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RECENT POPULATION DECLINE OF THE MARBLED MURRELET IN THE PACIFIC NORTHWEST

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Abstract. We document here a decline of nearly 30% in the Marbled Murrelet (*Brachyramphus marmoratus*) population of Washington, Oregon, and northern California between 2000 and 2010. The Northwest Forest Plan is an ecosystem-management plan for federal forest lands in the Pacific Northwest of the United States that incorporates monitoring to determine if species' conservation objectives are met. To evaluate the plan's effectiveness in conserving populations of the murrelet, a species associated with older, late-successional forests, we estimated the murrelet's density in near-shore marine waters of Washington, Oregon, and northern California south to San Francisco Bay. We sampled annually, using line transects and distance estimation. We divided the study area of about 8800 km² into five geographic subareas corresponding to existing murrelet-conservation zones. Annual population estimates for the plan ranged from an estimated 23 700 (95% CI: 18 300 to 29 000) birds in 2002 to a low of 16 700 (95% CI: 13 100 to 20 300) in 2010, representing an average rate of decline of 3.7% annually (95% CI: -4.8 to -2.7%) from 2001 to 2010. This annual rate suggests a total decline of about 29% during this period. We documented downward trends for Washington (conservation zone 1) and for the outer coast of Washington (conservation zone 2). These declines coincide with reductions in the amount of nesting habitat. Further research to evaluate the potential marine and terrestrial factors responsible for the declines is planned.

Key words: *Brachyramphus marmoratus*, Marbled Murrelet, Northwest Forest Plan, old-growth forest, population decline, population trends, seabird.

Disminución Reciente de la Población de *Brachyramphus marmoratus* en el Noroeste Pacífico de Norteamérica

Resumen. Documentamos aquí una disminución de casi el 30% de la población de *Brachyramphus marmoratus* de Washington, Oregón y el norte de California entre 2000 y 2010. El Plan Forestal del Noroeste es un plan de gestión de los ecosistemas boscosos federales del noroeste pacífico de los Estados Unidos que incorpora el monitoreo para determinar si los objetivos de conservación de especies se cumplen. Para evaluar la efectividad del Plan en la conservación de las poblaciones de *B. marmoratus*, una especie asociada con bosques maduros de estadios sucesionales tardíos, se estimó la densidad anual de la especie cercana a la costa en las aguas marinas de Washington, Oregón y el norte de California al sur a la Bahía de San Francisco. Se realizaron muestreos anuales a partir del 2000 hasta el 2010 utilizando transectas lineales y estimaciones de distancia. El área muestreada de aproximadamente 8800 km² fue dividida en cinco subáreas geográficas correspondientes a las actuales zonas de conservación de la especie. Las estimaciones anuales de la población para el Plan van desde un estimado de 23 700 aves (95% IC: 18 300 – 29 000) en 2002 a la estimación más baja, de 16 700 (95% IC: 13 100 – 20 300) en 2010. Se evaluaron las tendencias poblacionales de la zona del Plan (todas las cinco zonas combinadas) y para cada zona. Se encontró una disminución de la población para el área del Plan, con una tasa estimada promedio de disminución anual del 3.7% (95% IC: -4.8 a -2.7%) para el período del 2001 al 2010. Esta tasa anual indica una disminución total de alrededor de 29% durante este período. Hemos documentado una tendencia descendente para el norte de Washington (zona de conservación 1), que incluye el Estrecho de Puget, las Islas San Juan y el Estrecho de Juan de Fuca, y para la costa exterior de Washington (zona de conservación 2). Estos descensos observados coinciden con las reducciones en la cantidad de hábitat de nidificación. Se planean realizar investigaciones futuras para evaluar los factores potenciales marinos y terrestres responsables de los descensos.

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INTRODUCTION

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small seabird that spends most of its time foraging in coastal waters of the eastern Pacific Ocean, from central California to the Aleutian Islands. Unlike most seabirds, however, the murrelet flies up to 50 km inland to nest (Nelson 1997). In most of its range, it is strongly associated with late-successional and old-growth forests, nesting mostly on large branches or other suitable platforms in large trees (Ralph et al. 1995, McShane et al. 2004, Piatt et al. 2007). Largely because of timber harvesting, only a small percentage (5 to 20%, depending on region) of original old-growth coastal forest remains in the Pacific Northwest south of Canada (Morrison 1988, Norheim 1996, 1997, Stritholt et al. 2006), mostly in relatively small, fragmented patches or in forest parks and reserves.

In 1992, the Marbled Murrelet was listed as threatened in Washington, Oregon, and California under the federal Endangered Species Act. Degradation of habitat from logging, exacerbated by catastrophes including fire and wind storms, were the primary factors contributing to its listing (USFWS 1992). In the three-state area, murrelet populations continued to decline after listing (McShane et al. 2004, Strong 2003, USFWS 2009). The small isolated population at the southern end of the species' range in central California appears to be at risk for further decline (Peery et al. 2006). In the northern portion of its range, where it is most numerous, the species appears to have declined in Alaska by about 70% over a period of 25 years, with similar declines likely in British Columbia (Burger 2002, Piatt et al. 2007).

