COMPARISON OF AERIAL AND BOAT-BASED SURVEY METHODS FOR MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* AND OTHER MARINE BIRDS

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SUMMARY

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We compared density estimates for marine birds off central California from simultaneous aerial and boat-based surveys, with a special emphasis on Marbled Murrelets *Brachyramphus marmoratus*. We surveyed 44 eight-kilometer transects in nearshore waters of Monterey Bay, California, from December 2005 through March 2006. We found that density estimates of all birds combined and of Western *Aechmophorus occidentalis* and Clark's *A. clarkii* Grebes were significantly greater from the air than from the boat, but no significant differences in density were noted for four other taxa. Density estimates for Marbled Murrelets were nearly identical from the two platforms, with a high degree of correspondence correlation (0.82). Mean species richness was significantly greater from the boat than from the air. For taxa that occurred in large flocks (grebes and gulls), density estimates from the air were substantially greater when abundance was greater. Our results indicate that aerial surveys may provide more accurate density estimates than do boat-based surveys for some taxa, under certain conditions. However, density estimates were similar for most taxa, and density estimates from the two platforms based on certain survey methods may be similar enough to be considered directly comparable.

Key words: Aerial survey, seabirds, Marbled Murrelet, survey techniques

INTRODUCTION

Aerial surveys have been used successfully for several decades to assess the distribution and abundance of marine birds (e.g. Bradstreet 1979; Harrison 1982; Briggs et al. 1985a, 1985b, 1987; Dean et al. 2003; Ford et al. 2004; Nysewander et al. 2005; Mason et al. 2007). Aerial surveys have several advantages over boat-based surveys: they allow for coverage of a large area in a relatively short amount of time; they are less limited by sea state than are surveys from small boats; they make it possible to simultaneously survey for oil in the event of an oil spill; they avoid the need for adjustments for ship-following or ship-avoiding birds; and given that the movement rate of the birds is slow relative to the aircraft, they also avoid the need for flux corrections for birds in flight (Spear et al. 2004). Boatbased surveys for marine birds have been used since the early 20th century and are considered by many to be the standard technique to assess abundance and distribution (Tasker et al. 1984). These surveys have distinct advantages as well: observers have more time to identify birds to species and age, surveys are less often limited by high fog, diving birds are less likely to be missed while underwater, and concurrent data can be collected on the biologic and physical characteristics of the ocean.

Density estimates from both aerial and boat-based surveys have been published with little reference to the relative accuracy of these methods. We are aware of only one published study that compared density estimates for marine birds derived from simultaneous aerial and boat-based surveys. Briggs et al. (1985b) compared density estimates of seabirds from simultaneous aerial (using a Cessna 337 Skymaster) and ship-based surveys (using a 20-m vessel) and found that densities of large birds were 3-4.5 times greater from aerial surveys than from ship-based surveys, and that densities of less conspicuous birds were up to 6.2 times greater from aerial surveys than from ship-based surveys—presumably because boat-based observers failed to detect birds in the outer portion of strip transects (400 m on each side for large birds, 150 m for less conspicuous birds). Their "simultaneous" surveys were conducted with delays of up to 4.0 hours, and they found that the correlation between aerial and boat-based counts decreased with increasing delay. Additional comparisons in that study, conducted on a regional scale using data from surveys that were not conducted simultaneously, revealed no significant difference between density estimates from the two platforms.

More recently, Ford *et al.* (2004) compared regional density estimates of Common Murres *Uria aalge* and phalaropes *Phalaropus* spp. from aerial and boat-based surveys conducted during similar seasons, but not simultaneously, off central California. Density of Common Murres was similar between survey platforms; density of phalaropes was greater from aerial surveys. For both taxa, zero counts within 10×10-minute cells (degrees of latitude and

longitude) were more common on boat-based surveys, and aerial surveys detected more large flocks of phalaropes.

Results from both of the foregoing studies indicate that the typically patchy and dynamic distribution of seabirds at-sea can affect comparisons of survey methods on a fine scale, and that on a larger scale, natural variability in distribution may be greater than the variability between different survey techniques.

Marbled Murrelets Brachyramphus marmoratus, which are among the smallest diving birds off California, may be difficult to detect from a fast-moving airplane, particularly if weather conditions are less than ideal. Few studies have attempted to assess the accuracy of aerial surveys for Marbled Murrelets, yet accurate density estimates are important in determining population status and at-sea habitat used by this threatened species (Becker et al. 1997, Rachowicz et al. 2006). Varoujean & Williams (1995) used murrelet decoys on flat water to conduct a cursory test of aerial survey methods. They found that observers on the non-glare side of the plane missed 9%–30% of the decoys, but the layout of the trials had problems, and density was substantially greater than that expected in nature. In preliminary unpublished studies, Piatt et al. (1991) found no difference between density estimates from boat-based and aerial surveys conducted during the breeding season in Southeast Alaska, but Nysewander et al. (2005) found that fewer Marbled Murrelets were detected in aerial surveys than in boat-based surveys. It is possible that aircraft type alters the detectability of birds from the air: relatively small, quiet aircraft such as the Partenavia Observer or Cessna 337 Skymaster (Briggs et al. 1985a, 1985b; Varoujean & Williams 1995; Dean et al. 2003; Ford et al. 2004; Mason et al. 2007) may result in less avoidance (e.g. birds diving) than is seen with larger, noisier aircraft such as the deHavilland Beaver or Hunting Pembroke (Briggs et al. 1985a, Piatt et al. 1991, Nysewander et al. 2005).

