Land and Seascape Patterns Associated with Marbled Murrelet Abundance Offshore

Sherri L. Miller[1], Carolyn B. Meyer[2] and C. John Ralph[3]

[1]Pacific Southwest Research Station, Redwood Sciences Laboratory, U.S. Forest Service,
1700 Bayview Dr., Arcata, CA 95521 USA
smiller02@fs.fed.us

[2] Department of Botany, P.O. Box 3165, University of Wyoming, Laramie, WY 82071 USA

[3]Pacific Southwest Research Station, Redwood Sciences Laboratory, U.S. Forest Service,
1700 Bayview Dr., Arcata, CA 95521 USA

Abstract. —We measured offshore Marbled Murrelet (*Brachyramphus marmoratus*) abundance from April through October between 1989 and 1998, in northern California and southern Oregon and investigated its relationships with marine and terrestrial habitats. We found that higher murrelet abundance offshore was strongly related to the presence of large, clustered and unfragmented old-growth forests on nearby inland areas. Murrelets were most abundant offshore of contiguous old-growth forest adjacent to relatively abundant medium-sized, second-growth coniferous forests. Compared to the forest habitat, marine habitat was relatively unimportant in determining murrelet abundance offshore; high marine primary productivity and nutrients were not associated with high murrelet numbers. Tidal flat shorelines were weakly associated with more murrelets, independent of inland habitat. Our findings suggest management efforts to conserve the Marbled Murrelet should focus on protecting or creating large, contiguous blocks of old-growth habitat, features which currently are rare in the study area.

Key words.—*Brachyramphus marmoratus*, fragmentation, landscape, Marbled Murrelet, marine habitat, offshore habitat, seascape.

Waterbirds 25(1): 100-108, 2002

The Marbled Murrelet (*Brachyramphus marmoratus*) is a seabird that forages in the northeastern Pacific Ocean from Alaska to central California, and breeds inland from April through September, mostly on large branch platforms in old-growth forests, and in second-growth forests that have residual large trees (Hamer and Nelson 1995). The species' decline and listing as a threatened species in the southern part of its range is believed to be primarily due to loss and fragmentation of its nesting habitat (Miller *et al.* 1997; Meyer and Miller in press; Meyer 1999). In southern Oregon and California, we have found murrelets are most likely to nest in unfragmented old-growth forests in a matrix of forests with mature second-growth (Meyer *et al.* in press). These forests were located relatively close to river mouths, fine sandy beaches, and marine waters with high chlorophyll concentrations, an indicator of high primary productivity (Joint and Groom 2000; Robinson 1990). Proximity to submarine canyons and bays were also important. Nesting is generally restricted to areas with frequent fog, such as the Coast Redwood zone in California and the Western Hemlock zone in southern Oregon (Meyer 1999). Although these features are associated with inland habitat, it is still unknown what broad-scale land- and sea-scape patterns affect murrelet abundance offshore in their marine habitat. Marine habitat characteristics that relate to offshore murrelet densities have not been well-defined. One objective of our research was to determine which marine characteristics and inland spatial patterns, measured in broad-scale regions of southern Oregon and California, were correlated with offshore murrelet numbers during the breeding season. A second objective was to determine which was more limiting to offshore abundance, the marine habitat or the inland nesting habitat. In particular, we wished to determine if the same characteristics that predicted inland nesting habitat use were important to predicting marine habitat use.

We predicted that regions with the highest offshore murrelet densities would have both high quality inland and offshore habitats. Specifically, we expected offshore murrelet densities to be positively correlated with inland regions that contained closely-spaced, large blocks of old-growth forests and a high percentage of land with medium-sized trees (61-90 cm diameter at breast height). After taking into account the effect of inland habitat, we expected murrelet densities to be highest in regions with abundant sandy shorelines, tidal flats, river mouths, submarine canyons, and high spring and summer marine chlorophyll concentrations, as proximity to such characteristics are important in predicting nesting habitat (Meyer *et al.* in press). Murrelets should also be more abundant in marine waters with high nutrient levels, as such waters are indicative of coastal upwelling, a process which increases nutrient availability and prey density (Ainley and Boekelheide 1990).

