-sea hotspots of murrelet abundance therefore reflect not only suitable marine foraging habitat but primarily the proximity of suitable inland nesting habitat.

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1. Introduction

Spatial and temporal factors that influence the distribution and abundance of species are of considerable interest to effective conservation planning. Identifying hotspots of abundance can help identify areas to focus protection or other conservation measures (Amorim et al., 2009; Barbaree, 2011; Game et al., 2009; Nur et al., 2011; Suryan et al., 2012). Knowledge of these factors can also help us understand potential areas of conflict between human uses and important habitats to species (Winiarski et al., 2013). For example, understanding seabird distribution can help select locations for alternative energy developments (wave, tidal, wind) that minimize impacts to seabirds (e.g., Fox et al., 2006; Winiarski et al., 2013). In addition, understanding habitat relationships helps identify the factors that, if they can be manipulated, might be managed to have the greatest influence on population distribution and abundance.

The marbled murrelet (*Brachyramphus marmoratus*), a seabird in the Alcidae family, forages in nearshore waters along the coast of North America from the Aleutian Islands south to central California. It was declared Threatened under the United States Endangered Species Act (ESA) in the portion of the range from the Washington–British Columbia border to the southern end of its range (USFWS, 1997). As a result of the murrelet's legal status, there is great interest in understanding its biological status and trend as well as the factors that act as stressors on the population and that may contribute to species recovery. Unlike other seabirds, the murrelet nests up to 80 km inland, generally on the limbs of older coniferous trees but occasionally on the ground or on cliffs. Because of its inland nesting behavior and distance constraints on how far it forages from nests, the at-sea distribution of murrelets, especially during the nesting season, is likely to be influenced by the distribution of suitable nesting habitat. A nesting murrelet can be thought of as a central place forager (Orians and Pearson, 1979) with the nest as the central place. Other alcids, such as the common murre (*Uria aalge*), are colonial nesters and forage from a fixed colony site. In that case, available foraging habitat is subject to energetic constraints and is

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therefore restricted to some radius around the colony location (Burke and Montevecchi, 2009; Elliott et al., 2009). The murrelet, however, is not a colonial nester, but similar constraints may apply (Raphael et al., 2011; see the Methods section 2.2).

Given the dispersed distribution of the murrelet's nesting habitat, we were interested in how the amount of that habitat influences the local at-sea abundance of the murrelet during the breeding season. Marine conditions, specifically the amount of suitable prey, should also affect the at-sea distribution of murrelets (Ainley et al., 1995; Haynes et al., 2011), but previously we did not know the relative strength of influence of marine versus terrestrial habitat features on their distribution. We were also interested in the functional shape of the relationship between murrelet at-sea abundance and marine or terrestrial habitat features, as well as interactions between habitat features. To investigate these questions, we developed a statistical model relating murrelet abundance at sea to a suite of both marine and terrestrial attributes.

2. Methods

2.1. Marbled murrelet abundance

As part of the Effectiveness Monitoring Program for the Northwest Forest Plan (Huff et al., 2006; Raphael, 2006), we counted murrelets in nearshore waters from small boats by using line transect methods with distance estimation to account for detectability (Buckland et al., 2001; Raphael et al., 2007). We followed at-sea transects within primary sampling units (PSUs) that were roughly rectangular areas of about 20 km of coastline and that were generally contiguous over the entire sampling area. We divided each PSU into nearshore and offshore subunits corresponding to changes in murrelet density with distance from shore; the nearshore subunit was further subdivided into 4 5-km segments. Transect lines in each segment were parallel to shore and located at randomly assigned distances from shore up to 1.5 or 2.0 km from shore depending on location (Fig. 1; see Raphael et al., 2007 for details). Offshore transects were laid out in a zig-zag pattern out to a maximum of 8 km from shore (Fig. 1). For this study we restricted our analysis to the nearshore segments as these had the most complete coverage and because murrelet density decreases with distance from shore. Sampling began in year 2000 and extended to year 2012. All samples were obtained between May 15 and July 31, a period that corresponds with murrelet nesting.

We used the software program DISTANCE (Thomas et al., 2010) to estimate density of murrelets in each segment each year. We computed a detection function based on the distribution of sighting distances to each group of murrelets, an estimate of group size, and the exact transect length for each segment. We then computed the area of each segment based on length along coast and overall distance from shore

and multiplied density by that area to compute abundance (estimated number of murrelets per segment).

To identify murrelet “hotspots” (Nur et al., 2011; Sydeman et al., 2006) along the coast, we examined patterns of mean and coefficient of variation (CV) in murrelet abundance; the CV provides a measure of temporal variability in abundance. We defined coastal hotspots as those 5-km segments that had higher mean abundance (upper 20th percentile of all segments) and lower CVs (lowest 20%).

2.2. Covariates

We calculated all covariates annually from 2000 to 2012 for each at-sea survey segment. Covariates varied spatially (by segment), temporally (by year), or both spatially and temporally (Table 1). Covariates were also associated with either marine foraging habitat suitability or terrestrial nesting habitat suitability (Table 1).