As datasets from at-sea surveys accumulate, and in some cases are combined into larger databases (e.g. Bonnell & Ford 2001, Ford *et al.* 2004, Skov *et al.* 2007), it is becoming increasingly important to determine if the data collected using different techniques can be directly compared or combined (Pyle 2007). In the present study, we conducted simultaneous aerial and boat-based surveys to assess the relative accuracy and comparability of these techniques, with a particular emphasis on Marbled Murrelets. Our initial assumption was that boat-based surveys would provide accurate density estimates from which we could develop correction factors for aerial surveys.

METHODS

Survey methods

We conducted six days of aerial and shipboard at-sea surveys during winter 2005/06 in northern Monterey Bay, California. Surveys were conducted on 6 December 2005, and 17 January, 24 January, 8 February, 21 February, and 8 March 2006. Weather conditions ranged from Beaufort 0 (calm) to Beaufort 3 (small whitecaps forming). On each survey day, near-simultaneous (within 219 minutes) aerial and boat-based surveys were conducted. Surveys were conducted along transects eight kilometers in length parallel to the shore and spaced at 200-m intervals from 400-m offshore to two kilometers offshore. From five to 12 paired near-simultaneous surveys were conducted each day, for a total of 44 paired transects. Navigational error on both platforms was estimated to be <20 m.

For aerial surveys, a Partenavia Observer (now marketed as Vulcanair P-68) aircraft was flown at a speed of $145 \,\mathrm{km} \cdot \mathrm{h}^{-1}$ (90 kts) and an altitude of 60 m (200 ft.). This high-wing twinengine airplane is particularly quiet, and it can fly at slow speeds. One trained observer on either side of the airplane conducted independent strip transects, recording all sightings of Marbled Murrelets and other marine birds within 75 m (data from the sunny side of the plane were excluded from analyses because of poorer visibility related to glare; see Briggs *et al.* 1985a). Each observer calibrated his or her strip-width estimate using a clinometer, and all observers had >80 hours of experience estimating a transects 75 m in width at the study altitude. No line transects were conducted from the airplane. Time-referenced sighting data for all bird and mammal species were entered on hand-held recorders.

Boat-based surveys were conducted from a 9-m (30-ft.) boat, the R/ V Sheila B, traveling at 15 km•h⁻¹. Two experienced observers (one on each side, working independently) sat on an observation platform with eye-level approximately 3.5 m off the water. Each observer recorded data for transects on his or her side of the boat, from the centerline to perpendicular to the track line. Line transects were conducted for Marbled Murrelets, for which perpendicular distance off the trackline was estimated visually for each group of murrelets. Before each survey, surveyors calibrated distance estimation using a laser rangefinder on objects (e.g. buoys) at a variety of distances. In addition, all birds were recorded within a 100-m strip transect (50 m on either side of the boat and 100 m ahead). Care was taken to avoid double-counting flying birds; obvious ship attraction or ship following was not observed. Birds observed within the transect but more than 100 m ahead that dove or took flight from the transect were recorded if it appeared that the behavior occurred in response to the research vessel. Time-referenced sighting data were recorded on hand-held recorders.

Data processing and analyses

Aircraft and boat position and time were recorded using global positioning system (GPS) units linked to onboard computers running dLOG software (Ford 1999). Every five seconds, dLOG recorded times and positions and provided an instantaneous display of aircraft or boat position relative to the target transect to assist with navigation. Position of bird sightings was estimated by interpolation, assuming straight transects at a constant speed over each five-second interval.

For each transect, densities of each species of bird (birds•km⁻²) were calculated from aerial surveys and boat-based surveys. For strip surveys (aerial surveys and boat-based surveys for most species), density was calculated as the number of birds multiplied by the area surveyed (e.g. 8 km × 100-m strip width = 0.8 km²). No compensation was made for potential bias associated with counting birds in flight (Spear *et al.* 1992). Given the narrow strip corridor and the high speed of the airplane, aerial surveys effectively used the instantaneous count method for flying birds (Tasker *et al.* 1984, Gould & Forsell 1989, van Franeker 1994). For boat-based surveys, flux of flying birds may have resulted in a slight overestimation of density, but only 13.5% of all birds recorded on boat-based surveys (primarily gulls) were in flight, and the narrow strip width reduced the potential bias associated with flux (Spear *et al.* 1992).