Murrelets appear to show a delayed response to recent fragmentation and continue to use small forest fragments for several years before abandoning the area (Meyer *et al* in press). In our study area, large amounts of old-growth forest have been harvested in the last 20 years. The lowered reproductive success expected as a result of loss and fragmentation of inland nesting habitat would not strongly affect the offshore abundance until enough time had passed for substantial numbers of the adults to die and not be replaced. Therefore, offshore murrelet abundance, estimated from surveys in the 1990s, is expected to be more strongly related to vegetation conditions in the mid- to late 1980s than conditions in the 1990s. We addressed this potential lag in response to habitat changes by quantifying inland habitat during the mid-1980s. Unfortunately, we could not verify whether this mid-1980s map was more predictive than a map from the 1990s because habitat maps in the 1990s were not available at the same resolution and consistency across the study area. Nevertheless, we obtained very good results using the 1980s map.

STUDY AREA

The study area extends from Coos Bay, Oregon to Point Lobos at the southern end of Monterey Bay in California, 1,088 km of coastline (Fig. 1). The adjacent inland habitat is the southern extent of the known nesting range of the Marbled Murrelet (Ralph *et al.* 1995). Nesting habitat for the murrelet was generally restricted to within 40 km of the coast and to the inland fog zone (Meyer *et al.* in press). Old-growth forests adjacent to the coast in areas without fog were not occupied by murrelets. Within the murrelet nesting area, the vegetation was predominantly in the Western Hemlock zone in southern Oregon and the Coast Redwood zone in California (Franklin and Dyrness 1973, Agee 1993). The marine habitat in the study area comprises a 6-km wide strip along the coastline, where most murrelets forage (Ralph and Miller 1995; Strong *et al.* 1995).

METHODS

The study area was divided into nine regions, which ranged from 2,121 to 6,504 km^2 and extended 40 km inland (Fig. 1), a distance which contained all known occupied nesting areas (Meyer *et al.* in press). Regions were centered on major clusters of old-growth forest, and the boundaries were selected to minimize high rates of bird movement between regions, assuming birds do not frequently travel much more than 20 km north and south of their nesting habitat (F. Cooke, unpublished data in British Columbia, Canada; Kuletz

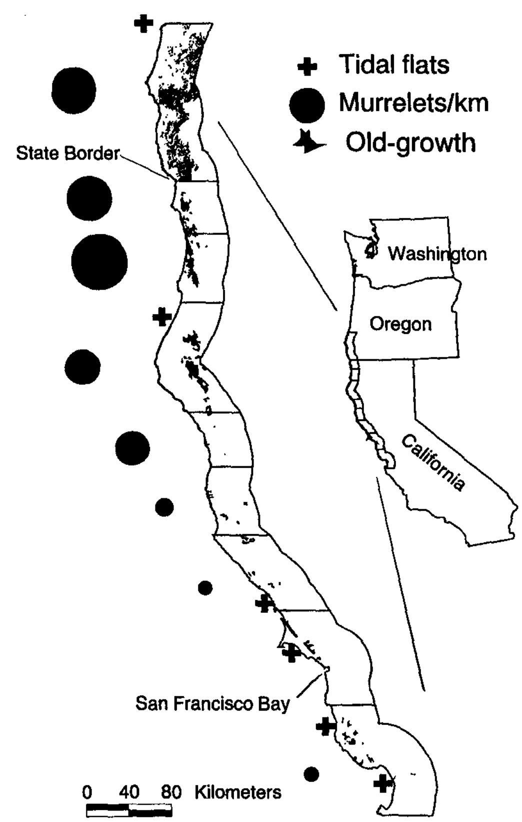

Figure 1. Study area divided into nine regions in southern Oregon and northern California. Potential old-growth nesting habitat for the murrelet is shown. Tidal flat locations and murrelet densities (proportional to areas of circles) are also shown.

et al. 1995; E. Burkett, unpublished data in central California). Within regions, the 6-km strip of marine habitat ranged from 366 to 1230 km^2 (Fig. 1).

We compiled available Geographic Information System (GIS) databases of marine features, marine water quality, old-growth forest and other land cover types within the nine regions. Using ARC/INFO (Environmental Systems Research Institute, Inc., Redlands, California, USA, v. 7.1), we calculated marine and terrestrial habitat variables including old-growth fragmentation patterns within each region and searched for relationships between habitat variables and offshore murrelet densities. Below we describe in more detail how we obtained our datasets.

