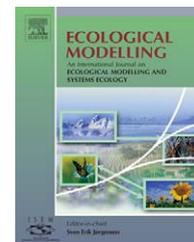


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Evaluating at-sea sampling designs for Marbled Murrelets using a spatially explicit model

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ABSTRACT

Spatial environmental gradients can greatly affect the distribution of organisms, but studies investigating how the spatial arrangement of samples along these gradients influences power of monitoring programs to detect trends are lacking. Spatial gradients in environmental processes may remain relatively constant, or change over different time intervals and spatial dimensions. We investigated the influence of transect layout and replication on the power to detect population declines in the Marbled Murrelet (*Brachyramphus marmoratus*), a threatened seabird found in a highly dynamic nearshore environment. In Marbled Murrelet populations in our study area, no a priori gradient along the shoreline was apparent, whereas a predictable decline in abundance offshore occurred. We characterized the spatial and temporal variation in the offshore gradient by: (1) fitting flexible curves to historical abundance data from 13 site–year combinations in California and Oregon and (2) applying clustering routines to the fitted offshore probability distributions to reveal three distribution patterns that varied among sites and annually within sites. Power of sampling schemes was derived by a simulation where nine transect designs of equal effort detected population declines over 10 years within an 80 km × 2.5 km sampling unit either with or without stratification, based on data-generating distributions that were an approximation to the observed data. Our simulations suggested several designs had high power to detect trends at an annual decline rate of 2, 4, and 6%, produced relatively unbiased population estimates and slopes of the trend, and were logistically feasible: (1) stratified and unstratified zigzags and (2) ten 8 km transects placed at random distances parallel to shore in two strata. For murrelets, layouts that adequately sample along-shore and offshore in both high-density and low-density areas were most robust to heterogeneity and shifting environmental gradients in both along-shore and offshore dimensions. Our approach shows how pilot survey data and an understanding of spatial gradients or heterogeneity can help design a powerful sampling layout.

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1. Introduction

Detecting declines in wildlife populations is critical for initiating conservation measures that prevent biodiversity loss (Holt et al., 1987; Doak, 1995; Burgman et al., 2001). To detect a decline, sampling designs must accurately estimate range size, population size, or some index of the population over time (Gerrodette, 1987; Peterman, 1990; Steidl et al., 1997). Physical and biological processes in the environment that affect the distribution of organisms often occur along spatial gradients in one or more dimensions and interact to affect spatial distributions of organisms. Spatial environmental gradients and their associated variability should be incorporated into sampling schemes at an appropriate scale. In highly dynamic systems, such as marine environments, spatial gradients in environmental processes may be relatively constant (e.g., bathymetry) or may change over hourly (e.g., tides), daily or seasonally (e.g., upwelling), or yearly (e.g., El Niño Southern Oscillation [ENSO]) intervals. Processes creating gradients may occur in a predictable (e.g., tides and bathymetry) or less predictable (e.g., upwelling and ENSO) manner. In nearshore marine environments, spatial gradients may differ in their along-shore (parallel to the shoreline) and offshore (perpendicular to the shoreline) dimensions. As a result, distributions of marine organisms may be unpredictable and characterized by heterogeneity. Previous work has suggested that sampling across spatial gradients or sampling almost exclusively in high-density areas of a species range can increase power to detect a trend (Gerrodette, 1987; Strayer, 1999; Buckland et al., 2001). However, focusing on high-density areas can be difficult if locations change over time, which is likely for mobile species and species in highly dynamic systems.

Here, we investigate spatial aspects of line transect designs for monitoring species found in landscapes with underlying but shifting environmental gradients that affect distributions. Line transects are a widely used sampling method for detecting population trends (e.g., Fisher et al., 2000; Srivastava et al., 2001; Okouyi et al., 2002), and their ability to accurately estimate abundance has been improved with the development and application of distance sampling theory (Buckland et al., 2001). Previous studies have primarily focused on the power advantages of increased transect replication (Gerrodette, 1987; Thompson et al., 1998; Strayer, 1999; Wilson et al., 1999). However, few studies have investigated the impact of the spatial arrangement of transects on trend detection (but see Van der Meer, 1997). In this paper, we use a simulation approach to study how the complicated juxtaposition of transect layout and variability in species distribution in space and time affect the detection of trends in abundance.

Simulation studies involving explicit models of species distributions have been used to evaluate the relative merits of various designs (Austin and Adomeit, 1991; Hirzel and Guisan, 2002). The goal of these studies was to find the best design for minimizing the error of predicting habitat suitability. However, this basic approach can be adapted for any function of the distribution of species over space and time. Our goal is to use simulation studies to quantify the relative performance of survey designs at detecting a trend over time in the abundance of a particular species within the study area.

Specifically, we develop a spatially explicit model to examine how the spatial arrangement of line transects influences power to detect population trends in the Marbled Murrelet (*Brachyramphus marmoratus*), a federally threatened seabird that spends most of its life nearshore in a highly dynamic ocean ecosystem but nests in old growth forests (Binford et al., 1975; Sealy, 1975; Carter and Sealy, 1990). Marbled Murrelets are rare in large portions of their former nesting range in California, Oregon, and Washington (Marshall, 1988; Carter and Erickson, 1992; Nelson et al., 1992; Ralph, 1994) due to logging of old growth forests, oil spills, increased predation, and decreased food supply (Stein and Miller, 1992; USFWS, 1992; Peery et al., 2004a). Although demographic models from some areas suggest that murrelets may be declining at a rate of at least 4–6% per year (Beissinger, 1995; Beissinger and Nur, 1997), current population trends are uncertain (Becker et al., 1997; Cam et al., 2003; USFWS, 2003). Monitoring murrelets in forest stands typically is not used for estimating population trends due to the bird's secretive nesting behavior (Nelson and Hamer, 1995; Paton, 1995). Radar has been used effectively to count murrelets flying up watersheds (Burger, 2001; Cooper et al., 2001; Cooper and Blaha, 2002; Raphael et al., 2002), but it only detects the proportion of birds that fly inland attempting to nest (Peery et al., 2004b). At-sea monitoring is an effective method for estimating murrelet abundance because during the breeding season it detects nesting and non-nesting murrelets, when murrelets occur mostly within 2–3 km of shore near inland nesting areas (Ralph and Miller, 1995; Strong et al., 1995; Becker et al., 1997; Meyer et al., 2002), although birds are occasionally seen up to 10 km from shore (Ainley et al., 1995). At-sea distributions of Marbled Murrelets vary both offshore and along-shore. Bathymetry creates a relatively predictable gradient affecting offshore abundance, while upwelling, sea surface temperature, and prey availability significantly affect the distribution of murrelets along-shore (Becker and Beissinger, 2003; Yen et al., 2004). The latter factors vary within and among years and suggest that abundance along-shore is likely to be less predictable and more heterogeneous than offshore abundance.

In this paper, we develop a model to examine the effectiveness of a variety of at-sea sampling designs for Marbled Murrelets, which display spatial and temporal variation in abundance associated with shifting environmental factors. Using available at-sea data, we first develop techniques to estimate offshore and along-shore abundance patterns and to examine how patterns vary from site-to-site and year-to-year throughout Oregon and California. We then utilize these patterns in a simulation model that uses data-generating functions to distribute murrelets over space with daily and annual variability and tests nine different transect designs and two sampling frequencies. We evaluate designs based on their ability to detect population trends and their bias in population estimates and declines.

2. Methods

The value of population monitoring increases when trends can be related to a set of candidate factors that could potentially cause population change (Greenwood et al., 1993).

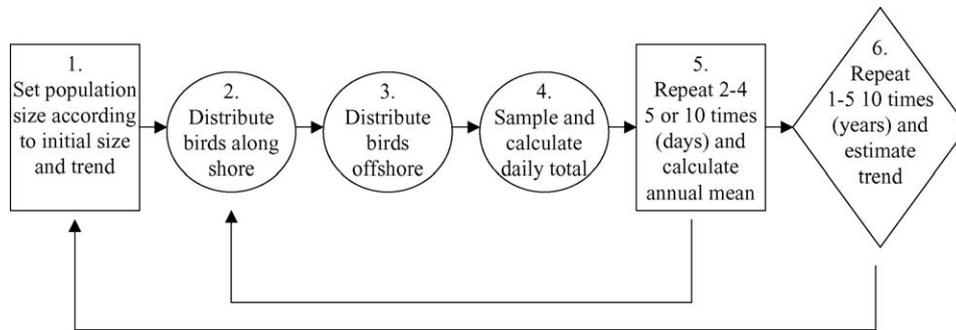


Fig. 1 – Schematic of one simulation of 10 years. For every unique combination of sampling design and offshore distribution, we repeated this 500 times to estimate power and bias. Circles, rectangles, and diamonds represent steps performed daily, yearly, and every 10 years, respectively.