The first three marine covariates in Table 1 were based on proximity to terrestrial features that may influence observed at-sea abundance of murrelets, presumably due to effects on foraging conditions. These included the mean perpendicular distance (m) from the survey transect to shore for all at-sea surveys in a segment for the given year, the distance (km) from the survey segment center to the nearest major river (defined by a flow $> 166 \text{ ft}^{-3} [4.7 \text{ m}^{-3}]$ based on the USGS Enhanced River Reach Data 2.0 from 2003), and the predominant shoreline type. Shorelines were classified based on the Environmental Sensitivity Index (NOAA, 2002), which categorizes shorelines into 21 major classes. We simplified these into 11 classes and then calculated the predominant shoreline type within each survey segment boundary. This calculation resulted in 7 types represented in our study area (Table 2).

The remaining marine covariates in Table 1 were based on oceanographic conditions that may influence prey availability (primarily fish) and therefore murrelet abundance at sea. Because foraging conditions within each survey segment are likely to be influenced by marine conditions at broader scales, we calculated the remaining marine covariates that vary spatially based on the mean or sum (depending on the covariate) of values within a 10-km moving window. We then extracted the mean values of the moving window result within each survey segment (i.e., the mean of all moving window centers that fell within the segment boundary).

We obtained monthly mean sea surface temperature (SST) and chlorophyll-*a* concentration (ChlorA) data from the NASA Earth Observations (2012) portal. Data from 2000 to 2002 were collected by the SeaWiFS platform and data from 2003 to 2012 were collected from the MODIS Aqua platform (http://aqua.nasa.gov/about/instrument_modis.php). We then calculated the mean SST ($^{\circ}\text{C}$) and ChlorA concentration (mg/m^3) within 10 km of the survey segment during two seasons, summer (values from May to July) and winter (values from Dec to Feb). All data were raster images with a resolution of 0.1° latitude/longitude.

We quantified marine human footprint based on a raster model of human threats to marine ecosystems (Halpern et al., 2008), including commercial shipping, pollution, commercial and recreational fishing, climate change (ocean acidification, ultraviolet radiation, and changes in sea temperature), invasive species, and benthic structures. This covariate was calculated based on the mean value within 10 km of the survey segment.

To quantify bathymetric influences on murrelet abundance, we used two approaches. First, we calculated the mean depth within 10 km of the survey segment based on a 250-m digital elevation model (USGS). Second, based on the same bathymetric data, we summed the area (km^2) of depths suitable for foraging within 10 km of the survey segment, hereafter referred to as “foraging area.” Suitable foraging depths were based on a threshold ($< 25 \text{ m}$ deep, except for the San Juan Islands and northern Puget Sound, for which the threshold was $< 40 \text{ m}$); the thresholds were based on natural breaks observed in the plots of murrelet abundance versus depth.

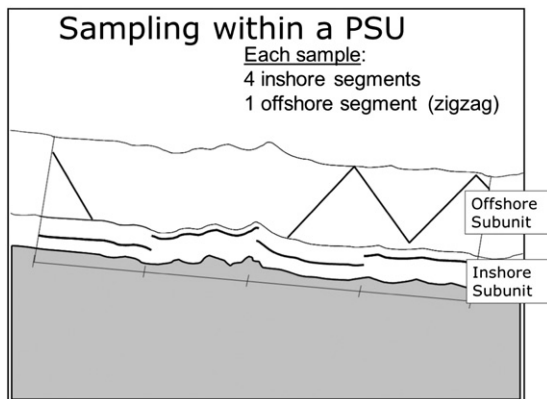


Fig. 1. Layout of at-sea transects used to estimate density of marbled murrelets. In this study, we analyzed data from only the inshore subunits.

Table 1

Description, abbreviation, variability (spatially, temporal, or both spatial and temporal), and habitat component (marine or terrestrial) represented for each covariate evaluated.

Covariate	Abbreviation	Variability	Habitat
Survey distance to shore (m)	ShoreDistance	Spatial & temporal	Marine
Distance to major river (m)	DistToMajorRiver	Spatial	Marine
Majority shoreline type	ShoreType	Spatial	Marine
Chlorophyll <i>a</i> summer (May–July) (mg/m ³)	ChlorA_summer	Spatial & temporal	Marine
Chlorophyll <i>a</i> winter (Dec–Feb) (mg/m ³)	ChlorA_winter	Spatial & temporal	Marine
Sea surface temperature summer (May–July) (°C)	SST_summer	Spatial & temporal	Marine
Sea surface temperature winter (Dec–Feb) (°C)	SST_winter	Spatial & temporal	Marine
Marine human footprint	MarHumanFoot	Spatial	Marine
Depth (m)	Depth	Spatial	Marine
Foraging area (km ²)	ForagingArea	Spatial	Marine
Biological spring transition day	BioTransDay	Temporal	Marine
Physical spring transition day	PhysSprTransDay	Temporal	Marine
Upwelling season duration	UpwellSeasonDur	Temporal	Marine
Upwelling anomaly	UpwellAnom	Temporal	Marine
Oceanic Niño index summer (May–July)	ONI_summer	Temporal	Marine
Oceanic Niño index winter (Dec–Feb)	ONI_winter	Temporal	Marine
Pacific Decadal Oscillation index summer (May–July)	PDO_summer	Temporal	Marine
Pacific Decadal Oscillation index winter (Dec–Feb)	PDO_winter	Temporal	Marine
Nesting habitat area	NestingHabitat	Spatial & temporal	Terrestrial
Nesting Habitat Cohesion	NestHabitatCohesion	Spatial & temporal	Terrestrial
Terrestrial Human Footprint	TerrHumanFootprint	Spatial	Terrestrial