Estimates of Murrelet Regional Numbers

We used methods detailed in Ralph and Miller (1995) to estimate the numbers of murrelets offshore for eight regions in California (883 km). Sections of the coast, 20 to 30 km in length, were surveyed and counts recorded for each 2-km segment of line transect. We estimated a 200-m effective survey width using line transect methods (Buckland *et al.* 1993). Estimates of the number of murrelets in each region were based on 5,739 two-km segments surveyed during April through October, from 1989 to 1998. The entire coastline was surveyed repeatedly using line transects parallel to the coastline at 800 m and 1,400 m from the shore. In addition, to determine the murrelet distribution at right angles to the shoreline, 25% of the coastline in the three northern regions of California and one location south of San Francisco Bay were intensively surveyed at increasing distances (400 m, 800 m, 1.4 km, 2 km, 3 km and 5 km) from the shore, in coastal sections 6 to 8 km long. Based on the intensive surveys, a linear regression was developed to estimate the number of murrelets in each of the eight regions. The independent variables were the average murrelet counts per 2-km segment at 800 m and 1,400 m transect distances for all intensive survey locations and the response variable was the extrapolated number of murrelets in a 6 km wide x 2 km coastal segment. The resulting regression equation and the mean counts at 800 m and 1,400 m were then used to estimate the total number of murrelets for each coastal section in California:

$$\text{Estimate of numbers in section} = 6.417 + 4.189 \cdot \bar{x}_{800m} + 5.190 \cdot \bar{x}_{1400m}$$

We summed the section numbers within each region to estimate the number of murrelets in the region (Table 1).

We obtained an estimate of numbers for the southern Oregon region by averaging those reported by Strong (1996). Strong's density estimates for southern Oregon were based on 343 transects, each 2 km long and with an effective survey width (Buckland *et al.* 1993) of 0.2 km. Surveys parallel to the coastline were conducted during June and July in 1992, 1993, and 1995 from boats at 300 to 750 m from the shore (Strong *et al.* 1995; Strong 1996). Additional surveys were conducted in 1995 at right angles to the shoreline in two 4-km long intensive survey areas to determine the proportion of murrelets offshore compared to the inshore (300-750 m) transect. Murrelet density was calculated in each transect by adding the proportion estimated to be farther offshore to the inshore counts. Densities were

Table 1. Murrelet offshore region population numbers and survey effort from April to October 1989 to 1998 for regions in California and southern Oregon.

Region name	Coastline length (km)	No. 2-km segments surveyed 800 m from shore	No. 2-km segments surveyed 1,400 m from shore	Total estimated birds	SE	Total birds per km coastline
South Oregon	205	343[1]	5	3495	243	17.0
Klamath	61	823	764	1178	42	19.2
Trinidad	72	534	576	1904	79	26.6
Humboldt Bay	127	1302	1257	1406	33	11.0
Kings Range	61	23	44	275	16	4.5
Point Arena	73	44	25	199	—[2]	2.7
Russian River	98	43	42	180	—[2]	1.8
San Francisco	233	35	33	0	0	0
Santa Cruz	158	109	85	717	93	4.5
Total	1088	3256	2831	9354	134	8.6

[1]These surveys were conducted between 300 and 750 m from shore in Oregon. Total surveyed lengths exceed coastline length because coastlines were repeatedly surveyed.
[2]Standard errors were not calculated for these regions because errors are based on number of pairs of 800 m and 1,400 m counts (Ralph and Miller 1995), but no 2-km segments were ever surveyed at both 800 m and 1,400 m distances from the shore for these areas.

extrapolated to the area surveyed in the region to obtain an estimate of numbers. For California and Oregon, we divided the estimate of total birds by the length of coastline in each region to obtain numbers of murrelets per km of coastline (Table 1).

Vegetation Databases

To map murrelet habitat, we created GIS maps from several sources. For California, we used an old-growth 1985-86 vegetation map developed from aerial photographs (Redwood Mapping Project, Larry Fox, Humboldt State University, 16 ha minimum mapping unit). For Oregon, we used two 1988 databases (Congalton *et al.* 1993 and BLM Western Oregon Digital Image Project, 1.2 to 6 ha minimum mapping unit) based on LANDSAT TM imagery. The final GIS maps for both states included old-growth only, defined as having >40% canopy cover and ≥10% cover in old, large trees present before Europeans arrived (typically >91 cm diameter at breast height in California). We used a third LANDSAT TM-based GIS map (CTTF 1993) to calculate percentage of land with medium-sized trees (61-90 cm diameter at breast height) in California.