Regional and local changes in population size of Marbled Murrelets could be monitored in dozens of local survey areas (e.g., 50–100 km of coastline) and compared with differences or trends in terrestrial habitat (e.g., amount, degree and fragmentation of old growth, and density of nest predators) and oceanographic conditions (e.g., marine habitat features and fish populations) to evaluate their relative importance (USFWS, 1997; Peery et al., 2004a). Therefore, we choose an 80 km length of shoreline as our sampling unit, which is large enough to encompass overlapping home ranges of 500–700 nesting and non-nesting murrelets in central California (Peery et al., 2004b; M.Z. Peery, unpublished data).

We created a spatially explicit simulation model to compare a variety of sampling schemes under different environmental conditions to find designs that were efficient in detecting declines subject to annual and daily changes in the at-sea distribution of murrelets. We chose a Monte Carlo simulation model over an analytic model because of the difficulty of deriving analytic models that can incorporate a high level of spatial and temporal variation at daily and annual scales (Bendetti-Cecchi, 2001), which occurs in murrelet distributions (Ralph and Miller, 1995; Becker et al., 1997; Becker and Beissinger, 2003). The simulation model (Fig. 1) proceeds by: (1) randomly distributing, both along-shore and offshore, a fixed number of birds (1000 in year 1) in a virtual ocean for each day; (2) setting an annual decline (2, 4, 6, 8, or 10%); (3) setting the transect layout (nine different layouts) and number of days per year to be sampled (5 or 10 days); (4) counting the number of birds detected for 50 m on both sides of a virtual boat that passed through the ocean according to the assigned transect layout, assuming a detection probability of 1.0. Becker et al. (1997) examined distance sampling techniques in our system and found detectability remained high to 50 m on either side of a transect; (5) calculating the mean annual number of birds detected, fitting a regression to the means over 10 years, and determining if a significant trend is present. Details of parameter estimation and model structure are below.

2.1. Characterizing offshore and along-shore distributions

2.1.1. Offshore distribution of murrelets

Our first objective was to estimate offshore distributions by fitting functions to historical survey data of murrelets by year

and location, and then to cluster these functions into general patterns of offshore distribution in order to evaluate spatial and temporal variation. Functions were later used to distribute birds offshore in the simulation program.

Past data available to us from Oregon and central and northern California yield indirect estimates of the offshore distribution of murrelets (13 site and year combinations; Table 1 and Appendix A). The California and Oregon segments of the Marbled Murrelet range are characterized by open ocean and linear shorelines (Carter and Erickson, 1992; Nelson et al., 1992). In other areas, Marbled Murrelets are found primarily in protected bays and fiords, where at-sea monitoring must take different strategies into account (Aglar et al., 1998; Kuletz and Kendall, 1998; Yen et al., 2004).

To characterize offshore distributions of murrelets in the available data, we evaluated families of curves that were flexible enough to reflect the rapid changes in abundance with distance offshore found in the survey data. Because abundance was measured at only a few distances from shore, we concentrated on curves that contained a minimal number of parameters (2–4). These included polynomial (quadratic and cubic), quadratic splines, and exponential models. Exponential curves fit some offshore distributions very well, but were not used because they only yield a monotonic decline and could not reflect the other patterns of abundance observed. We used the Akaike Information Criterion corrected for small sample size (AIC_c) to compare fits of curves (Sakamoto et al., 1986; Burnham and Anderson, 2002). The quadratic spline fit the data equal to other polynomial curves for all 13 site-year combinations, with ΔAIC_c values for the other models ranging from –0.6 to 0.8 (AIC values within 2 are considered indistinguishable; Burnham and Anderson, 2002). Quadratic splines are flexible functions that can be used to estimate an infinite variety of underlying curves, and assign a “knot” or a data point where the fitted function can bend quickly (de Boor, 1978). We then used quadratic splines to estimate the probability distribution (density) of birds offshore for each site-year combination (see Appendix B for details).

We used a clustering technique to group the probability density functions for the 13 site-year combinations to yield a smaller number of characteristic sets of offshore patterns. We used a weighted Euclidean distance between pairs of normalized curves, which totaled 78 unique combinations, by calculating the difference between two curves every 50 m from

Table 1 – Region–site–year combinations used to estimate offshore distributions of Marbled Murrelets with their abbreviations, kilometers of coastline sampled, and sources of data for each region

Region	Site	Year	Abbreviation	Kilometers	Reference
Central California	Año Nuevo Bay	1996	ANB96	10	Becker et al. (1997); S. Beissinger and B. Becker (unpublished report)
		1997	ANB97	10	
		1998	ANB98	10	
	Half Moon Bay Santa Cruz	1996	HMB96	10	
		1998	SC98	10	
Northern California	Agate Beach	1997	AGBE97	6	C. Ralph, B. O'Donnell, L. Long, S. Miller, and T. Shaw (unpublished report)
	Crescent Beach		CRBE97	4	
	North Jetty		NOJE97	4	
	Trinidad south		TRSO97	8	
Oregon	Central	1996	Central96	4	C. Strong (unpublished report); C. Strong and M. Fisher (unpublished report)
		1997	Central97	4	
	South	1997	South97	4	

0.5 to 5.0 km from shore (see Appendix C for derivation). We constructed a 13×13 symmetric distance matrix from these weighted distance measures and used it to cluster the probability densities to examine similarities in the offshore distributions of murrelets among years and sites using a hierarchical clustering routine (Venables and Ripley, 1997). Three main patterns of offshore distribution were identified and used in the simulations: nearshore, offshore, and midshore patterns.

2.1.2. Along-shore distribution of murrelets

The only data available for characterizing along-shore distribution of birds were abundance data from an 80 km line transect placed nearshore, parallel to the shoreline, in central California and replicated approximately weekly for 2 years during the breeding season. Average annual density of murrelets was recorded in 4 km segments (Fig. 2) and used to

describe two along-shore distributions: (1) a “uniform” distribution that assigned an equal probability of occurrence to each segment, similar to the distribution observed in 1996 and (2) a “clumped” distribution that used the distribution observed in 1997 to calculate a probability of occurrence for each segment by dividing the abundance in each segment by the sum of all segment abundances.

2.2. Sampling design evaluation

We evaluated the properties of different potential survey designs by: (1) power to detect a population trend over time; (2) bias in annual population estimates and in the slope of a simulated decline over 10 years; (3) variability in annual population estimates and in the slope of a simulated decline over 10 years. Because our simulation model could not include all

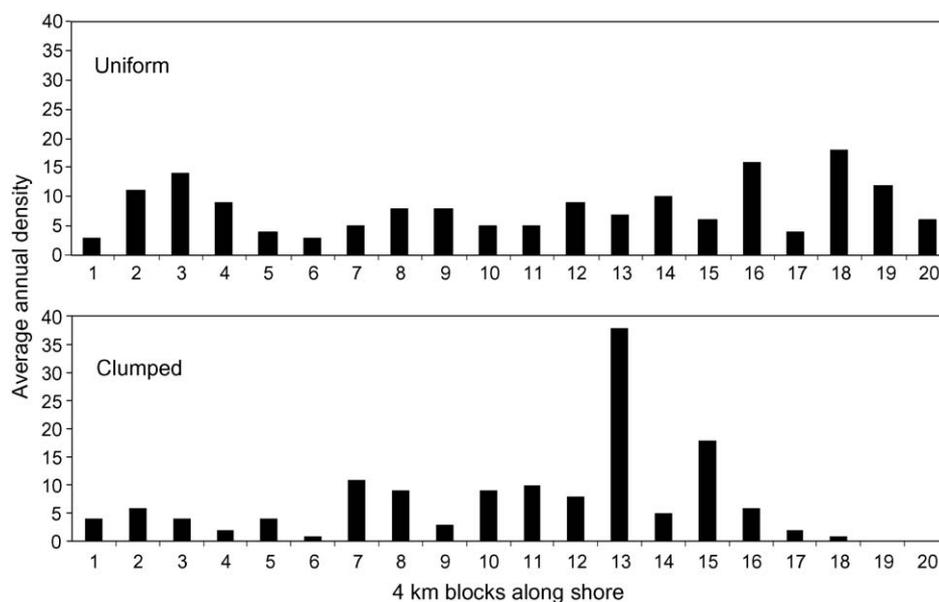


Fig. 2 – Distribution of Marbled Murrelets along an 80 km length of coastline from Half Moon Bay to Santa Cruz in central California over 2 years: uniform (1996) and clumped (1997). Each block represents a 4 km segment of coastline, with block 1 farthest north and block 20 farthest south.

variation encountered in real populations, the power, bias, and population estimates should be viewed as relative measures used to compare the designs rather than as absolute estimates for the sample design in a real murrelet population. In addition, we recorded the total driving distance by surveyors in boats, which affects the costs and time required to perform surveys.