The next four marine covariates were indices of temporal (but not spatial) variation in local Pacific Ocean conditions based on measurements from the NOAA Northwest Fisheries Science Center (NWFS, 2012) NH05 sampling station 9 km offshore of Newport, Oregon. The biological spring transition day was calculated as the date when the zooplankton community composition changes from a winter to a summer mix. The physical spring transition day was based on the date of the minimum value of the cumulative upwelling index (Schwing et al., 2006). Upwelling season duration was calculated as the number of days between the spring physical transition and the fall physical transition (i.e., transition from summer to winter upwelling conditions). Upwelling anomaly was defined by the difference in upwelling between the current year and the mean upwelling index from 1946 to the present.

The last four marine covariates were indices of broader Pacific Ocean conditions, including the Pacific Decadal Oscillation (PDO; Mantua et al., 1997) and the El Niño Southern Oscillation (ENSO; Trenberth, 1997). The PDO index (JSAO, 2012) is based on variation in North Pacific SST from 1900 to the present. The Oceanic Niño Index (ONI), a measure of the state of the ENSO, is based on variation in equatorial Pacific SST (NOAA Climate Prediction Center, 2012). Both indices are calculated on a monthly basis, which we then averaged for two seasons, summer (values from May to July, representing conditions during the central murrelet nesting season) and winter (values from December to February, representing the period preceding nesting).

To quantify the terrestrial habitat influences on at-sea marbled murrelet abundance, we calculated three covariates that quantified the amount and fragmentation of nesting habitat as well as degradation by human modification. Murrelets can commute up to 124 km from foraging to nesting sites (Whitworth et al., 2000), but studies show great variation in observed distance between nest sites and foraging sites

(Barbaree et al., 2014; Hébert and Golightly, 2008; Nelson, 1997; Peery et al., 2009; Raphael and Bloxton, unpublished data). For purposes of this analysis, we calculated an average foraging range of about 80 km from these published studies and used that distance to define an 80-km moving window around each survey segment. We then calculated the mean of the moving window result within each survey segment (i.e., all moving window centers that fell within the segment boundary). Although our main study area did not extend north of Washington State, in some areas of Washington the 80-km window included terrestrial habitat in British Columbia, Canada. We quantified terrestrial nesting habitat based on a marbled murrelet nesting habitat spatial model produced for the United States portion of our study area (Raphael et al., 2011). This model classified nesting habitat into four categories. However, for our analysis we converted it into a binary model using the highest habitat quality class and grouping the other categories as less suitable. Temporal variation in nesting habitat was represented by modeling habitat changes between 2000 and 2012. For the British Columbia terrestrial areas, we defined nesting habitat based on areas designated by the Ministry of Forests, Lands, and Natural Resource Operations as Old Growth Management areas (FLNRO, 2012). We also calculated the fragmentation of nesting habitat using the patch cohesion metric in Fragstats (McGarigal et al., 2012), also within an 80-km moving window. Finally, we calculated the mean terrestrial human footprint within an 80-km moving window based on a model of anthropogenic landscape modifications, including human habitation, roads, railroads, irrigation canals, power lines, linear feature densities, agricultural land, campgrounds, highway rest stops, landfills, oil and gas development, and human induced fires (Leu et al., 2008).

2.3. Statistical analysis

We used boosted regression trees with a Poisson loss function to explore the relationship between murrelet at-sea abundance and our suite of marine and terrestrial covariates. Boosted regression tree (BRT) is a machine learning approach combining regression trees with a boosting procedure that adds new trees to the model fit to the residuals of the prior trees (Elith et al., 2008; Haynes et al., 2011). The BRT prediction is optimized based on two main parameters, the learning rate and tree complexity. The learning rate, also called shrinkage rate, determines the contribution of each new tree added to the model, while tree complexity determines the number of nodes per tree. Following recommendations of Elith et al. (2008), we used a learning rate of 0.01 and a tree complexity of 5 throughout our analysis. The optimal number of trees

Table 2

Frequency of shoreline types (ShoreType) among 5-km coastal segments.

Type	Code	Frequency	Percent
Exposed rocky shores	1	1082	26.0
Exposed wave-cut platforms, scarps, and steep slopes	2	590	14.2
Fine- to medium-grained sand beaches	3	1168	28.1
Coarse-grained sand beaches	5	216	5.2
Gravelly beaches	6	869	20.9
Exposed tidal flats	7	206	5.0
Man-made structures, riprap	11	25	0.6

was selected based on training the model to one half of the data and then assessing the fit of the model to the remaining half. When new trees began to reduce the fit of the model to the test data, no new trees were added. Final model parameters were derived from an ensemble of all trees weighted by the learning rate.

Because our sample units were contiguous 5-km segments of coastal waters, they might exhibit spatial autocorrelation. To account for spatial autocorrelation in the BRT model residuals, we calculated a residual autocovariate term (RAC), as in Crase et al. (2012), by plotting the residuals from the BRT model to raster grid cells representing each survey segment, calculating the mean residual within a 25 km moving window, and then extracting the moving window result for each survey segment grid cell. We then refit the BRT model as before but included the RAC term.