Variables Sampled

Within each entire region, we quantified the major old-growth fragmentation and marine habitat variables that we found were important in Meyer *et al.* (in press) using FRAGSTATS (raster version, McGarigal and Marks 1995; Table 2). Because the area outside the Coast Redwood and Western Hemlock zones had very low murrelet use, we calculated old-growth variables only after eliminating any old-growth forest in the region that fell outside those zones (Fig. 1). We also included annual marine nitrate concentration, sampled at the surface of the ocean in 1 degree blocks along the coastline (NOAA 1994), as a variable because of its importance as an indicator of potential year round marine productivity (Granéli *et al.* 1990; Maranon *et al.* 2000) Nitrate concentrations during just the murrelet breeding season (spring and summer) were not available from NOAA for our entire study area. Latitude of the center of the region was included as an index of north to south changes in climate, which might affect murrelet abundance.

Data Analyses

Because the map resolution and methods used to calculate regional numbers were different in Oregon than California, we analyzed the data using California alone, and then with southern Oregon included. First, we calculated simple Pearson correlation coefficients between each variable and murrelets per km of coastline (Neter *et al.* 1989). Then we used best subsets linear regression to determine two-variable functions that best predicted murrelets per km. Best subsets regression calculates all possible subsets of the candidate variables. The adjusted R^2 and Mallows' C_P (C_P estimates bias and random error to assess fit) were the criteria used to select the best subset of variables (following Neter *et al.* 1989). Because we had only nine data points (regions), we needed to limit the number of candidate variables. Therefore, the inland variables included as candidates in the two-variable regressions were only those that had a significant correlation coefficient ($P \leq 0.05$). To evaluate our hypothesis that marine variables would be important after accounting for the effect of inland habitat, we also specifically searched for regression functions that were significant when a marine variable was combined with the most significant inland variable.

Because Oregon had a smaller map resolution (1.2-6 ha) than California (16 ha), map resolution may affect the variables that measure patch size. Therefore, we added minimum mapping unit to the regressions to see if they changed the results, which they did not.

RESULTS

When we correlated each variable separately with murrelet offshore abundance, we found abundance increased as old-growth forest fragmentation decreased in the regions (more old-growth and core area, more area in the largest patch, high proximity index; Table 3). The mean proximity index of old-growth, a measure of old-growth patch isolation (see Table 2), had the highest correlation with abundance. Specifically, closely spaced, large old-growth stands were associated with high bird numbers offshore. Abundance also increased with more medium-sized conifer forests in the regions. Trinidad, the region with the most birds had almost 5% of the land in old-growth core area (interior habitat) and 15% in medium-sized conifer forests (Table 4). No marine variables were positively correlated with murrelet numbers (Table 3). Annual marine nitrate concentrations were negatively correlated to murrelet abundance in California, but when Oregon was included, this relationship disappeared. Also, as latitude increased, murrelet densities increased. Such an increase may be an artifact of the greater nesting habitat availability farther north.

In the two variable regression model that best predicts murrelet offshore abundance, only inland variables were included (Table 5). The inland habitat variable with the most explanatory power (92% of the variance) was the mean proximity index, followed by either the percentage land in old-growth (California only) or the percentage land in the largest patch of old-growth (includes Oregon). No marine variables, except percent coastline in tidal flats were significant once an inland habitat variable was in the model. Once proximity index of old-growth was accounted

Table 2. Habitat variables measured in regions of California and southern Oregon.

Inland Fragmentation Variables (from FRAGSTATS)	
OG[1] (%)	Mean OG patch size (ha)
Mean proximity index of OG[2]	Largest OG patch (%)
OG core area (%) (50-m edge distance)	Edge old-growth per area of old-growth (m/ha)
Medium-sized conifer (%) (61-90 cm dbh)	
Marine Variables	
Tidal flats (% of coastline)	River mouths (no/km of coastline)
Mean (1978-1986) spring marine chlorophyll (mg/m^3 and % of coastline > 10 mg/m^3) (18-km pixel)	Mean (1978-986) summer marine chlorophyll (mg/m^3 and% > 10 mg/m^3 (from NASA coastal Zone Color Scanner)
Submarine canyons (no/km) within 22 km of shore (from NOAA bathymetry)	Sandy beach (% of coastline)[3]
Rocky coast (% of coastline)	Annual mean nitrate concentration (µmol/I from 1900-1990 (1-degree pixel along coastline, NOAA 1994)
Latitude (degrees at midpoint of region)	

[1]OG = old-growth forest.