2.2.1. *Transect layout*

We chose sampling designs for evaluation based on suggestions by the US Fish and Wildlife Service's Marbled Murrelet At-Sea Working Group, their statistical desirability and their feasibility. We chose a sampling frame from just beyond the surf zone at 0.5–3.0 km from shore. Data on the distribution of murrelets were not consistently available from closer distances due to surf and bathymetric constraints, and past surveys found few murrelets (≤ 3 –10%) from 3.0 to 5.0 km from shore (Becker et al., 1997; S.R. Beissinger and B. Becker, unpublished data; C. Ralph, B. O'Donnell, L. Long, S. Miller, and T. Shaw, unpublished data; C. Strong, unpublished data; C. Strong and M. Fisher, unpublished data).

Nine transect designs of approximately equal sampling effort over 80 km were evaluated. Two general types of designs were used: population indices and population estimators. A population index is a measure derived from counting some portion of a population with an unknown but approximately proportional relationship with the actual population size. In our simulation, population indices were produced by repeatedly sampling the same transect placed at one distance from shore in an area of high density, which produced a temporal trend, but abundance could not be extrapolated to estimate the population size. A population size estimator is a measure which is intended to reflect the actual population size and is extrapolated over the entire range of a population to produce a population size estimate. In our simulation, population estimators were produced by repeatedly sampling a number of transects, placed to cover multiple areas in the sampling frame. The *population indices* consisted of one 80 km transect placed parallel to shore at either 550 m from shore (550 m) or 950 m from shore (950 m). These sampling schemes imitate designs initially used for monitoring murrelets (Ralph and Miller, 1995; Strong et al., 1995; Becker et al., 1997). The remaining seven designs yielded *population estimators* and consisted of transect segments that sampled various distances from shore between 0.5 and 3.0 km. Five of the population estimators were *stratified sampling designs* that placed transect segments into a *nearshore* stratum, extending from 0.5 to 1.5 km from shore, and an *offshore* stratum, extending from 1.5 to 3.0 km from shore (Fig. 3). Designs of this type included: (1) four 20 km transect segments parallel to shore at random distances from shore, with three in the nearshore stratum and one in the offshore stratum (3 nearshore/1 offshore); (2) four 20 km transect segments parallel to shore at random distances from shore, with two in the nearshore stratum and two in the offshore stratum (2 nearshore/2 offshore); (3) ten 8 km transects parallel to shore, with seven placed at random distances in the nearshore stratum and three placed at random distances in the offshore stratum (7 nearshore/3 offshore; Fig. 3); (4) ten 8 km transects parallel to shore, with five placed at random distances in the nearshore stratum and

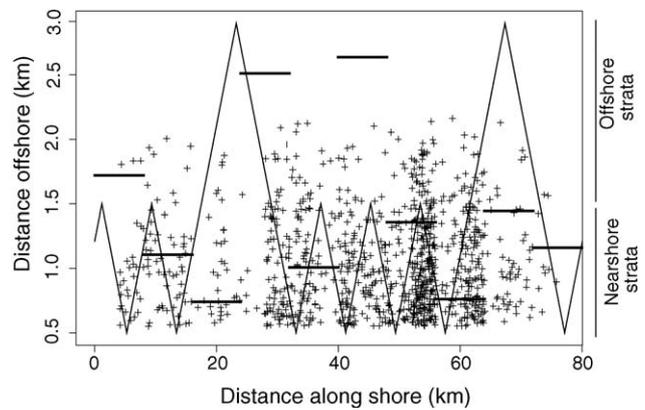


Fig. 3 – One realization of 1000 birds distributed along the 80 km shoreline between 0.5 and 3.0 km offshore used in the simulation, according to a clumped along-shore distribution and a 50% nearshore/50% midshore offshore distribution. Most designs break the offshore distribution into two strata, a nearshore strata (0.5–1.5 km from shore) and an offshore strata (1.5–3.0 km from shore). The 7 nearshore/3 offshore and stratified zigzag sampling designs are illustrated (see text for details).

five placed at random distances in the offshore stratum (5 nearshore/5 offshore); (5) a zigzag transect running at a 13° angle from the shoreline that spent 75% of the time in the nearshore stratum and 25% of the time in the offshore stratum (stratified zigzag; Fig. 3). Completely traversing the 80 km study area with this zigzag required 82.2 km of transect. These stratified sampling schemes are similar to the type of designs currently used for surveying murrelets, where short transect lines are randomly placed close to shore and a zigzag transect line is placed farther offshore (Huff, 2005). We also evaluated two *unstratified sampling designs*: (1) ten 8 km transects placed parallel to shore at random distances between 0.5 and 3.0 km from shore (10 random) and (2) a zigzag transect running continuously between 0.5 and 3.0 km from shore at a 15° angle from the shoreline (unstratified zigzags). Completely traversing the 80 km study area with this zigzag required 82.8 km of transect.

2.2.2. *Simulation mechanics*

The general sequence of the simulation is illustrated (Fig. 1). We evaluated each sampling design under a variety of along-shore and offshore distributions. We assigned all 10 years of a given simulation either to a 4 km clumped or a uniform along-shore distribution. Each bird was assigned to a segment along-shore by the probabilities calculated for the clumped or uniform distribution. We then distributed birds in the offshore direction from 0.5 to 3.0 km from shore in each simulation using patterns described from clustering analysis. Since the clustering routine revealed that distributions from shore differed from site-to-site and from year-to-year within the same site, each simulation over 10 years used one of two combinations of offshore patterns: (1) an equal chance of either a nearshore or a midshore distribution for each year (50% nearshore/50% midshore), which resembled distributions of murrelets in central California and in central Oregon and (2)

an equal chance of a nearshore or an offshore distribution for each year (50% nearshore/50% offshore), which provided the most variation in the annual offshore distribution and partly resembled distributions in northern California and southern Oregon.

Once the annual offshore distribution type was chosen, we incorporated daily variation in the distribution pattern using a linear mixed effects model based on survey data (Laird and Ware, 1982). For a specific cluster of offshore patterns (nearshore, offshore, or midshore cluster; see results of clustering analyses below), c is the density at a distance offshore and x can be represented as,

$$\text{Density}(x|c) = \beta_0^c + \beta_{0i}^c + (\beta_1^c + \beta_{1i}^c)x + (\beta_2^c + \beta_{2i}^c)x^2 + (\beta_3^c + \beta_{3i}^c)(x - x_0)_+^2,$$

where i is a particular day within a cluster, c , and the superscript represents the fact that the fixed effects (β_0^c , β_1^c , β_2^c , β_3^c) are estimated separately by major cluster. Given a particular cluster, c , the simulation chooses among daily random effects (β_{0i}^c , β_{1i}^c , β_{2i}^c , β_{3i}^c) to derive a curve that varies randomly around the mean distribution pattern. As a result, each day within a year's assigned cluster had a different distribution from shore, derived from the mixed effects models. Thus, the distribution of birds from shore used in the simulation incorporated daily, annual, and random variation.

2.2.3. Simulation evaluation

Each simulation was iterated 500 times and upon completion, we calculated the average index or population estimate per year and its coefficient of variation (CV). We estimated the average population of murrelets for the entire study area by multiplying the number detected per kilometer by the area of the sampling frame if no strata were involved in the layout. If based on stratified sampling, we estimated the overall density by a weighted average of the densities estimated separately within each strata, where the weights were proportional to the total area of the strata.