Although declines of Marbled Murrelet populations have been predicted by demographic models (USFWS 1997, McShane et al. 2004) and suggested by field observations, ours is the first robust assessment of population size and trends for the species' range south of Canada. This assessment is part of a program to monitor the effectiveness of a forest-management plan, the Northwest Forest Plan (the Plan), to conserve murrelet populations. Established in 1994, the Plan represented a major change in how federal forest lands are managed in western Washington, Oregon, and northwestern California, taking an ecosystem approach to the management of about 10 million hectares of federal lands. One objective of the Plan is to support stable or increasing populations of the Marbled Murrelet by conserving nesting habitat.

Conservation of the Marbled Murrelet requires knowledge of the status and trends of both populations and nesting habitat and of interactions between the two (Ralph et al. 1995, USFWS 1997, Raphael 2006, Piatt et al. 2007); the Plan monitors both (Madsen et al. 1999). Nesting habitat is monitored by combining ground-based data with remote imagery to model habitat conditions and trends (Raphael et al. 2011). Because murrelets are cryptic at their nests and individuals cannot be reliably counted in the forest, population size and trends are best estimated by monitoring at sea (Madsen et al.

1999, Miller et al. 2006, Raphael et al. 2007). Our paper presents results of murrelet population monitoring from 2000 to 2010 in the coastal waters off the Northwest Forest Plan area.

METHODS

SAMPLING DESIGN

Our monitoring plan was designed to estimate the trend of the murrelet population in coastal waters between the U.S.–Canadian border and San Francisco, California (Fig. 1). This area encompasses five of the six Marbled Murrelet conservation zones designated by the Marbled Murrelet Recovery Plan (USFWS 1997) and lies offshore of the Plan area. Zone 6 at the southern end of the species' range was not included in our sampling because that zone fell outside the boundary of the Plan. The target population is also defined by the area of navigable waters within 2 to 8 km of shore (distance varies by zone), and temporally from mid-May through the end of July, when breeding birds at sea are likely to be associated with inland nesting habitat. Within each conservation zone (zones 1–5) (Fig. 1), we designated two or three geographic strata based



FIGURE 1. The five marine Marbled Murrelet conservation zones adjacent to the Northwest Forest Plan area. The inland breeding distribution within the Plan area is shaded, and the Plan boundary is outlined.

on patterns of murrelet density (Miller et al. 2006, Raphael et al. 2007). The distance from shore of the offshore boundary for the target population varied by zone and stratum. By using available historic data on the murrelet's relative abundance in relation to shore (Miller et al. 2006, Raphael et al. 2007), we selected offshore boundaries to include in each sample area at least 95% of the murrelets on the water. Sampling was designed to allocate more sampling effort to strata with higher densities (Raphael et al. 2007). The design accommodates augmented sampling in strata with particular conservation questions. For instance, Zone 4, Stratum 2 received additional sampling effort from 2000 through 2003, when a private timber company required monitoring of murrelets offshore of the area of its habitat-conservation plan.

Primary sampling units (PSU) were roughly rectangular areas of approximately 20 km of coastline and were contiguous over the entire sampling area (Raphael et al. 2007). Each zone included from 14 to 22 unique PSUs, except for Zone 1, where the complex shoreline of Puget Sound resulted in 98 PSUs. PSUs were divided into inshore and offshore subunits (Fig. 2). The inshore subunit extended to either 1.5 km or 2 km from shore, except in Stratum 2 of Zone 1, where narrow inlets and passages between opposite shorelines limited the inshore subunit to waters within 500 m of shore (Raphael et al. 2007). Inshore subunits generally have higher murrelet densities, so we sampled them with more effort, using transects parallel to shore. Offshore subunit transects were oriented diagonally to the shoreline, often in a zigzag configuration (Fig. 2) to sample across the gradient of murrelet density that, generally, declines with distance from shore (Ralph and Miller 1995). Details of the PSUs for each zone and stratum are summarized in Raphael et al. (2007).

Annual monitoring began in 2000 for all zones, although year 2000 data from zones 1 and 2 were later excluded from analyses (see Methods below). Our target sample size in zones 2 to 5 was 30 PSU surveys per zone per year; most or all PSUs

in these zones were sampled each year, in a random order (Raphael et al. 2007). In Zone 1, an initial sample of 30 PSUs was randomly selected from the total of 98, and each selected PSU was sampled twice each year (Raphael et al. 2007). To minimize variance by year, this same random subsample was sampled each year. Zone 5, which supports less than 1% of the target population, was not sampled in 2006, 2009, or 2010 because of limited funding, and the sampling effort in this zone was reduced to 15 PSU surveys in 2004. Boundaries of PSUs and strata remained constant over the study.

Each survey used two observers, one on each side of the boat's centerline and facing forward, surveying a 90° arc to the left or right of the bow. We estimated murrelet density by line-transect methods (Buckland et al. 2001, Thomas et al. 2010), recording the perpendicular distance to each bird or group of birds detected. Accuracy of distance estimates is key to density estimates based on line transects. Training of observers and calibration of distance estimates, as described in Miller et al. (2006) and Raphael et al. (2007), were repeated throughout the season to maintain consistency. Description of the complete survey protocol is provided in Raphael et al. (2007), and in Miller et al. (2006).

STATISTICAL ANALYSES

Density and population estimates. Our goal was to estimate the density and population for each zone and for the entire target population of the five zones combined for each year from 2000 to 2010 (Miller et al. 2006, Raphael et al. 2007). The density estimate for the five zones combined was a weighted average of the individual zones' densities, with the weights being the area (km²) sampled in each zone. For reasons discussed below, we excluded the year 2000 from all analyses that included data from Zone 1 or Zone 2.