[2]Quantifies size and distance of neighboring old-growth patches within a 5-km radius to distinguish sparsely spaced, small old-growth patches (low value) from clusters of large old-growth patches (high value). Large consolidated patches or fragmented, yet very closely spaced small patches, have a high mean proximity index (McGarigal and Marks 1995).

[3]This variable was only available in California (from a state shoreline map).

Table 3. Correlation coefficients (r) between number of murrelets offshore per km coastline and the highest ranked (using r) inland and marine (including latitude) habitat variables in California and Oregon or California alone.

Variable	California and Oregon (N = 9)	California (N = 8)
Mean proximity index OG[a]	0.95	0.96
OG (%)	0.85	0.91
OG core area (%)	0.91	0.90
Medium-sized conifer (61-90 cm dbh) (%)	-	0.86
Nitrate (mg/m^3)	n.s[b]	-0.86
Largest patch OG (%)	0.70	0.85
Latitude (degrees)	0.81	0.81

[a]OG = old-growth forests

[b]not significant

for, the partial correlation coefficient for tidal flats was 0.82. However, tidal flats explained only an additional 5% of the overall variance. The three best 2-variable regression models were highly predictive ($R^2 \geq 0.96$ and $P < 0.0001$; Table 5).

DISCUSSION

Inland habitat was by far more important than marine habitat in affecting murrelet regional numbers, accounting for up to 98% of the variance in offshore numbers (Table 5). Although we had expected that inland habitat would be more important, we had also expected the marine habitat to contribute to explaining a portion of the variation in murrelet abundance. The regions we selected for our study were relatively large scale. A smaller scale analysis may provide stronger relationships between marine habitat and offshore abundance.

Inland Habitat

As predicted, higher fragmentation of habitat inland would decrease murrelet abundance offshore. Regions with abundant murrelets contained some large blocks of contiguous old-growth forest, which increased old-growth clumping and percentage of land in the largest patch size (Fig. 1). Such large patches provide more core areas, which was also found to be important in our study of inland birds at smaller scales (Meyer *et al.* in press). Core area provides sites for nests away from the edge, where young are more likely to fledge successfully due to lowered predation rates (Paton 1994; Nelson and Hamer 1995).

Our prediction that the region with the most birds offshore would contain proportionally more forests with medium-sized trees than younger seral stage forests with smaller trees, was supported. Such a land-

Table 4. Offshore murrelets per km of coastline compared to average characteristics of old-growth (OG) and conifer forests, and coastline habitats of the regions in the study area.

Region name	Birds per km	OG (%)	OG core area (%)	OG mean proximity index	Largest patch OG (%)	Medium conifer (%)
South Oregon	17.0	7.49	4.40	305.25	0.20	—
Klamath	19.2	4.01	3.55	289.49	1.91	15.50
Trinidad	26.6	5.39	4.80	354.35	2.07	14.70
Humboldt Bay	11.0	4.55	4.19	41.86	2.07	12.00
Kings Range	4.5	0.43	0.29	31.31	0.09	7.40
Point Arena	2.7	0.51	0.43	0.45	0.17	9.24
Russian River	1.8	0.52	0.43	0.00	0.19	6.82
San Francisco	0.0	0.60	0.54	11.92	0.53	2.50
Santa Cruz	4.5	0.99	0.83	24.99	0.30	2.25

Table 5. Predictor variables and coefficient statistics in linear regression models of offshore murrelets per km of coastline in California alone or with southern Oregon included. Old-Growth conifer forest is represented in the table as "OG."