We calculated power for each sampling design using the linear trends approach (Gerrodette, 1987; Taylor and Gerrodette, 1993; Nickerson and Brunell, 1997) by fitting a linear regression on the annual average number of birds detected for the indices, or on the annual average estimated population size for designs that yielded population estimates. Power was calculated as the proportion of iterations with a statistically significant negative slope using a two-sided α -level of 0.05. Hatch (2003) criticized over-simplified versions of standard power calculations that extrapolate estimates of within-year variation to between-year components of variance. We avoided this problem both by accurately characterizing within and between-year variation and by performing linear regressions on the average annual population estimates. We used linear models, not because we think the underlying process of population decline is strictly linear, but because such models allow estimation of power using well understood statistical methods, and linearity is a useful first approximation. Linear and exponential models often fit declines equally well (Hatch, 2003), which would be expected in our study because we evaluated a short period of decline (10 years).

We considered two types of bias for the population-estimating designs: bias in the population estimate and bias in the trend (details in Appendix D). We also calculated the CVs of the estimated population sizes and estimated slopes. Finally, we calculated the maximum possible travel distances for each design, which included the distance of transects and the distance traveled between transects.

3. Results

3.1. Offshore distribution estimation and clustering

Most Marbled Murrelets were observed within 2 km of shore during the previous at-sea surveys (Fig. 4). In central California and central Oregon, murrelet abundance was usually highest in the transect nearest shore (0.4 and 0.5 km, respectively) and declined rapidly thereafter; however, in some years the greatest density was at 0.9–1.0 km from shore (Fig. 4A and C). In southern Oregon and northern California, murrelet density was greatest at 1.0–2.0 km from shore and declined at closer and farther distances (Fig. 4B and C). Truncated quadratic splines fit the observed data well, mimicking the shapes of the offshore distributions apparent from the raw data (Fig. 4). In 16 of 75 (21%) survey days, however, a small number of birds were detected beyond the truncation point of the fitted curve, resulting in the exclusion of 2.6% of the total birds observed.

Clustering routines detected three distinct groupings of sites from their probability density functions and one outlying site (Fig. 5). One cluster had the greatest density of birds nearshore and density declined rapidly with distance from shore ("nearshore"; Fig. 5A). Another cluster had humped distributions, with the highest probability of detecting a bird around 1.0 km from shore, and density declined slowly to 3.0 km ("offshore"; Fig. 5C). The third cluster was similar to the second cluster except that the probability of detecting a bird from shore declined more quickly, which resulted in a higher hump ("midshore"; Fig. 5D). The fourth cluster included only 1 site-year, an outlier with a small sample size that showed no distinct trend in density with distance from shore (Fig. 5B).

3.2. Evaluation of sampling designs

3.2.1. Power and bias of sampling designs

The greatest differences in power among various transect designs was for populations declining slowly at 2–4% per year. For rapidly declining populations (>6% per year), sampling regimes showed little variation in their power to detect trends. Thus, our results focused on the ability of designs to detect slowly to moderately declining populations (2, 4, and 6% declines).

Ranking the designs according to their relative power to detect a trend produced a similar order of designs for all combinations of replication, offshore distribution, and along-shore distribution. The ranking of the designs from highest to lowest power was: (1) stratified and unstratified zigzags; (2) 7 nearshore/3 offshore and 5 nearshore/5 offshore; (3) 3 nearshore/1 offshore and 2 nearshore/2 offshore; (4) 10 ran-

dom; (5) 550 m (see Fig. 6, for examples). The single 950 m transect was the only design whose rank changed with changing offshore distributions of birds and ranged from high power to low power. Overall, zigzag designs had higher power than designs that placed transects parallel to shore, parallel designs with shorter transects (10 transects of 8 km each) had higher power than longer parallel transects (4 transects of 20 km each), and stratified parallel designs had higher power than the unstratified parallel design.

Although the ranking of designs persisted over all combinations of distributions, replication, and rate of decline, some designs lost more power than others with changes in offshore and/or along-shore distributions and the number of replicates. All population-estimating designs were relatively robust to changes in the offshore distribution (power changed by <10%) compared to the population index measures (550 and

950 m), which, for example, lost 63 and 23% of their power, respectively, when birds occurred farther from shore (50% nearshore/50% offshore) at a 4% annual decline rate (Fig. 7A). Power was higher for most designs when murrelets occurred uniformly along-shore than when clumped (Fig. 7B). Zigzag designs and population indices were robust to a clumped along-shore distribution (lost <5% power when birds were clumped), while the parallel density-estimating designs lost 20–37% power by clumping. Overall, power increased when replication doubled from 5 to 10 days each year (Fig. 7C). For example, the population estimators gained from 33 to 89% power at a 2% annual decline rate with the increase in replication. Replication had less impact on the indices than the population-estimating designs.

Designs with the lowest variability around the population estimate and around the mean slope of the trend were

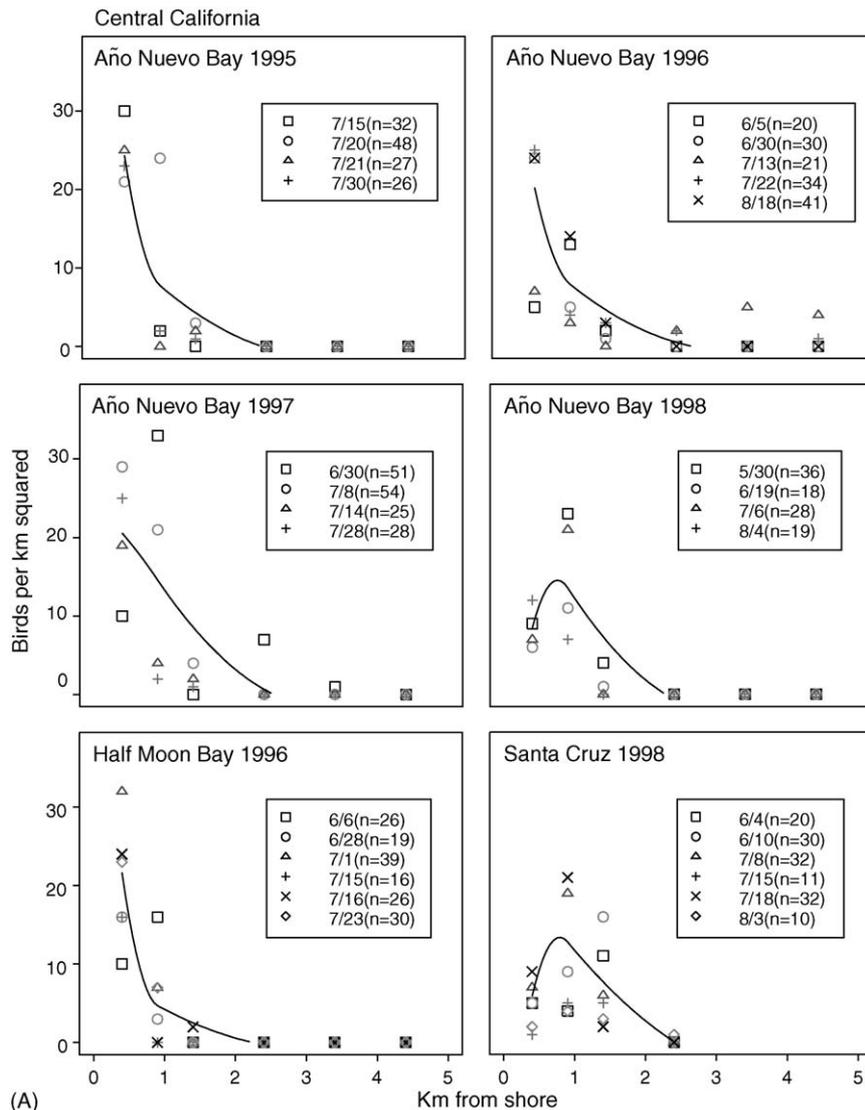


Fig. 4 – Truncated quadratic spline curves fit to the density of Marbled Murrelets offshore where each symbol type represents one survey day for: (A) three sites in central California during 1995–1998 based on 100 m strip transects, (B) four sites within northern California during 1997 based on 200 m strip transects, and (C) two sites within Oregon during 1996–1997 based on 100 m strip transects. Month and day for each survey is given. N is the total number of birds counted that day. See Table 1 for definitions of site abbreviations.