We estimated the murrelet's average densities (average daily counts of birds per km²), with an associated estimate of precision. We used the software program DISTANCE (Buckland et al. 2001, Thomas et al. 2010) to estimate $f(0)$, the probability density function of perpendicular detection distances evaluated at the transect line and the mean number of birds per group [or cluster size, $E(s)$] for each year and zone from surveys of inshore and offshore subunits. We truncated the distance data prior to analysis by discarding for each zone the 5% of observations at the greatest distances, which can improve modeling of detection functions, as recommended by Buckland et al. (2001). DISTANCE used the mean observed cluster size as the estimate for $E(s)$ unless an internal test found evidence that detection was a function of cluster size, in which case DISTANCE applied a correction (Buckland et al. 2001). Because of low numbers of birds in Zone 5, we combined zones 4 and 5 for these estimates. DISTANCE also provided the number of groups of birds observed per km (ER, encounter rate) for each subunit survey. We then estimated density (birds per km²) for each subunit of a PSU surveyed (Raphael et al. 2007) by using the

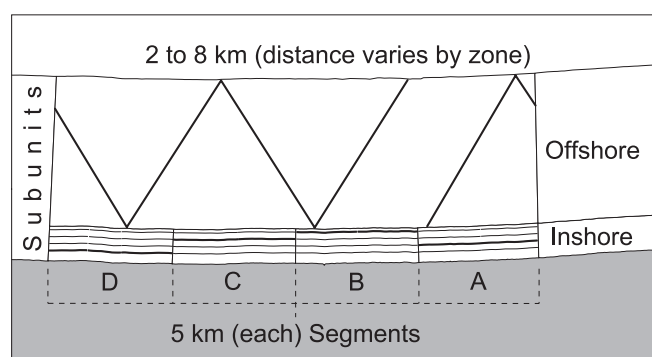


FIGURE 2. Schematic primary sampling unit for Marbled Murrelet surveys, with parallel and zigzag transects in inshore and offshore subunits, respectively. The inshore subunit is divided into four segments of equal length (~5 km each) and four bins of equal length (bands parallel to and at increasing distances from shore). One bin is selected without replacement (bold lines) for each segment of transect.

estimates and encounter rate from DISTANCE with the following formula:

$$\hat{d} = 1000 \cdot \hat{f}(0) \cdot \hat{E}(s) \cdot \frac{ER}{2}$$

The “hats” over the letters designate estimates. We estimated densities for strata, zones, and all zones combined from average densities weighted by the area of the respective geographic scale.

We generated population estimates for each zone and for the five zones combined by standard methods for stratified sampling (Cochran 1977, Sokal and Rohlf 1981). We used the total area within each stratum, density estimates from DISTANCE, and associated estimates of precision to estimate the average total numbers of birds by zone and for the five zones combined for the target period. For estimates of precision we used bootstrap resampling methods with consideration of PSU samples that might be clustered in time or space (Miller et al. 2006, Raphael et al. 2007). Because the total area (area sampled) and the sampling effort were constant over the study for all zones and years, density and population estimates are equivalent for purposes of trend detection, since population is simply density multiplied by area. Details of methods used to calculate population estimates and confidence intervals are in Raphael et al. (2007).

Estimating trends. We used annual density estimates to evaluate trends in the Plan area from 2000 to 2010 (see Miller et al. 2006 for details) for each zone and for all zones combined. Departures from the protocol in zones 1 and 2 in 2000 may have affected density estimates for those zones, so we used data from only 2001 through 2010 for trend estimates for all zones and for zones 1 and 2. For zones 3 and 4, we used data from 2000 through 2010. For Zone 5, we used data from 2000 through 2005, 2007, and 2008. For the years without Zone 5 estimates, the all-zone analyses used the 2008 Zone 5 estimate for 2009 and 2010 and an interpolation of 2005 and 2007 estimates for 2006. Because Zone 5 supports less than 1% of the target population, missing data had minimal effect on population estimates and no measurable influence on the magnitude or significance of trend; we confirmed this empirically by analyzing trends for the Plan area with and without Zone 5 included.

We used a regression model to estimate population trend. We fit a linear regression to the natural logarithm of annual density estimates to test for declines and to characterize the change over time as a constant percent change per year in zones 1 through 5 and in all zones. For our analysis, the natural logarithm best fits and tests existing demographic models (USFWS 1997, McShane et al. 2004) that predict the murrelet population is declining by a constant percentage each year. We tested the null hypothesis that the slope equals zero or greater (no change or increase in murrelet numbers) against the alternative hypothesis of the slope being less than zero (i.e.,

a one-tailed test for a decrease). We tested the significance of the slope at the level of $\alpha = 0.05$.

We used the 2001 to 2010 data for Zone 1 to evaluate potential effects of sea condition (Beaufort sea state) and observer (crew) on our density and population-trend estimates. For each year, we estimated murrelet density with software DISTANCE (Thomas et al. 2010) for three models (sea condition, crew, and sea condition plus crew) as well as the default no-covariate model. We used AIC methods to identify the best model for each year (Johnson and Omland 2004). We evaluated the effect of covariates on the population-trend estimate for Zone 1 by using the regression methods described above to compare the trend estimated from the no-covariate model with the trend based on density estimates from the best model for each year.