We assessed variable importance based on the number of times that a variable was used for splitting, weighted by the squared loss of deviance due to each split, and averaged over all trees; deviance measures the loss in predictive performance due to a suboptimal model, thus reducing deviance represents improved model fit. The result was scaled such that the sum of all variable importance scores added to 1, allowing them to be interpreted as percent contributions to the final model. We assessed model performance using a ten-fold crossvalidation procedure that involved training the model on ten random subsets (90%) of the full data and then evaluating the model predictions against the portion of the data withheld (10%) from the model. All BRT models were fit in R (version 3.0, R Core Team, 2012) using the dismo package for species distribution modeling (Hijmans et al., 2012).

To reduce model complexity, we used a jackknifing procedure where we removed one variable at a time (based on the variable of the lowest importance), refit the model, and repeated until removing a variable significantly increased the model deviance. This procedure resulted in a more parsimonious model that had similar explanatory power to the full model.

3. Results

3.1. Murrelet abundance

Murrelet density was highly variable along the coast, ranging in any one year from 0 to 147 birds/km² (Table 3). Areas representing the upper 20th percentile of abundance were evident along the Strait of Juan de Fuca in Washington, the central Oregon coast, and northern California (Fig. 2). These areas also showed consistently lower than

average variability among years (Fig. 2). Variation among segments was greater than variation within segments over time (Fig. 3).

3.2. Boosted regression models

Our boosted regression model using all covariates in Table 1 plus the residual autocorrelation term explained 84% deviance in murrelet abundance in all segments and 64% deviance in segments held out in cross-validation. After screening these covariates using a jackknife procedure, we dropped 6 that made little contribution to the model to produce a more parsimonious model (Fig. 4). Doing so had no effect on explained deviance; explained deviance was still 84% overall and 64% for cross-validated segments. Among the remaining covariates, Nesting Habitat Cohesion (23%) and Amount of Nesting Habitat (21%) had the greatest relative influences on the model; the next highest contributor was Shore Distance (7%) (Fig. 5). Murrelet abundance increased quite rapidly at levels of cohesion above the mean of 78 units and increased as Amount of Nesting Habitat increased (Figs. 2, 6). Murrelet abundance decreased with increasing Shore Distance and with increased index values of the Terrestrial Human Footprint. Response curves were less clearly defined for Sea Surface Temperature and Chlorophyll. Murrelet abundance was greater in waters associated with sandy shores (Shore Types 3 and 5), as well as with shores with man-made structures and rip-rap (Shore Type 11, Fig. 6), although the latter type was rare in the study area (Table 2).

We also observed a strong interaction between Amount of Nesting Habitat and Habitat Cohesion (Fig. 7). Areas with both high cohesion and greater Amount of Nesting Habitat were associated with greater density of murrelets in segments adjacent to those sites.

4. Discussion

Many studies have examined the role of physical and biological processes on seabird abundance and distribution in the California Current System (CCS) and elsewhere (e.g., Ainley et al., 1995; Haynes et al., 2011; O'Hara et al., 2006; Sydeman et al., 2009; Thayer and Sydeman, 2007). Few of these, however, have factored in the role of nesting habitat, or distance to nesting habitat, in the birds' distribution (but see Barbaree, 2011; Clarke et al., 2003; Peery et al., 2009). In our study, it is apparent that the location, amount, and especially landscape pattern of terrestrial nesting habitat are strong predictors of the spatial and temporal distributions of marbled murrelets at sea in the CCS and the Salish Sea. Murrelets are very different from most seabirds in their use of terrestrial habitats. Even within the alcid family they are unusual: they nest individually or at best semi-colonially, and in trees at inland locations up to 80 km from the coast; they forage at distances up to 120 km away from the coast in Alaska (Whitworth et al., 2000). Most seabirds nest on the ground in colonies with high densities, mostly on islands, near-coast rocks or narrow bands of coastal cliff. As a result, this dependence or terrestrial influence is not unexpected, given that the nesting murrelet is a central place forager. We certainly expected that proximity of nesting habitat would play some role in at-sea abundance. What we did not expect is that variation in murrelet abundance would be so highly correlated with amount and cohesion of terrestrial nesting habitat and variables describing marine foraging habitat would have a small role, compared to terrestrial factors. What this indicates perhaps is that a lot of potential murrelet foraging habitat exists but is un-used in the present, very low population status of this species.

It is possible that our suite of marine covariates does not adequately convey information on murrelet foraging habitat. The marbled murrelet is a pursuit diver that preys primarily upon small schooling fishes including sand lance (*Ammodytes hexapterus*), anchovy (family Engraulidae), herring (*Clupea pallasii*), and juvenile rockfish (*Sebastes* spp.) during spring and summer (Burkett, 1995; Nelson, 1997). We did not have information on the spatial and temporal distributions of these forage fishes that we could include in our models. Instead, we relied on

Table 3
Descriptive statistics for murrelet density and for each covariate evaluated. See Table 1 for descriptions and units.