Variables	Unstandardized coefficient	SE	Standardized coefficient[1]	t-value	P<
California (N = 8)	$R^2 = 0.981$				
Mean proximity index OG[2]	0.0424	0.0074	0.636	5.7	0.002
% land in OG	1.807	0.5006	0.403	3.6	0.02
Constant	0.930	0.8863		1.1	n.s.
California/Oregon (N = 9)	$R^2 = 0.965$				
Mean proximity index OG	0.0494	0.0060	0.801	8.3	0.0002
% in largest patch OG[2]	2.946	1.0016	0.285	2.5	0.03
Constant	1.416	1.0595		1.3	n.s.
California (N = 8)	$R^2 = 0.974$				
Mean proximity index OG	0.0666	0.0049	0.999	13.6	0.0001
coastline in tidal flats	14.026	4.3681	0.235	3.2	0.03
Constant	1.666	0.8580		1.9	

[1]The standardized coefficient and P value show the relative importance of each variable.

[2]This variable was also highly predictive with mean proximity index in a two variable linear regression for California alone, but % land in OG was slightly better.

scape, with old-growth in a matrix of even-aged older second-growth forest, may support fewer nest predators as it would provide less edge contrast. However, forests with medium-sized trees did not significantly explain any additional variance in murrelet offshore abundance, once fragmentation of old-growth forest was considered. More research that targets old-growth areas, with and without surrounding medium-sized forests, is needed to determine the effects of various matrix habitats.

Marine Habitat

None of the marine variables were good predictors of offshore abundance. Nitrate concentration was the only marine variable with a significant simple correlation to abundance, and it decreased as murrelet numbers increased. We expected nitrate, an indicator of marine productivity, to be positively, rather than negatively, associated with the birds. Notably, the addition of the Oregon data removed the significant relationship. Because the addition of Oregon data negated the importance of nitrate, the nitrate result in California is likely a statistical artifact, rather than an important biological result. Of the marine habitat relationships we felt would be important, only our expectation that murrelet numbers would be highest in regions with more tidal flats was supported. Tidal flats were uncorrelated with the old-growth proximity index (r = 0.17) and thus independently contributed to murrelet abundance. Tidal flats are within the bays and estuaries, and are nutrient rich, highly productive areas providing food for potential murrelet prey.

When inland habitat fragmentation patterns were included in the models, marine habitat appeared to have little effect on murrelet offshore numbers, accounting for ≤5% of the variation in offshore numbers. On a smaller landscape scale (Meyer *et al.* in press), we found areas with consistently high chlorophyll, were near inland nesting areas. However, in the present study, increased primary productivity, as evidenced by chlorophyll in the ocean, did not significantly increase murrelet numbers over and above the effect of unfragmented inland habitat. Within our study area, murrelet abundance appears most limited by the amount and degree of fragmentation of old-growth nesting habitat. However, the marine environment may have a stronger influence on abundance if nesting habitat increases. Our results suggest that conservation efforts for the Marbled Murrelet should focus on protecting or creating large, contiguous blocks of old-growth habitat, features which are uncommon in the study area.

ACKNOWLEDGMENTS

We thank Dennis Knight, William Reiners, William Baker, Stanley Anderson, and E. Raymond Hunt, Jr. for reviewing early versions of the manuscript. Howard Stauffer and Ken Gerow provided statistical advice. Field and office assistants included Stacey Vigallon, Linda Long, Tami Matsumoto, Adrienne Wright, Bill Hogoboom, and Robert Thurston. The U.S. Fish and Wildlife Service and many Forest Service employees assisted in collecting offshore data. The research was supported by a U.S. Environmental Protection Agency STAR Fellowship, the U.S. Geological Survey, the Andrew Mellon Foundation, and the National Park Service.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Ainley, D. G. and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands: ecology, dynamics and structure of an upwelling-system community. Stanford University Press, Stanford, California.

Cooke, F. 1999. Marbled Murrelet radio telemetry studies in Desolation Sound, British Columbia, Canada. Unpublished data. Simon Fraser University, Dept. of Biological Sciences, Burnaby, British Columbia.

Buckland, S.T, D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. New York: Chapman & Hall. 446 p.

Burkett, E. 1998. Marbled Murrelet radio telemetry studies in Central California. Unpublished data. California Department of Fish and Game, 1416 Ninth St., Sacramento, California, 95814.

Congaiton, R. G., K. Green and J. Teply. 1993. Mapping old-growth forests on national forest and park lands in the Pacific Northwest from remotely sensed data. Photogrammetric Engineering and Remote Sensing 59: 529-535.

CTTF (California Timberland Task Force). 1993. The report of the California Timberland Task Force. California Department of Forestry and Fire Protection, Strategic Planning Program, 1419 9th Street, Sacramento, California.