RESULTS

Beginning in 2000, we monitored the population in all five zones, except Zone 5, each year. The total area of ocean surveyed each year was about 8785 km². Each year, we conducted 150 to 200 PSU surveys and recorded 4000 to 6000 murrelet observations along roughly 5500 to 6500 km of transect. In each year, we completed the largest number (~60) of PSU surveys in Zone 1 because of the greater length of coast in this zone. From 2000 to 2004, to meet the requirements of another project for more precise stratum-level population estimates, we conducted about 25 additional surveys per year in Stratum 2 of Zone 4. In 2005, the Zone 4 survey effort reverted to the target of 30 PSU surveys. Because a PSU may be sampled more than once in a year, the number of unique PSUs sampled annually is less, about 90–95 for the five zones combined (Raphael et al. 2007).

POPULATION ESTIMATES

Estimates of density and population size by zone and for all zones combined are presented by year in Appendix 1, available at <http://dx.doi.org/10.1515/cond.2012.110084>, and Table 1 respectively. The highest population estimated at the all-zone scale was about 23 700 in 2002 (95% CL: 18 300–29 000; Table 1). The estimate for 2010, the lowest annual estimate for all zones, was 16 700 birds (95% CL: 13 100–20 300; Table 1). Of the individual zones, 1 and 3 had the two highest estimated populations in all years except 2008, when they were larger for zones 3 and 4 (Appendix 1). The population estimated in zone 5 was far smaller than for any other zone, never exceeding 300 birds.

Because population estimates are the product of both density and area of coastal waters, density patterns by zone did not closely track population estimates. This is largely because the area sampled in Zone 1 (about 3500 km²) is more than double that of the next largest zone (about 1650 km², Zone 2). Murrelet density varied from 0.05 km⁻² in Zone 5 to >3 or 4 birds km⁻² in zones 3 and 4 (Appendix 1). Within a zone,

TABLE 1. Summary of estimated density and population (rounded to nearest 100 birds) of the Marbled Murrelet in all zones surveyed (conservation zones 1–5), 2001–2010.

Year	Density (birds km ⁻²) ^a	Population ^b
2001	2.52 (0.27)	22 200 (17 600–26 800)
2002	2.69 (0.31)	23 700 (18 300–29 000)
2003	2.53 (0.24)	22 200 (18 100–26 400)
2004	2.43 (0.25)	21 400 (17 000–25 800)
2005	2.30 (0.25)	20 200 (16 000–24 500)
2006	2.14 (0.17)	18 800 (15 900–21 700)
2007	1.98 (0.26)	17 400 (12 800–21 900)
2008	2.03 (0.18)	17 800 (14 600–21 000)
2009	2.02 (0.21)	17 800 (14 200–21 300)
2010	1.90 (0.21)	16 700 (13 100–20 300)

^aBootstrap SE in parentheses.

^b95% CL in parentheses.

densities at the scale of a PSU varied by more than an order of magnitude (from <1 to >10 km⁻²), except in Zone 5, where density was uniformly low (Fig. 3). For all zones combined, the mean density varied by year (Table 1) from 1.9 (2010) to 2.7 km⁻² (2002).

POPULATION TREND

From 2001 to 2010, the population estimated for all zones combined declined at a rate of 3.7% per year (95% CI = –4.8

TABLE 2. Estimates of average annual rate of population change. Trends for all zones combined and zones 1 and 2 are based on data from 2001 to 2010, those for other zones on data from 2000 to 2010; see text for details.

Zone	Annual change (%)		95% Confidence limits		Adjusted R ²	P
	Estimate	SE	Lower	Upper		
All zones	–3.7	0.4	–4.8	–2.7	0.89	<0.001
1	–7.4	1.6	–11.2	–3.5	0.67	0.002
2	–6.5	2.9	–13.1	0.06	0.29	0.06
3	–1.5	1.7	–5.4	2.6	0.00	0.41
4	–0.9	1.2	–3.9	2.0	0.00	0.47
5	–0.5	9.3	–21.7	26.3	0.00	0.97

to –2.7%; Table 2, Fig. 4). This is equivalent to a total decline of 29% (SE = 3%) over this period, based on an exponential model of population change. The evidence is strong for a decline at this scale ($P < 0.001$, adjusted $R^2 = 0.89$, Table 2).

At the scale of the individual zone, in Zone 1, we found a significant rate of decline of 7.4% per year (95% CI = –11.2 to –3.5%; Table 2). This represents a total decline of about 46% over the 10 years. Evidence of a decline was also strong in Zone 2, at a rate of 6.5% per year (95% CI = –13.1 to 0.06%, $P = 0.06$; Table 2). The trends for the other zones were not statistically significant.