Covariate	n	Minimum	Maximum	Mean	SD
Murrelet density (n/km ²)	4182	.0	147.0	6.3	13.5
ShoreDistance (m)	4069	150.0	2925.0	840.6	428.3
ChlorA_winter (mg/m ³)	3012	.5	29.6	2.9	2.7
ChlorA_summer (mg/m ³)	3682	.6	24.1	7.9	4.1
SST_winter (°C)	4037	6.6	13.2	9.0	1.6
SST_summer (°C)	3918	9.1	17.2	12.3	1.2
ForagingArea (km ²)	4182	130.7	3694.4	932.1	672.7
Depth (m)	4182	13.4	158.0	53.3	30.7
BioTransDay (Julian day)	4182	64	230	118.9	41.8
PhysSprTransDay (Julian day)	4182	70	142	105.7	20.3
UpwellAnom	4182	-55	9	-21.4	18.4
UpwellSeasonDur	4182	129	218	174.3	23.6
MarHumanFoot	4182	4.7	33.4	15.8	6.6
TerrHumanFootprint	4182	2.7	6.0	4.2	1.0
NestingHabitat (km ²)	4082	.1	151.5	59.9	40.1
ONI_winter	4182	25.0	28.3	26.4	1.0
ONI_summer	4182	26.9	28.3	27.6	.4
PDO_winter	4182	-2	2	-1	1.1
PDO_summer	4182	-1.3	1.2	-1	.7
DistToMajorRiver (km)	4182	1.1	59.7	13.8	11.3
NestHabitatCohesion	4182	24.5	93.3	77.9	8.7

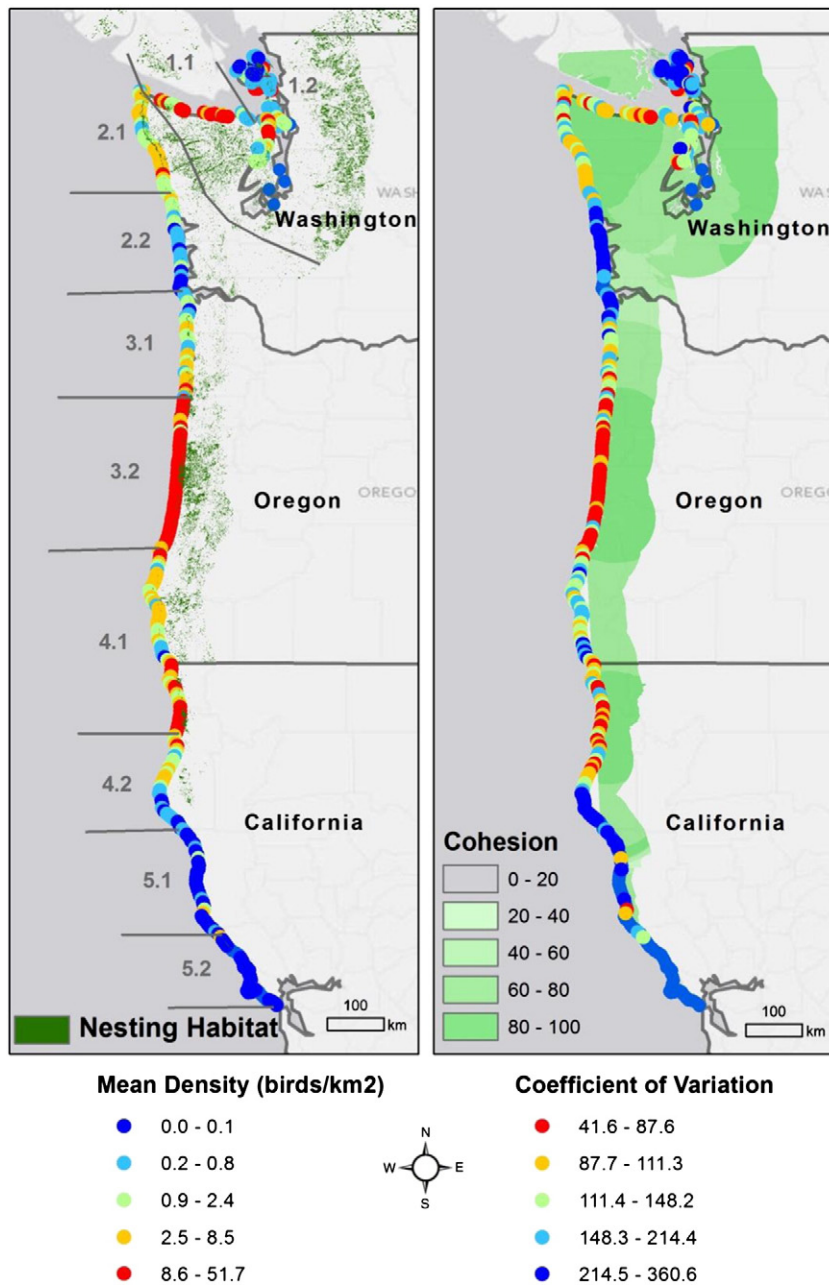


Fig. 2. Mean density and coefficient of variation (CV) in marbled murrelets in 5-km segments in nearshore waters of the Pacific Coast, USA. Red ovals denote “hotspots” with higher than average murrelet density and lower than average CV. Amount of suitable nesting habitat is depicted in the left figure; cohesion of that habitat is depicted on the right figure. Cohesion is indexed from 0 (no cohesion) to 100 (high cohesion). Numbers denote coastal strata.

oceanographic features such as SST, chlorophyll concentration, and upwelling, which have been used as indicators of prey availability (Emmett, 2006; Hooff and Peterson, 2006; Peterson et al., 2010). Particularly in the depleted status of the murrelet population, we assume a bottom-up process whereby SST and upwelling drive prey availability as follows:

upwelling → nutrients → plankton → forage fish → murrelets.