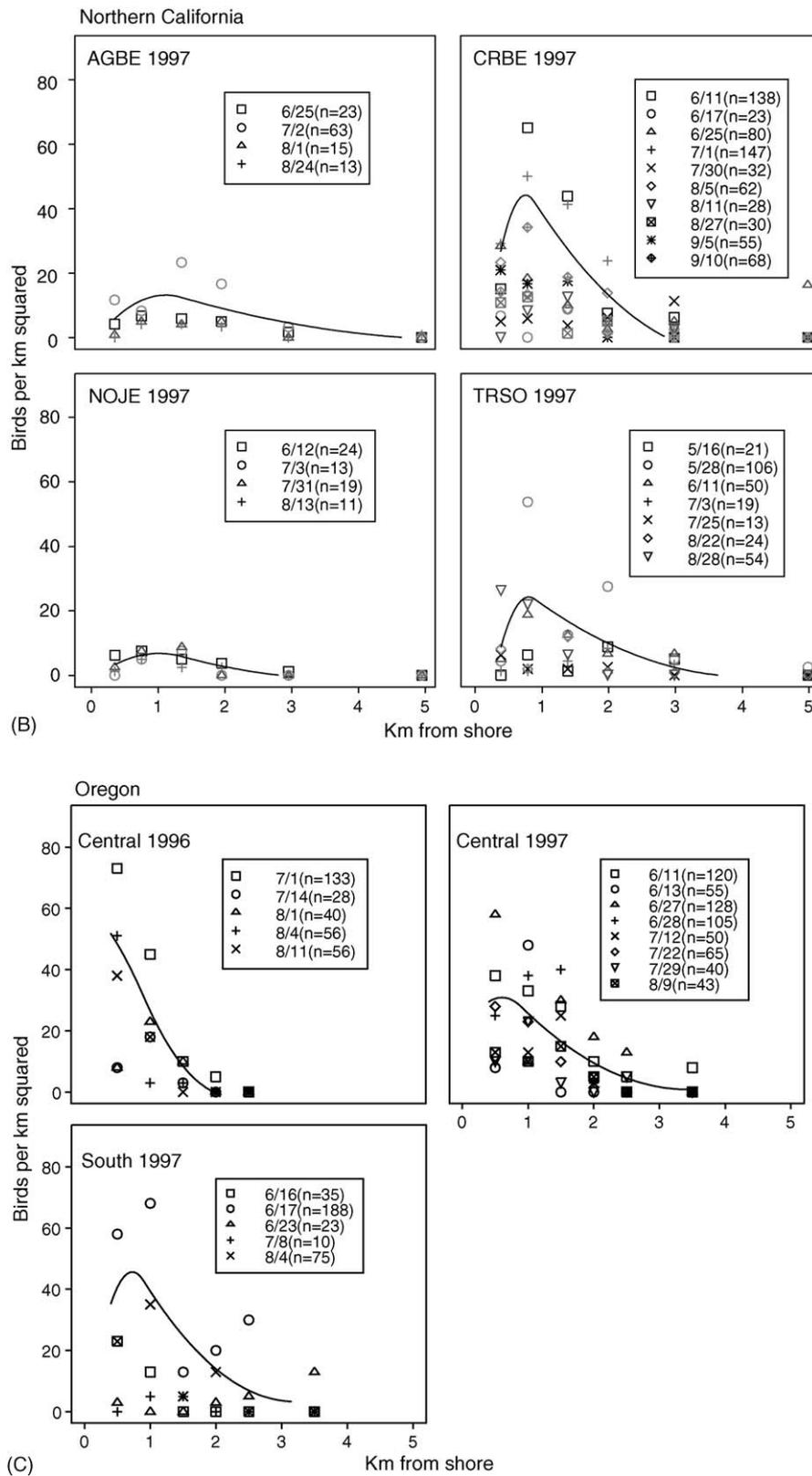


Fig. 4 - (Continued).

the designs with the highest power, which was expected. Given a declining trend, power is a monotonically decreasing function of the variation in the estimated slope, which itself is a decreasing function of the variation in the esti-

mated number of birds. The zigzag designs and stratified short parallel transect designs (7 nearshore/3 offshore and 5 nearshore/5 offshore) showed the least variation and the unstratified parallel transect design had the most varia-

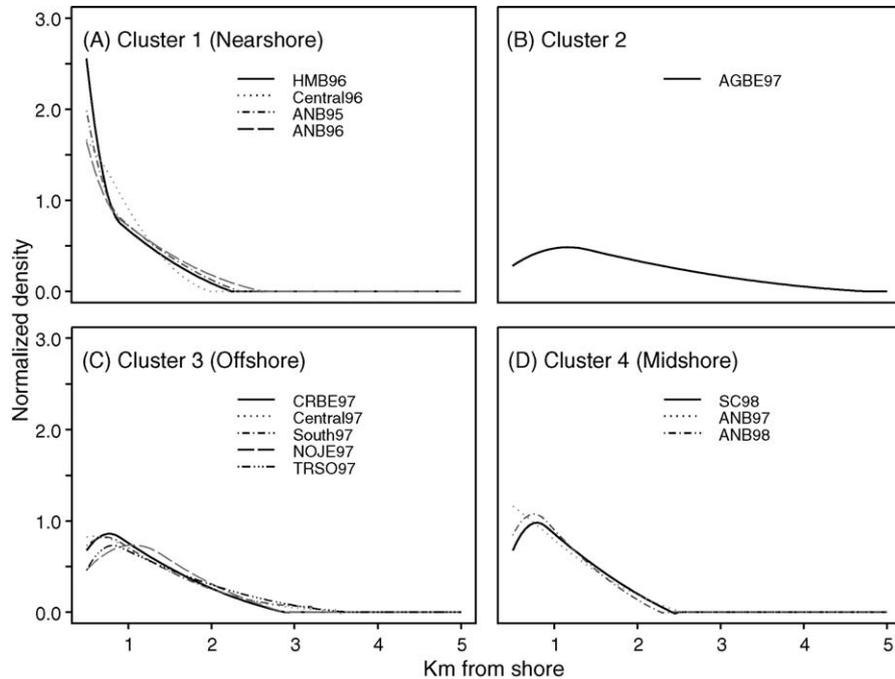


Fig. 5 – (A–D) Clusters of site with similar probability densities of Marbled Murrelets. Variation in abundance pattern of birds is seen spatially (by sites within a region) and temporally (by year). See Table 1 for definitions of the site abbreviations.

tion for nearly all measures (Table 2). Overall, the CVs for each estimating design increased when the along-shore distribution changed from uniform to clumped but did not change significantly with changes in the offshore distribu-

tion, as also reflected in the power estimates (Table 2 and Fig. 7A and B).

In general, the population-estimating designs had low bias in the population estimate and slope of the decline; variabil-

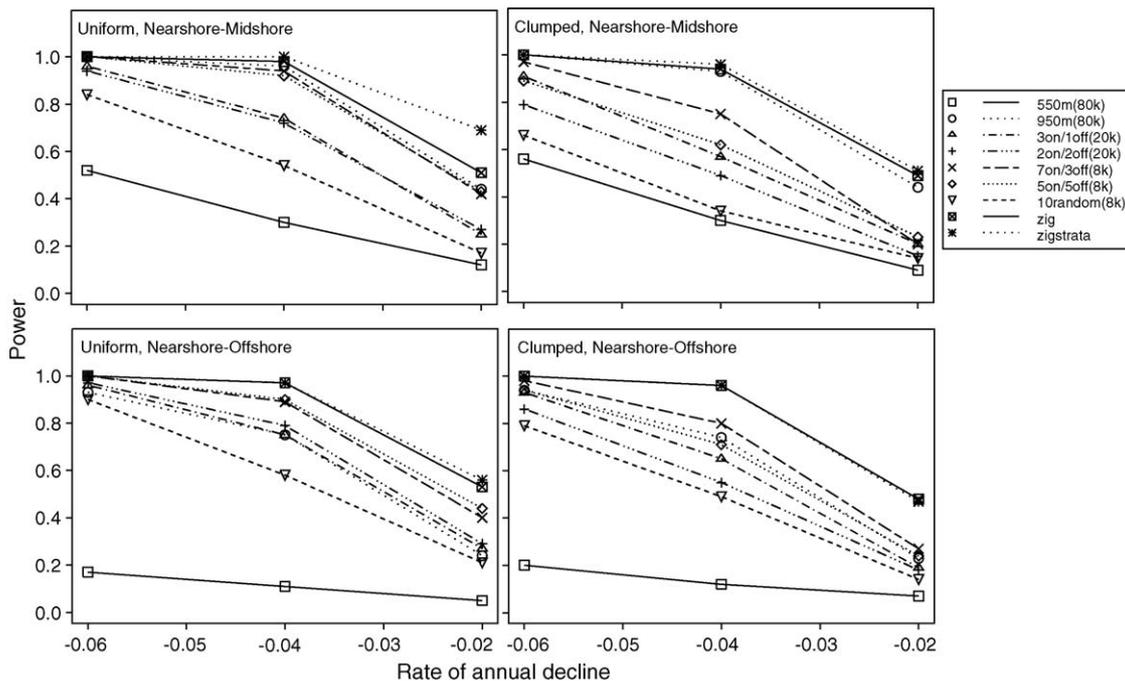


Fig. 6 – Power of nine transect designs to detect different annual rates of population decline for five daily replicates per year over 10 years assuming a uniform along-shore distribution and an offshore distribution varying among years with either a 50% chance of a nearshore distribution and a 50% chance of a midshore distribution each year, or a 50% chance of a nearshore distribution and a 50% chance of an offshore distribution each year. See the text for definitions of the transect layout abbreviations.