Effects of observer and sea condition on density and trend estimates. For each year, we identified the best-fit models for

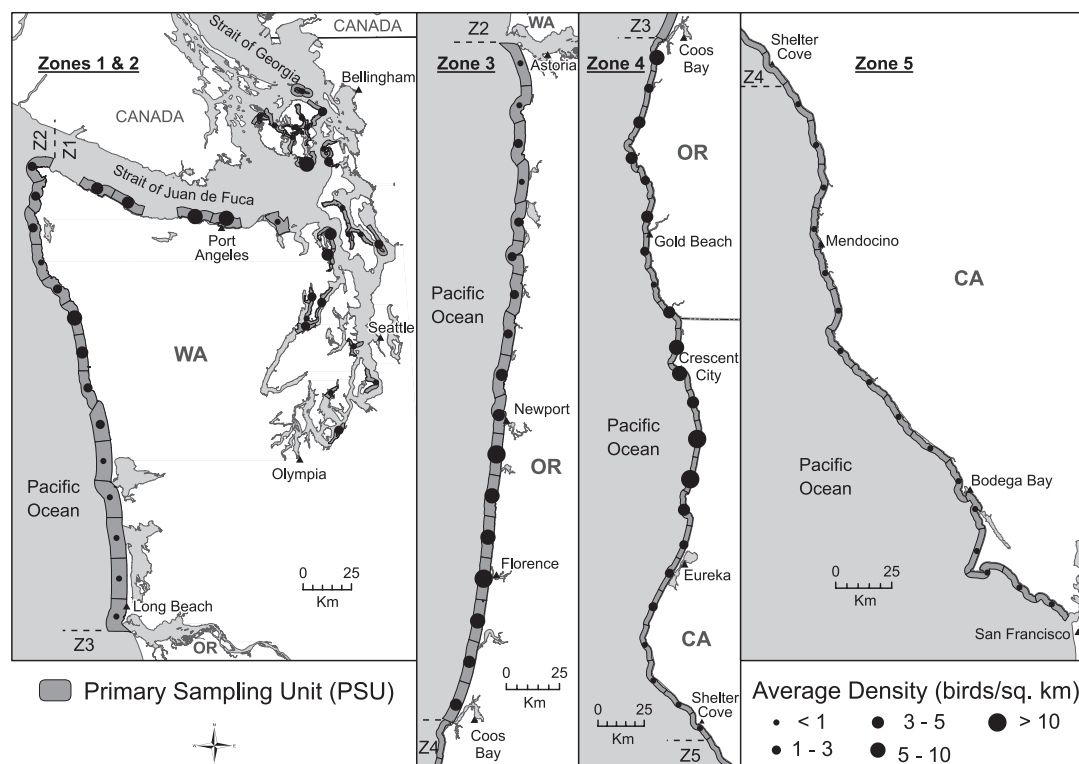


FIGURE 3. Average Marbled Murrelet densities at sea by primary sampling unit for each conservation zone of the Northwest Forest Plan area. Based on mean densities recorded from 2001 to 2010.