Each of the linkages in this conceptual model involves some unknown time lag, spatial variation, and other sources of uncertainty so we expect our measures of marine condition to be imprecise estimates of murrelet prey availability. In the CCS, wind-driven upwelling and the subsequent advection of the upwelled water in the form of cold,

chlorophyll-rich filaments and the associated eddies has strong influences on secondary ocean productivity (Castelao et al., 2006; Kahru et al., 2012; Strub et al., 1991) and previous research has established the utility of these linkages to seabirds (e.g., Ainley et al., 1993, 2009; Becker et al., 2007; Black et al., 2010; Peery et al., 2009; Santora et al., 2011).

One of the defining features of seabirds is that they breed on land and yet they spend most of their lives and obtain their food from the sea. As a result, their distribution and abundance at-sea during the breeding season is influenced by both terrestrial and marine factors (Haynes et al., 2011; Peery et al., 2009). Based on the relative importance of covariates in our model, we hypothesize that murrelet at-sea habitat selection during the breeding season may be hierarchical. Because the amounts of high quality and highly cohesive nesting habitat

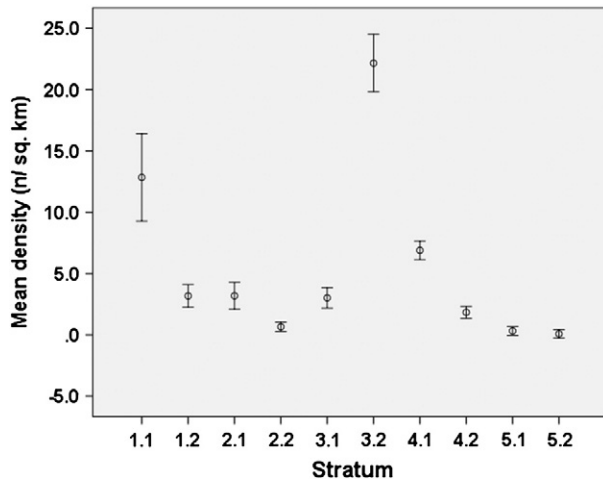


Fig. 3. Mean density of marbled murrelets across coastal strata from Washington south to California (see Fig. 2 for locations of each stratum). Variation within strata across years (2000 to 2012) is represented by error bars.

are the most influential variables in our model, we suggest that murrelet coastal abundance at broad spatial scales is initially driven by the proximity of the marine environment to these terrestrial habitats, and as noted there is a lot of suitable foraging habitat that is un-used in the low population state of this species.

Extensive landscapes of high quality and cohesive nesting habitat are likely to attract more nesting murrelets (Meyer and Miller, 2002) resulting in higher densities of murrelets in the adjacent marine waters (Raphael, 2006). Within these suitable stretches of coast, small-scale space use by murrelets at-sea is likely driven by suitable foraging conditions which, in turn, are influenced by an interaction between prey resources, oceanographic conditions (e.g., SST), and physical features (depth, distance to major rivers, and foraging area) (Balance, 2007). In the absence of suitable forage fish data across our study area, chlorophyll-*a*, which can be remotely sensed at large spatial scales, provides insights into spatio-temporal patterns of primary productivity (Field et al., 1998) and can be used to indirectly identify areas with high levels of trophic transfer (Henson and Thomas, 2007). This relationship between trophic transfer and chlorophyll-*a* concentrations is grossly imperfect and usually results in high but variable correlations between at-sea abundance of seabirds and chlorophyll-*a*, except at the largest scales (Nur et al., 2011; Suryan et al., 2012). At the same time,

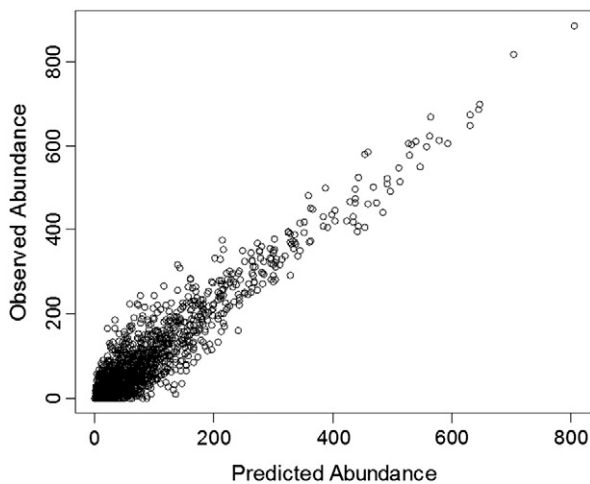


Fig. 4. Boosted regression model fit for abundance of marbled murrelets in 5-km segments along the Pacific Northwest Coast, USA, based upon the full set of covariates listed in Table 1 less those that made little contribution to explained model deviance.