Franklin, J. G., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. General Technical Report PNW-8. U.S. Forest Service, Portland, Oregon.

Graneli, E., K. Wallström, U. Larsson, W. Granéli and R. Elmgren. 1990. Nutrient limitation of primary production in the Baltic Sea area. Ambio 19:142-151,

Hamer, T. E. and S. K. Nelson. 1995. Characteristics of marbled murrelet nest trees and nesting stands. Pages 69-82 in Ecology and conservation of the marbled murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael and J. F. Piatt, Eds.). General Technical Report PSW GTR-152. U.S. Forest Service, Albany, California.

Joint, I. and S. B. Groom. 2000. Estimation of phytoplankton production from space: current status and future potential of satellite remote sensing. Journal of Experimental Marine Biology and Ecology 250: 233-255.

Kuletz, K. J., D. K. Marks, D. A. Flint, R. A. Burns and L. M. Prestash. 1995. Marbled murrelet foraging patterns and a pilot productivity index for murrelets in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project Final Report (Project 94102), U.S. Fish and Wildlife Service, Anchorage, Alaska.

Maranon, E., P. M. Holligan, M. Varela, B. Mourino and A. J. Bale. 2000. Basin-scale variability of phytoplankton biomass, production, and growth in the Atlantic Ocean. Deep Sea Research Part I, Oceanographic Papers 47: 825-857.

McGarigal, K. and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW GTR-351. U.S. Forest Service, Portland, Oregon.

Meyer, C. B. 1999. Marbled murrelet use of landscapes and seascapes during the breeding season in California and southern Oregon. Unpublished Ph.D. Dissertation, University of Wyoming, Laramie, Wyoming.

Meyer, C. B. and S. L. Miller. In press. Marbled murrelet use of fragmented landscapes for nesting in southern Oregon. Conservation Biology.

Meyer, C. B., S. L. Miller and C. J. Ralph. In press. Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas. Landscape Ecology.

Miller, G. S., S. R. Beissinger, H. R. Carter, B. Csuti, T. E. Hamer and D. A. Perry. 1997. Recovery plan for the threatened marbled murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California. U.S Fish and Wildlife Service, 2600 SE 98th Ave. Suite 100, Portland, Oregon.

Nelson, S. K. and T. H. Hamer. 1995. Nest success and the effects of predation on marbled murrelets. Pages 89-97 *in* Ecology and conservation of the marbled murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael and J. F. Piatt, Eds.). General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, California.

Neter, J., W. Wasserman and M. H. Kutner. 1989. Applied linear regression models. Richard D. Irwin, Bunridge, Illinois.

National Oceanic and Atmospheric Administration (NOAA). 1994. World ocean atlas 1994. National Environmental Satellite Data and Information Service, National Oceanographic Data Center, Ocean Climate Laboratory. Washington D.C.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8: 17-26.

Ralph, C.J., G. L. Hunt, Jr., M. G. Raphael and J. F. Piatt. 1995. Ecology and conservation of the marbled murrelet in North America: an overview. Pages 3-22 *in* Ecology and conservation of the marbled murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael and J. F. Piatt, Eds.). General Technical Report PSW GTR 152. U.S. Forest Service, Albany, California.

Ralph, C. J. and S. L. Miller. 1995. Offshore population estimates of marbled murrelets in California. Pages 353-360 *in* Ecology and conservation of the marbled murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael and J. F. Piatt, Eds.). General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, California.

Robinson, I. S. 1990. Remote sensing-information from the colour of the seas. Pages 19-38 *in* Light and life in the sea (P. J. Herring, Ed.), Cambridge University Press, Cambridge, England.

Strong, C. S., B. S. Keitt, W. R. McIver, C. J. Palmer and I. Gaffney. 1995. Distribution and population estimates of marbled murrelets at sea in Oregon during the summers of 1992 and 1993. Pages 339-353 *in* Ecology and conservation of the marbled murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael and J. F. Piatt, Eds.). General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, California.

Strong, C. S. 1996. At-sea research on marbled murrelets in Oregon, 1992-1995: measures of density, distribution, population size, and productivity. Final report to the Oregon Department of Fish and Wildlife. Crescent Coastal Research, Crescent City, California.