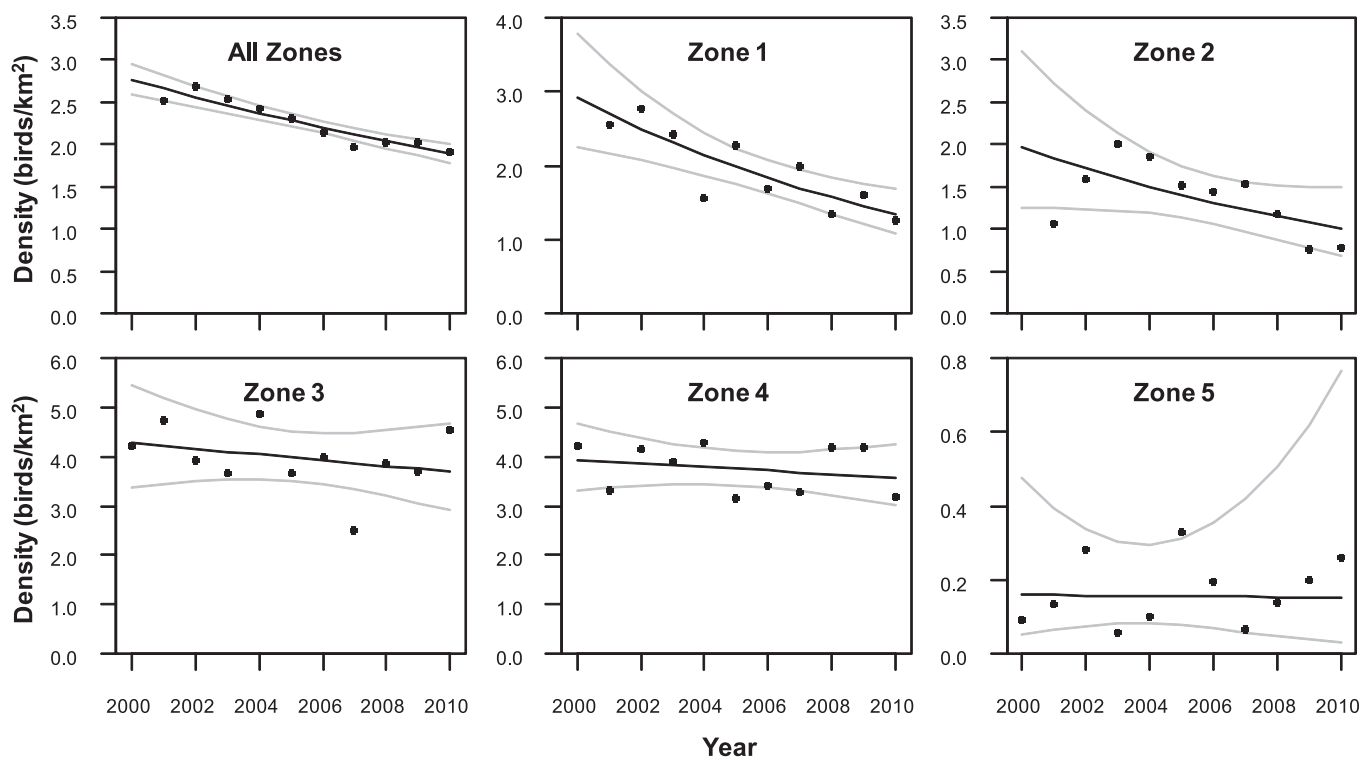


FIGURE 4. Results of analyses of trends in the Marbled Murrelet population of the Northwest Forest Plan, at the scales of all zones combined and five individual zones, 2000–2010. Graphs show fitted regression lines through the annual population estimates with 95% confidence limits.

Zone 1 density by the model with the lowest AIC_c . While the best model in most years included one or more covariates, the effect on density was minor, with estimates by the no-covariate and best-fit models being very similar in all years (Fig. 5). Also, no one model was consistently the best; each model (no-covariate, crew, sea condition, crew plus sea condition) performed best in at least one year. On the basis of the density estimates from the best model for each year, the population trend estimated for Zone 1 was -6.8% per year, compared to our estimate of -7.4% per year based on the no-covariate model, and well within the confidence limits of that estimate.

DISCUSSION

For the five zones of the Plan area, we observed an overall decline of about 29% (3.7% per year) from 2001 to 2010. This is consistent with earlier power analyses that estimated about 10 years of annual monitoring would be required to detect a decline of this magnitude with 95% power (Miller et al. 2006).

A key objective of the Northwest Forest Plan is the conservation of nesting habitat to support stable or increasing populations of the Marbled Murrelet. However, murrelet populations were not expected to respond rapidly to protection of their nesting habitat on federal lands, nor to the Plan's measures to increase the amount of old forests on its lands. New murrelet nesting habitat—forest with large old trees—is expected to take a century or more to develop on cutover lands

(USFWS 1997). Our results indicate that the population has not yet stabilized, particularly in Washington state, where the decline was strongest. The observed decline, particularly the

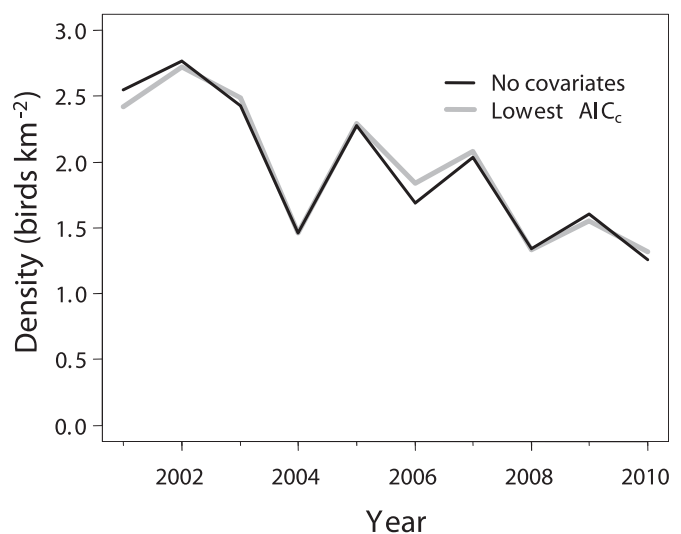


FIGURE 5. The effect of including covariates in the models used to estimate Marbled Murrelet density each year for Conservation Zone 1 (Washington: San Juan Islands, Puget Sound, and Strait of Juan de Fuca). The two lines represent annual density as estimated by a simple DISTANCE model with no covariates and by the best-fitting DISTANCE model with covariates (sea conditions, observer, or sea conditions plus observer) based on the lowest AIC_c value, for 2001 to 2010.

7% decline estimated in northern Washington (Table 2), suggests that conservation measures have not been sufficient to arrest the species' decline.

POTENTIAL UNCERTAINTIES IN SAMPLING

We reviewed several sources of potential bias to assure ourselves of the observed trends. For example, we anticipated a seasonal increase in murrelet density during the sampling period as chicks hatched and incubating birds returned to the water to forage, making only short flights inland to feed chicks (Peery et al. 2007). However, examination of the data early in the monitoring program (Miller et al. 2006) did not find a temporal trend within a season. This lack of a seasonal trend may be due to a variety of factors, including a small proportion of birds breeding in any one year or the early return to the ocean of breeders whose nests failed during incubation. Our objectives in this study were to estimate the average number of birds in our target area between 15 May and 31 July and to be able to detect trends in those estimates. Our sampling design, which distributed sampling effort consistently through this period, allowed us to meet our objectives even if the number of birds on the water during the sampling period was not constant.

We devoted more effort to the inshore subunit of each PSU, where results from our previous work indicated that densities were highest. All but seven of the 115 PSUs sampled fit this pattern. Five of these seven PSUs were clustered in the southern half of Zone 2, suggesting local conditions may affect this pattern. This rare pattern should not influence the trends inferred for the entire population because it arose in such a small percent of the total area covered and represented relatively few birds. At these few locations, however, we may not have met our goal of surveying far enough offshore to sample 95% of the local population. We will continue to sample the offshore subunit to account for any short-term shift in the murrelets' distribution, for instance, if the birds forage farther offshore in some years. This will also allow us to detect a long-term (multi-year), systematic shift of the murrelets farther offshore; such a shift could affect our ability to assess population trends if it resulted in a substantial change in the proportion of murrelets occurring beyond the waters sampled.