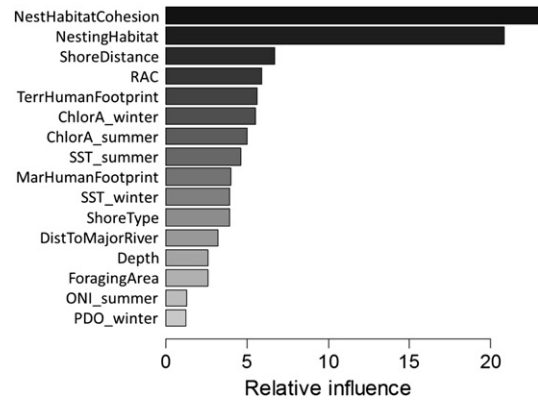


Fig. 5. Relative influence of marine and terrestrial covariates in boosted regression model of marbled murrelet abundance in 5-km segments along the Pacific Northwest Coast, USA. See Table 1 for information about each covariate.

seabird occurrence is affected by physical features that enhance productivity, and concentrate prey, such as surface currents, fronts and water masses (Ainley et al., 2009; Balance, 2007; Ballance et al., 2006; Croll et al., 2005; Yen et al., 2004). In this study, the influences of marine conditions (SST), productivity (chlorophyll-*a*) and physical features (near-by rivers, depth and shore type) were much smaller than the influences of terrestrial features, but we cannot rule out the possibility of complex interactions among these marine factors in shaping their small-scale, at-sea space use in areas adjacent to extensive patches of suitable nesting habitat.

We observed much greater spatial variation of murrelet density among different segments along the coast than temporal variation (among years) within segments (Fig. 3). It is not surprising, therefore, that covariates with a spatial variation component (Table 1) were all more influential on our model than covariates with only temporal variation. Our indices of upwelling and Pacific Decadal Oscillation were the lowest ranked in our model; the remaining temporal indices were all excluded from our more parsimonious model because they contributed so little to the explained deviance. The covariates that varied only temporally were all marine attributes, and if we had finer-scaled spatial and temporal data for these covariates, we might have been able to better detect marine influences on murrelet distribution, such as upwelling fronts and plumes (e.g., Ainley et al., 2009).

4.1. Management implications

We identified several hotspots of higher than average murrelet abundance along the Pacific coast. These areas can now be used to identify broad areas of potential conflicts between murrelet conservation and other human activities such as alternative energy development, fishing, and boat traffic and to target important areas for protection. Finer-scale research will be needed, however, to more closely target management opportunities within these broadly defined areas of higher murrelet abundance.

Although our results do not establish causal relations between murrelet abundance and the covariates that we modeled, our observation that variables describing the amount and pattern of suitable nesting habitat dominated our model do imply that the distribution of murrelets in our study area currently is best explained by the distribution of nesting habitat. If this observation reflects underlying processes, then conservation of the murrelet will require conservation of suitable nesting habitat. Landscape pattern of nesting habitat, as estimated with our cohesion index, interacts with the amount of that habitat such that areas with both greater amount of habitat and high cohesion are associated with greater offshore density of murrelets (Fig. 7). Land managers might target those areas with both high cohesion and high amounts of nesting habitat as supporting the greatest numbers of