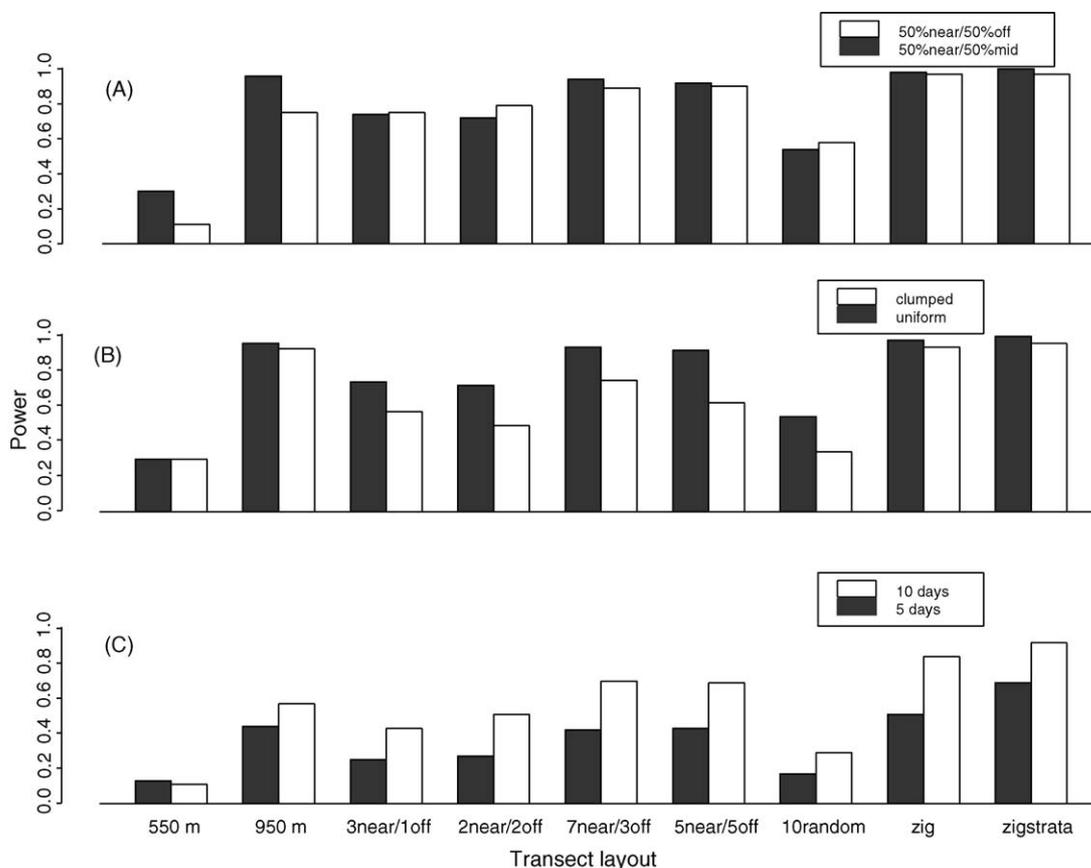


Fig. 7 – Power of nine transect designs to detect population declines for 10 years comparing: (A) two offshore distributions (a 50% chance of a nearshore distribution and a 50% chance of a midshore distribution vs. a 50% chance of a nearshore distribution and a 50% chance of an offshore distribution each year) with a 4% decline per year, a uniform along-shore distribution, and 10 days of sampling per year, (B) two along-shore distributions (uniform vs. clumped) with a 4% decline per year, a 50% chance of a nearshore distribution and a 50% chance of a midshore distribution each year, and 10 days of sampling per year, and (C) two levels of daily replication (5 samples vs. 10 samples per year) with a 2% decline per year, a uniform along-shore distribution, and a 50% chance of a nearshore distribution and a 50% chance of a midshore distribution each year. See text for definitions of the transect layout abbreviations.

ity in the population estimate and slope of the decline was a more informative measure of the relative statistical performance of the designs. All the designs estimated the population size within 5.5% of the true number (1000) in the first year (Table 2). An unbiased slope is important for estimating the magnitude of the decline rate in the population, beyond simply the statistical detection of a negative trend. The true slope of the best-fit linear line with an imposed decline of 6% per year was -47.3 , interpreted as a loss of 47.3 birds per year. The mean slopes of the best-fit lines from the designs in the simulation ranged between -47.7 and -44.4 (within 6.5% of the true decline; Table 2). Bias changed little with changes in the along-shore distribution, and population-estimating designs produced slightly more biased population estimates and slopes when the offshore distribution of birds increased away from shore (Table 2).

Power was low for the index designs compared to estimating designs, even though indices detected high numbers of birds with little variability. The 550 m design detected 108–131 birds and the 950 m design detected 71–83 birds in the index

sampled for the various along-shore and offshore distributions in the first year (Table 2). The CVs associated with the number detected were relatively low for the population indices (0.13–0.18; Table 2).

To evaluate the degree to which our simulation incorporated the amount of variation seen in the field, we compared CVs from our simulation to CVs calculated from field data. Simulation CVs ranged from 0.13 to 0.18 for population indices (Table 2) and were similar to CVs of 0.16–0.21 in California but lower than CVs of 0.20–0.45 in Oregon from at-sea surveys of similar design (S.R.B. and B. Becker, unpublished data). Coefficients of variations for the stratified zigzag transects (0.13–0.18; Table 2) were also similar to CVs from at-sea surveys of similar designs employed in central California (0.09–0.19; B. Becker and M.Z. Peery, unpublished data).

3.2.2. Sampling logistics

Maximum distances that would be driven by boats varied by 25% (Table 3). Maximum travel distances for population esti-

Table 2 – Average bias and associated coefficients of variation (CV) in population size and trend estimates for two offshore distribution combinations (50% nearshore/50% midshore and 50% nearshore/50% offshore) and two along-shore distributions (uniform and clumped)

Transect layout (CV)	Nearshore/midshore				Nearshore/offshore			
	Uniform		Clumped		Uniform		Clumped	
	Population	Trend	Population	Trend	Population	Trend	Population	Trend
Unstratified								
10 random (8 km)	-31 (0.35)	0.9 (0.25)	-24 (0.45)	0.8 (0.30)	-54 (0.30)	1.8 (0.21)	-50 (0.38)	2.9 (0.27)
Zigzag	-33 (0.16)	0.9 (0.12)	-34 (0.18)	0.9 (0.13)	-52 (0.17)	2.7 (0.13)	-55 (0.18)	2.2 (0.13)
Stratified								
3 nearshore/1 offshore (20 km)	-17 (0.27)	1.1 (0.18)	-17 (0.32)	0.7 (0.21)	-48 (0.27)	2.1 (0.18)	-51 (0.31)	2.0 (0.20)
7 nearshore/3 offshore (8 km)	-15 (0.20)	0.4 (0.14)	-16 (0.25)	0.8 (0.17)	-43 (0.21)	2.3 (0.15)	-46 (0.25)	1.3 (0.17)
2 nearshore/2 offshore (20 km)	-14 (0.26)	1.1 (0.18)	-19 (0.38)	0.4 (0.26)	-43 (0.25)	2.2 (0.18)	-49 (0.34)	1.7 (0.24)
5 nearshore/5 offshore (8 km)	-22 (0.20)	0.8 (0.14)	-17 (0.32)	1.0 (0.22)	-47 (0.20)	1.5 (0.14)	-46 (0.28)	2.3 (0.19)
Zigzag	7 (0.13)	-0.4 (0.10)	-28 (0.17)	0.8 (0.13)	-26 (0.16)	0.9 (0.12)	-37 (0.18)	2.4 (0.14)

Bias in population size was calculated as average number of birds estimated for the first year minus the actual population size (1000). Bias in the trend was calculated as the average estimated slope minus the true slope (47.3 birds lost per year) of the linear regression of the estimated annual average number of birds over 10 years for a 6% annual decline. Calculations were based on 10 sampling days per year.