We acknowledge that the areas we surveyed do not include the entire murrelet population in our zones. In some zones, murrelets have been detected farther offshore, particularly where shallow waters and islets extend farther offshore (Ralph and Miller 1995, Speich and Wahl 1995, Strong et al. 1995). These studies indicate that only a small proportion of the population, generally less than 5%, is outside of our survey area (beyond 2 to 8 km from shore, depending on zone). Excluding these few birds has little effect on the estimates of the total population or trends.

Other studies have found effects of year, observer, and sea state on the murrelet's detectability and estimated density at sea (Ronconi and Burger 2009). We did not include these factors as covariates in the estimation of $f(0)$ in DISTANCE, as can be done. By design, our trend analyses accounted for year effects.

Sea-state effects are minimized by our protocol, which precludes surveys during rough seas (Beaufort force ≥ 3), and low turnover in crews and consistent training and audits should reduce any observer effect. We tested for any residual effect of sea state and observer on our results from Zone 1. We used this zone as it had strong evidence for a decline and is the most heterogeneous zone, with two of three strata in the relatively calm, sheltered waters of Puget Sound and the San Juan Islands and one stratum in the relatively exposed waters of the Strait of Juan de Fuca. While this analysis suggested that differences in observer and sea state can affect estimates of the murrelet's density, those effects were small and did not change our conclusion about the direction or magnitude of the population decline in Zone 1.

Given the goals of the Plan and the monitoring program, ideally, any population trends we observe through monitoring should reflect changes within the Plan area. However, biological systems are rarely closed, particularly when defined by political boundaries. It is likely that there is some movement of murrelets between the northern portion of our sampling area and Canadian waters to the north. Suitable nesting habitat continues north from Washington into British Columbia, both on the mainland and Vancouver Island, and such movements have been observed. In a telemetry study, Raphael (unpubl. data) recorded movements between U.S. waters and nesting sites on nearby Vancouver Island but no long-distance movements consistent with individuals shifting their distribution from Washington to areas north of our study area.

A northward shift of the murrelet's distribution from Washington into Canada could mimic the decline observed in Zone 1 (Puget Sound and Strait of Juan de Fuca) and could also affect trends in the coastal Washington zone, Zone 2. However, we know of no evidence or causal mechanism for such a shift from 2001 to 2010, and all data available indicate that such a shift is unlikely. The murrelet's distribution at sea during the breeding season generally coincides with the distribution of potential nesting habitat directly inland (Burger 2002, Miller et al. 2002, Raphael et al. 2002, 2006), suggesting that most murrelets observed on the water represent local breeding populations. A large northward population shift would suggest that breeding individuals are shifting nest locations, which is not supported by the limited information on nest-site fidelity. Nest-site fidelity is common in other alcids (Divoky and Horton 1995), and individual Marbled Murrelets re-nest in the same stands and trees in successive years, suggesting fidelity to nest areas (Hebert et al. 2003, Piatt et al. 2007). Also, population-trend data from British Columbia from the 1990s to 2006 do not support a shift to the north. Regression of data from multiple transects along the west coast of Vancouver Island and from a single transect in Haida Gwaii (Queen Charlotte Islands) implies a decline for that period, suggesting a large-scale decline (Piatt et al. 2007). Finally, Piatt et al. (2007) reported a substantial and continuing loss of likely murrelet nesting habitat on Vancouver Island and Haida Gwaii since the 1970s. If the murrelet's distribution has shifted north from Washington since 2001, it is not reflected in the population trend for British Columbia, nor does the trend

in that province's nesting habitat support the hypothesis of a northward shift.

POTENTIAL CAUSES FOR DECLINE

While the causes for the observed decline are unknown, potential proximal factors include the loss of nesting habitat, including cumulative and time-lag effects of habitat losses over the past 20 years (an individual's potential lifespan), changes in the marine environment reducing the availability or quality of prey, increased densities of nest predators, and emigration. Ultimately, these factors can contribute to a decline by affecting the demographic processes of survival and fecundity.

The population decline we observed was within the range of 3 to 8% per year predicted by demographic models (Beissinger and Nur 1997, McShane et al. 2004). Those models indicate that low fecundity, more than adult survivorship, may be responsible for the declines. On the basis of data from known nests and the ratio of juveniles to adults observed at sea during the fledging period, the murrelet's fecundity appears to be low (USFWS 1997, McShane et al. 2004, Hebert and Golightly 2007, Peery et al. 2007, Bloxton and Raphael 2008, Strong 2008, Long et al. 2010). One factor contributing to low productivity is the high rate of predation by avian predators, particularly corvids (jays and ravens) (Nelson and Peck 1995, Luginbuhl et al. 2001, Raphael et al. 2002, Peery et al. 2004, Hebert and Golightly 2007). Elevated predation rates may be the result of increased numbers of predators associated with anthropogenic food sources and habitat fragmentation. In parts of the Plan area, most of the murrelet's remaining nesting habitat lies in parks and other public lands. The parks and national forests generally provide recreational facilities such as hiking trails and campgrounds where human activities tend to increase or concentrate corvid populations (Marzluff and Neatherlin 2006), likely increasing the risk of corvid predation on murrelet eggs and nestlings. Experiments found that the rate of predation of artificial nests on the Olympic Peninsula is significantly correlated with corvid abundance and that increased abundance of the American Crow (*Corvus brachyrhynchos*) and Common Raven (*C. corax*) is associated with human settlements and campgrounds (Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006). Crows used campgrounds more frequently than other land-cover types, and crow abundance is positively correlated with campground size (Neatherlin and Marzluff 2004). Public education and consideration of moving campgrounds to outside of the murrelet's nesting habitat are some of the current attempts to reduce nest predation by corvids within parks.