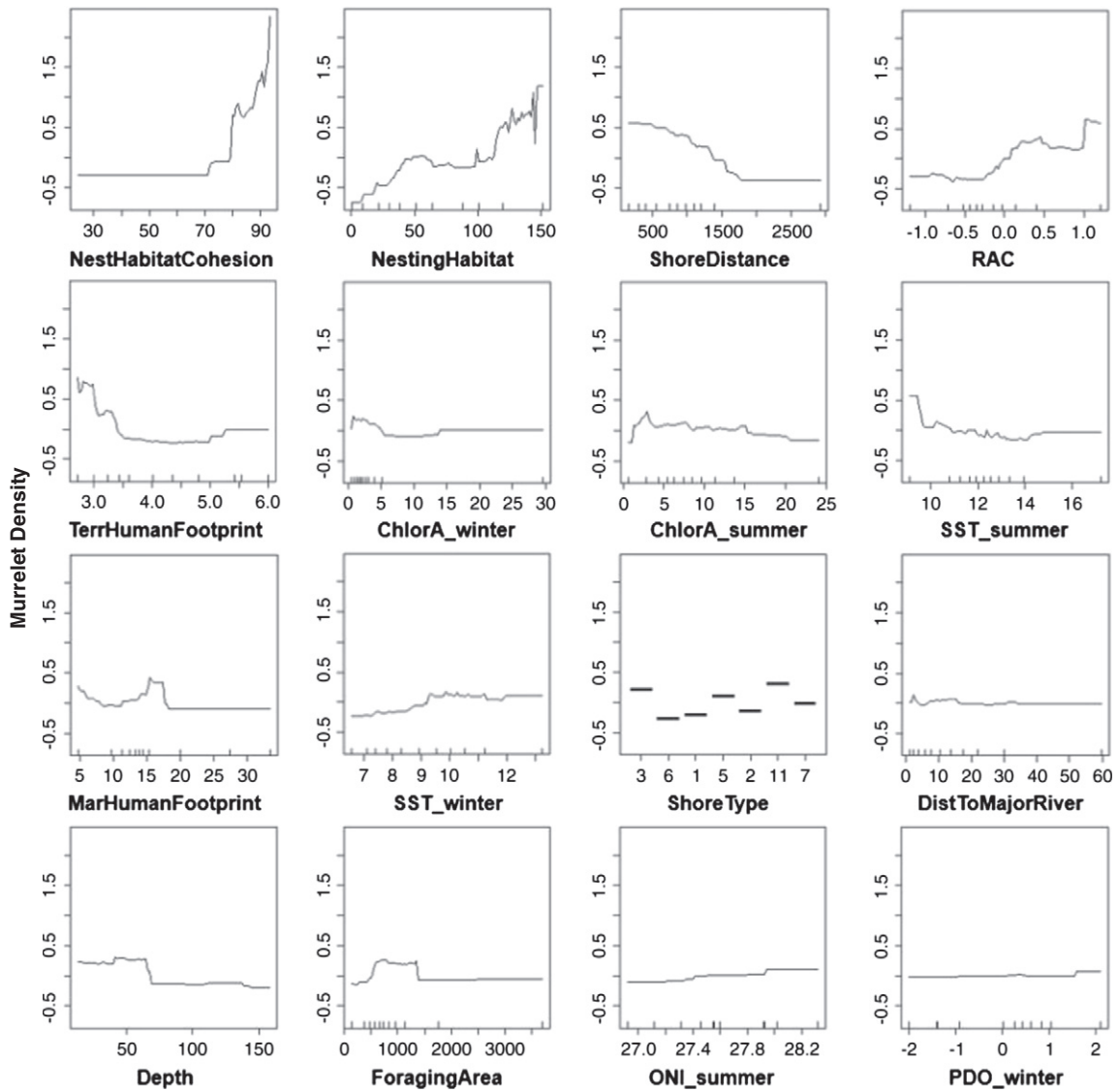


Fig. 6. Response curves (marbled murrelet density) for covariates depicted in Fig. 4. See Tables 1 and 2 for information about each covariate.

murrelets (as illustrated by the hotspots identified in Fig. 2). In addition, given the sharp non-linear increase in predicted at-sea abundance when the cohesion of nesting habitat was greater than 80 suggests a target range for managing the cohesion of nesting habitat to benefit the murrelets. Whereas nesting habitat is essential to murrelet conservation, managers cannot ignore foraging habitat nor the availability of certain forage species, not simply because murrelets require prey but also because prey availability can affect murrelet nesting success (Barbaree, 2011; Barbaree et al., 2014; Becker et al., 2007; Norris et al., 2007) and seabird survival (Sandvik et al., 2005). In addition, during the non-nesting season, murrelets may be less tied to coastal environments adjacent to suitable nesting habitat and their at-sea distribution may be more influenced by marine conditions that influence the distribution and abundance of prey resources (Ainley et al., 1995).

Murrelet numbers have seriously decreased over the past decades and continue to decline in our study area, especially in the waters of Washington State (Miller et al., 2012). The marine and terrestrial factors included in our research primarily explained the spatial distribution of murrelets but not temporal trends. Moreover, the marine factors included in our model had little influence on murrelet distribution at sea likely because the small population of murrelets under-utilizes available habitat. Despite this relatively weak spatial relationship, marine factors,

and especially decrease in forage species, may play an important role in explaining the apparent population decline, but this relationship is not evident in an analysis with such strong spatial factors. Indeed, for example, a number of smelt species, which as a group are important murrelet prey (Burkett, 1995), are themselves ESA listed within the murrelet's range. Consequently, we recommend additional analyses to identify the factors that influence temporal changes in abundance so that conservation actions can be better targeted to reverse apparent population declines.

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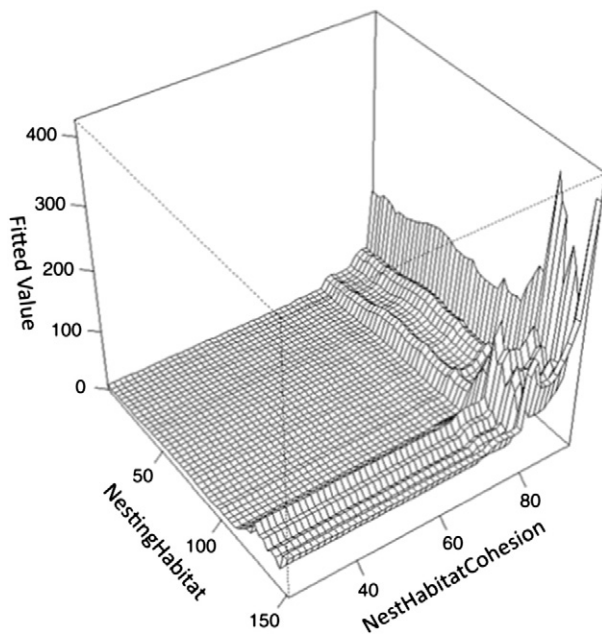


Fig. 7. Response of abundance of marbled murrelets (n/segment) in at-sea coastal segments (fitted value, y-axis) with interaction of cohesion of adjacent nesting habitat (NestHabitatCohesion) and amount of that habitat (NestingHabitat).

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