Table 3 – Number of transect segments, segment length, distance surveyed, and maximum boat driving distance for each sampling design

Sampling design	Number of transect segments	Segment length (km)	Distance surveyed (km)	Maximum travel distance (km)
Population indices				
550 m	1	80	80	80
950 m	1	80	80	80
Population estimators				
Unstratified				
10 random	10	8	80	102
Zigzag	1	83	83	83
Stratified				
3 nearshore/1 offshore	4	20	80	86
2 nearshore/2 offshore	4	20	80	87
7 nearshore/3 offshore	10	8	80	97
5 nearshore/5 offshore	10	8	80	102
Zigzag	1	82	82	82

mators were always higher than for indices because population estimators used few to many short transect segments and placed them both near and offshore. Travel distance was only slightly greater for zigzags than for index designs. Distance traveled increased from the actual distance surveyed by a maximum of 10% for population-estimating designs with long transects (2 nearshore/2 offshore and 3 nearshore/1 offshore) and by a maximum of 20% for designs with short transects (7 nearshore/3 offshore, 5 nearshore/5 offshore, and 10 random).

4. Discussion

To evaluate sampling schemes for Marbled Murrelets that are robust to shifting environmental gradients and heterogeneous distributions, we first used historical data to describe offshore and along-shore distribution patterns and how they varied

daily, annually, and regionally. We then used these descriptions to distribute birds in a spatially explicit simulation and compared performance of different sampling designs to detect population declines. A notable result is that certain transect layouts consistently had higher power than others under all environmental conditions and levels of replication. Although previous work has suggested that sampling almost exclusively in high-density areas of a species range can increase power to detect a trend (Gerrodette, 1987; Strayer, 1999; Buckland et al., 2001), we found that transect designs that sampled a range of areas had higher power than those concentrated in the high-density areas. Few studies have specifically looked at how to arrange transects in space to best detect trends in populations with strong environmental heterogeneity characterized by hierarchical sources of variation (e.g., daily, annual, and regional). Below we discuss our results and their implications for the spatial layout of transects under shifting distributions.

4.1. Offshore and along-shore distributions of murrelets

Differences in offshore distributions of murrelets at sea existed among sites, regions, and years. Three general distribution patterns emerged (Figs. 3 and 4): (1) a negative exponential pattern with greatest density nearshore and declining rapidly with distance from shore, which occurred in central California and central Oregon; (2) a humped pattern with highest density at 1 km and a quick decline in density after 1 km, which was found in northern California and southern and central Oregon; (3) a humped pattern with highest density at 1 km offshore and a gentle decline out to 3 km, which occurred in central California. Not all sites in the same year fell into the same cluster (e.g., 1997), and not all years from the same site fell into the same cluster (e.g., Año Nuevo Bay; Fig. 4). Thus, while there is a clear offshore gradient in murrelet density, the shape of the distribution is dynamic.

Variation in the shapes of the offshore distributions of murrelets is due to daily and annual shifts in the environmental factors causing the gradient and to regional ecological differences. Daily and annual variability in the offshore distribution of murrelets are likely due to changes in upwelling and annual differences in sea surface temperature (SST) that alter prey distributions (Hunt, 1995; Becker and Beissinger, 2003). Slight site-specific differences in bathymetry may drive regional differences in offshore distributions; the oceanic shelf declines 11.9 m/km from shore to 3.0 km in Oregon, 15.8 m/km in northern California, and 18.8 m/km in central California. Thus, interaction between SST, bathymetry, and prey depth preferences may partly explain regional, annual, and daily differences in the distribution of murrelets from shore.

The along-shore distribution of murrelets is far less well known. Range-wide, murrelets are closely associated with areas offshore of old growth habitat during the nesting season (Meyer et al., 2002), but fine-scale analyses of the daily and annual variation in distribution are not available. In central California, along-shore distribution of murrelets varied from nearly uniform to highly clumped (Fig. 2; Becker and Beissinger, 2003). Locations of murrelets at sea appear to be associated with topographic features such as river mouths, heads, and peninsulas, where upwelling may concentrate prey (Meyer and Miller, 2002; Meyer et al., 2002; Becker and Beissinger, 2003; Yen et al., 2004). Yet, oceanographic factors that create upwelling, which clump prey and murrelets around these features, can change annually (Becker and Beissinger, 2003). Thus, no a priori along-shore gradient is apparent, and distributions are likely to be heterogeneous and change unpredictably (as of now) from clumped in 1 year to uniform in another. Other seabirds, such as Atlantic Puffins (*Fratercula arctica*), Common Murres (*Uria aalge*), Rhinoceros Auklets (*Cerorhinca monocerata*), and Razorbills (*Alca torda*), tend to disperse over larger areas when prey is less available (Wanless et al., 1990; Davoren, 2000); changes in along-shore distribution of Marbled Murrelets could similarly be due to changes in prey distribution, possibly moving from a clumped to a more uniform distribution during years with less prey available.

4.2. Merits of various sampling designs under shifting environmental gradients

For mobile species that are distributed according to an underlying environmental gradient, spatial variability is likely to be high if changes in intensity or location of gradients occur (Fretwell and Lucas, 1970; Doak, 1995; Strayer, 1999). Shifting gradients create challenges for spatial design of transects, especially when such changes are unpredictable. Sophisticated sampling designs, such as adaptive sampling, which increase survey effort in areas of high animal density once they are located, recently have been developed (Thompson and Seber, 1996). This approach provides more statistical efficiency than conventional designs for sparse or clumped populations, but this advantage is lost when clumping is reduced (Pollard and Buckland, 1997; Christman and Lan, 2001; Khaemba and Stein, 2002; Pollard et al., 2002).

Like many mobile species, the at-sea distribution of Marbled Murrelets changes daily and yearly, but these changes occur in different dimensions, in different manners, and with different implications for sampling designs. There is a relatively predictable decline in abundance with distance offshore and an unpredictable and heterogeneous clumping of birds along-shore. A powerful sampling design must be able to capture this variability in abundance. In our model, because the distribution of the explanatory variable (time) is identical for all designs/analysis in our model, the only difference in the power of designs is the resulting variability in the day-to-day estimates of birds within each annual season. Thus, among designs that yield unbiased estimates of the trend, the most powerful designs will be those that give smallest day-to-day variability. In our simulation, the design that provides lowest residual (day-to-day) variance is that which optimally balances sampling in consistently high-density areas, where one finds consistently a high number of birds, and areas that are less consistent, but for which birds occasionally move from consistent high-density areas to these areas. If consistently high-density areas were very consistent (that is birds did not move in and out of them on a day-to-day or year-to-year basis), then sampling outside of them would provide lower benefit or even reduce the power. Our simulations, based upon the specific data-generating distributions used herein, suggest this optimal balance for the studied bird populations, requires sampling predominantly in the higher density areas but with forays outside to capture those less predictable birds.

Although the most economical method may be to sample only in habitats where the detection probabilities are highest (Zielinski and Stauffer, 1996), there may be power benefits of sampling in other areas, such as shown in our model. In our simulations, designs that did not sample fully in both offshore and along-shore dimensions fared poorly. A single transect at 550 m from shore had the lowest power of all designs, and a single transect at 950 m from shore lost ranking compared to other designs when murrelets shifted offshore although these designs detected a high number of birds and were completely robust to changes in the along-shore distribution. A fishery model finds that declines in abundance were not reflected in the most preferred, high-density habitats for several years, because changes first occurred in less preferred habitat; once

the lower density areas declined and were extinct, the high-density areas rapidly collapsed (MacCall, 1990). Likewise, a grizzly bear model concludes that both suitable and less suitable habitat must be sampled to have high power to detect a trend (Doak, 1995).