Landscape characteristics of the remaining old-growth forests also may be contributing to these high predation rates by reducing habitat quality for murrelets through fragmentation of the remaining forest patches. Fragmented patches often have high ratios of edge to interior, and edge habitats tend to support more predators (e.g., DeSanto and Willson 2001, Malt and Lank 2007). Planning reserves with

larger forest patches, with more core area and less edge, could reduce numbers of avian predators (Marzluff et al. 2000) and, consequently, improve the murrelet's nesting success.

The loss of nesting habitat was a major cause of the murrelet's decline over the past century and may still be contributing as nesting habitat continues to be lost to fires, logging, and wind storms (USFWS 2009, Raphael 2006). The Plan's monitoring of the murrelet's nesting habitat documented losses directly inland from the areas we sampled (Raphael et al. 2011). Within the three-state area, losses were greatest in Washington (9–11% from 1996 to 2006) and Oregon (5–17%, 1996 to 2006) and lower in California (2–6%, 1997 to 2007). This pattern of loss of older forest is independently supported by analyses of habitat for the Northern Spotted Owl (*Strix occidentalis caurina*) (Davis et al. 2011). Thus both populations and nesting habitat have recently declined in the northern part of our study area, in Washington and Oregon, suggesting a potential terrestrial mechanism for the population declines. This potential terrestrial mechanism of habitat loss warrants additional study because there is a strong positive correlation between the murrelet's population size and area of high-quality nesting habitat (e.g., Miller et al. 2002, Raphael et al. 2011), suggesting that the murrelet's numbers may be limited by the amount of high-quality nesting habitat, as suggested by Burger and Waterhouse (2009) and Raphael (2006).

In addition to the loss of quantity and quality of nesting habitat, factors in the marine environment may also be affecting the murrelet population. Oil spills have caused direct mortality throughout the murrelet's range (Kuletz 1996, Piatt and Ford 1996, McShane et al. 2004, USFWS 2009), although no oil spills killing murrelets have been recorded in waters off the Plan area since 1999 (USFWS 2009). The quality and composition of the murrelet's prey could be linked to changes in the distribution and abundance of that prey, which are, in turn, influenced by factors such as overfishing or oceanographic changes associated with climate change (Becker and Beissinger 2006, Becker et al. 2007, Norris et al. 2007). Changes in ocean conditions over the period of our monitoring could be affecting adults' survival and reproductive success by reducing the availability of prey in the nearshore waters where murrelets forage. Although data on the availability of the murrelet's prey over the period of our sampling are scarce, there is evidence of a warming of the coastal waters we surveyed (Sydeman and Elliott 2008, Ruckelshaus and McClure 2007) and for El Niño becoming more frequent, persistent, and intense during the last 20 to 30 years (Snyder et al. 2003), perhaps because of climate change. Much remains to be learned about potential effects of warming sea temperatures on the murrelet's prey, but northward shifts in the distribution of marine organisms can be expected as sea temperatures increase (Harley et al. 2006). Becker et al. (2007) suggested that in central California cooler water temperatures supported increased availability of the murrelet's prey and improvement in its reproductive success. In southern British Columbia, Norris et al. (2007) found

a strong correlation between the quality of the murrelet's diet and its abundance 3–4 years later, suggesting that diet could affect reproductive success. In southwestern British Columbia, Ronconi and Burger (2008) found that the murrelet's reproductive success was affected by annual variability in prey and oceanographic conditions, with increased foraging effort by parents ineffective at compensating for the effects of low prey availability during the poorest conditions.

One indication of marine rather than terrestrial causes of the observed decline would be a concurrent decline of seabirds that forage in the same marine environment as the murrelet but do not nest in the forest. During our murrelet surveys, we sampled other seabirds breeding locally by the same methods and tested for declines in these species from 2001 to 2009 in Washington, where the Marbled Murrelet declined in both zones 1 and 2. Among six species of alcids and three of cormorants, we found no species that had declined in both Puget Sound and along Washington's outer coast (zones 1 and 2; Pearson and Raphael, unpubl. data). In fact, two species appeared to be increasing in both regions and two demonstrated declines or increases in one region but not the other. These preliminary trends for other species do not support a hypothesis of systematically unfavorable marine conditions during the period of analysis.

The relationships between quantity and quality of inland forest, ocean conditions, and population densities at sea in the Plan area need further study. We plan to investigate these relationships, by integrating the results of this study with those of a complementary program that monitors the distribution and trend of nesting habitat (Raphael et al. 2011) and available oceanographic and prey data. A primary goal of this work will be to understand the causes of the population decline we observed and to provide information that may point to ways to better manage forests and other resources in the Plan area to conserve the Marbled Murrelet.

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