Unpredictable heterogeneity in distribution (i.e., not along a gradient) can have a surprisingly important influence on the relative power of sampling designs. Since all the designs in our simulation sampled the entire shoreline, changing the along-shore distribution (uniform to clumped) was not expected to influence the power of designs as much as changes to the offshore abundance pattern. However, variability in population estimates and consequently, power, was more influenced by changes in heterogeneity along-shore than shifts along the offshore gradient, especially for designs with parallel lines placed randomly (Table 2 and Figs. 6 and 7). Apparently, these parallel designs with randomly placed transects could miss crucial high-density clumps of birds, especially those designs with equal effort in both strata. The fixed parallel designs (index designs) and zigzag designs lost no to little power, respectively, with changes in the along-shore distribution (Table 2 and Figs. 6 and 7). Clumping had no impact on the fixed parallel designs because they sampled along the entire shoreline at the same distance offshore, thus detecting birds along-shore regardless of distribution. The zigzag designs were constantly cutting back and forth through clusters, so they retained power because they sampled the area more uniformly and with less variability than randomly placed parallel lines. For example, in one realization of 1000 birds, the stratified zigzag design can detect more birds than a random parallel design by sampling more of the clumps (Fig. 2).

The length of transect segments and the number of replicates were also important determinants of an effective sampling design. Stratified parallel designs with many shorter transect segments had lower CVs than similar designs with fewer, longer segments (Table 2). This result reflects that longer transects, though providing a nearly unbiased estimate of the average number of birds in a year, resulted in significantly more day-to-day variability than the shorter transects. Again, this may be because the longer transects were more likely to miss the crucial, high-density clumps than the shorter transects. Designs that used many short transect segments (10 random, 7 onshore/3 offshore, and 5 onshore/5 offshore) resulted in longer driving distances (Table 3), a trade-off that requires some consideration. The two zigzag designs that we evaluated yielded only modest increases in driving distances over the indices. Given the power benefits, the increased driving distances of the zigzag and even the many short transects over a less powerful single transect (as used previously in monitoring) likely would be worthwhile in the Marbled Murrelet system. For example, in central California these surveys with increased driving distances can still be accomplished in one day of surveying. Finally, the number of replicates per year greatly influenced power for the density estimators, as expected (Becker et al., 1997; Gerrodette, 1987; Kuletz and Kendall, 1998). When replication increased from 5 to 10 surveys per year in our simulations, power increased mainly for populations that were declining slowly (2–4% per year).

Allocation of transect segments between the two strata (7 onshore/3 offshore versus 5 onshore/5 offshore, 3 onshore/1 offshore versus 2 onshore/2 offshore and stratified versus unstratified zigzag) was not one of the important determinants of a powerful design in our study. Designs that allocated more transects to the higher density stratum (nearshore) than the lower density stratum (offshore) were slightly more powerful than equal allocation, but only among those simulations that had the birds in clumped distributions along-shore.

Here, we provided a model that characterized the spatio-temporal distribution for mobile organisms in a relatively non-parametric way (i.e., making few statistical assumptions and using exploratory statistical techniques such as clustering), used existing pilot data to characterize the sources of variation using a mixed models approach, and derived power by simulations based on data generalizing distributions which are a reasonable approximation to the observed data, rather than simplifying analytic models. Our model oversimplified by imposing a constant rate of decline, which is likely to vary in real populations and may include short periods of time when a population is increasing; trends in murrelet abundance may be curvilinear, oscillating, or varying significantly but without apparent pattern (see Dennis et al., 1991 for a thorough discussion of stochastic dynamics and trend detection). The method presented here could be easily augmented to apply to any type of trend. However, even if the true trend is a complicated curve (e.g., polynomial), the parameter of interest can still be the average decline with time (i.e., slope) as we have done here.

Another simplification of our model was the assumption that our virtual boat was able to detect all birds for 50 m on each side. This is not entirely realistic and a lack of complete detection in the field would likely result in lower power than found in our study; however, conclusions regarding the relative power of the various designs should remain valid in our study. Additionally, our simulation may have underestimated daily and annual variation in the distribution of birds along-shore. Neither of the two approaches we used to assign along-shore distributions yielded as much daily and annual variation in density estimates as we have recorded in central California (Becker and Beissinger, 2003). Based on CVs calculated from the simulation and compared to actual field surveys (see Section 3), variability in density estimates from the simulation model was similar to moderately less than variation from field surveys, depending upon the site.

In conclusion, spatial variation in distribution had a large influence on determining how transects should be laid out to maximize power. For a distribution along a gradient, density-estimating designs that are robust to variability (e.g., many short transect segments or zigzags placed in high-density and low-density areas) appeared to be the most powerful. For a heterogeneous distribution, fixed transects or zigzags were more powerful. If both environmental gradients and heterogeneity occur in differing dimensions, transects should sample as fully as possible in both dimensions to reduce variability in abundance estimates (e.g., zigzags). Pilot data or an understanding of the environmental factors that drive a gradient or changes in spatial heterogeneity is important for designing powerful sampling schemes as well.

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Appendix A. Description of pilot data used to parameterize simulations

Past surveys had placed short transects parallel to the shoreline at four to six distances from shore, using 100 or 200 m wide strip transects. Strip transects are more subject to observer bias than line transects, especially 200 m wide strips, because each bird within the designated strip transect is assumed to be detected whereas line transects take into account a loss in detectability away from the designated line. Nevertheless, they provided a useful starting point for estimating the shape and variation in offshore distribution. Surveys were replicated (4–10 days per year) and conducted from June to August during mornings when the ocean was calm and viewing conditions were good.

Central California surveys were conducted offshore of Santa Cruz (Santa Cruz County) and in Año Nuevo Bay and Half Moon Bay (San Mateo County). Northern California surveys took place in Humboldt County in three areas: (1) Agate Beach; (2) north of the Humboldt Bay jetties; (3) south of Trinidad Head. An additional site was located in Del Norte County at Crescent Beach. Southern Oregon surveys extended from Point Saint George, CA in Del Norte County to the Rogue River in Curry County, OR. In central Oregon, surveys extended from Florence in Lane County north to Gleneden Beach in Lincoln County.

Appendix B. Fitting quadratic splines for offshore distribution of birds

The quadratic spline curve that best-fit offshore distributions of murrelets was:

$$\text{Density}(x) = \beta_0 + \beta_1(x) + \beta_2(x^2) + \beta_3(x - x_0)_+^2$$

where x is the distance from shore in kilometers, x_0 the knot in kilometers from shore, and $\beta_3(x - x_0)_+^2$ is 0 unless, indicated by the subscript (+). We choose the location of the knot based on visual inspection of the data (Venables and Ripley, 1997). For 11 of 13 curves, the knot was set at 0.9 km from shore and the other two knots were set at 1.4 km from shore. We weighted daily observations by the total number of murrelets detected. Thus, survey days that provided more information about offshore distribution were given greater influence on curve fits. Quadratic spline curves were truncated if they intersected the x -axis (usually >2.5 km from shore) and we assumed no murrelets occurred farther offshore. Inspection of fit to the data

showed this assumption was reasonable. All curve fitting was done in S-PLUS (2000).

To estimate offshore distributions of murrelets that were not confounded by regional or annual differences in total abundance, we normalized each quadratic spline curve by dividing it by the total area under the curve. This provided an estimated probability density function of murrelets at all distances offshore for each year–site combination.

Appendix C. Distance matrix used for clustering

Distances from shore closest to offshore locations where data were field collected were given more weight, as were curves that were generated with larger sample sizes, because there was less uncertainty in these estimates. Let $D_{ij}(d)$ be the Euclidean distance between curves i and j at a distance, d , and $V_i(d)$ and $V_j(d)$ be the estimated variances of the estimated probability densities of curves i and j at distance d ; the variance estimates are the standard least-squares estimated prediction variances (Kleinbaum et al., 1988). The weighted total Euclidean distance between any two curves i and j was estimated as:

$$WD_{ij} = \frac{\sum_d (1/(V_i(d) + V_j(d))) D_{ij}^2(d)}{\sum_d 1/(V_i(d) + V_j(d))}$$

Appendix D. Calculation of bias in trend and population size

We calculated bias in the population estimate by subtracting the actual population size of 1000 birds from the mean of the first year estimate for the 500 iterations (before any decline was initiated). We calculated bias in the trend by subtracting the true slope (linear projection of the non-linear decline) from the average of the estimated slopes (500, 1 for each iteration) derived from linear regressions of the estimated annual average number of birds over 10 years.

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