For boat-based surveys, density of Marbled Murrelets was estimated using Distance 5.0 software (Buckland *et al.* 1993). Using this

program, we tested a variety of curves to model the decrease in detectability with increasing distance and chose the model with the best fit based on the lowest Akaike's information criterion (AIC) value. The Distance software uses this curve to determine the effective strip width (ESW). All missed detections inside the ESW equal the number of observed detections outside the ESW, meaning that density estimates using all observed data and a sample area based on the ESW theoretically represent 100% actual density. This methodology assumes that no individuals are missed on the trackline itself, which would not be the case if birds dive when they see the boat approaching. Although we found no evidence that murrelets dove within 50 m of the approaching boat, it is possible that some birds avoided detection by diving, and this problem is common to all line transect surveys of diving seabirds.

For boat-based data, we developed two density models for Marbled Murrelets based on observers' ratings of viewing conditions (fair/good or very good/excellent), and the model providing the lowest AIC value for each category was chosen for surveys with that viewing condition. Viewing condition ratings were based on a combination of factors, including sea state and glare; very good/excellent conditions generally corresponded to sea states of Beaufort 0–1.

For density estimates using distance sampling, data were truncated at 100 m and binned into five categories (0–20 m, 20–40 m, and so on). Density estimates for Marbled Murrelets under fair/good conditions were based on a uniform curve with one cosine adjustment (n = 84 sightings), and an estimated ESW of 67.8 m [95% confidence interval (CI) = 55.9 m to 89.2 m; Fig. 1]. That detection function was similar to a function reported by Becker *et al.* (1997), with slightly lower detectability close to the track line, and rapidly decreasing detectability outside of 40 m. Under very good/excellent conditions, detectability was greatest nearest the trackline, but remained relatively consistent out to 80 m. Density estimates for Marbled Murrelets under those conditions were based on a hazard–rate curve with one cosine adjustment (n = 128), and an estimated ESW of 86.2 m (95% CI = 76.8 m to 96.7 m).

For comparisons of density estimates between the two survey platforms, 44 samples of paired surveys were available, although

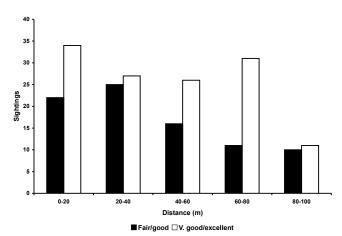


Fig. 1. Detection functions (number of detections by distance off the survey trackline) for Marbled Murrelets *Brachyramphus marmoratus* under fair/good and very good/excellent viewing conditions. All data were truncated at 100 m.

paired surveys in which no individuals of a particular taxon were detected on either survey were not used for comparisons of that taxon. We compared density estimates for all bird species combined and for Marbled Murrelet, Western Aechmophorus occidentalis and Clark's A. clarkia Grebes, all gulls combined, Brandt's Cormorant Phalacrocorax penicillatus, and all loons combined. Gulls included (in order of abundance) California Gull Larus californicus, Western Gull L. occidentalis, Bonaparte's Gull L. philadelphia, Heermann's Gull L. heermanni, Mew Gull L. canus, Glaucous-winged Gull L. glaucescens, Herring Gull L. argentatus, Black-legged Kittiwake Rissa tridactyla, Thayer's Gull L. thayeri, Ring-billed Gull L. delawarensis, and unidentified gulls. Loons included Pacific Loon Gavia pacifica, Common Loon G. immer, and Red-throated Loon G. stellata. Marbled Murrelets during this study were in basic (black and white) plumage; results may not apply to murrelets in alternate (brown) plumage.

Paired surveys were conducted within 219 minutes of each other, but initial analyses indicated that differences between density estimates from paired surveys may have increased with time between surveys. To control for this bias, we used linear regression to test for effects of elapsed time on the difference between paired survey density estimates, and we discarded paired surveys in a stepwise fashion when regressions were significant (P < 0.05). To test for potential effects of the first craft (airplane or boat) to survey an area (e.g. birds being scared away by the boat), we used t-tests to detect any effect of ordering (i.e. whether the boat surveyed first or the plane surveyed first) on differences between the mean differences between platforms. After discarding data as described earlier, we observed no significant differences between density estimates by time phase for all birds combined (boat: t = 0.86, df = 37, P = 0.40; air: t = 0.27, df = 37, P = 0.72) or for any individual taxon (all P > 0.05). These corrected datasets were used for further analyses comparing survey techniques.

Data were tested for normality using the Kolmogorov-Smirnov test (Zar 1996); all datasets except those for Marbled Murrelet and all species combined were square-root transformed to achieve normality. To test for effects of platform (airplane or boat) and viewing conditions on density estimates for Marbled Murrelets and all birds combined, we used analysis of variance to test for an interaction of date and platform on density estimates. For all taxa, paired t-tests (two-tailed) were used to compare density estimates from paired boat-based surveys and aerial surveys. These tests also were conducted for species richness (the number of species recorded per transect). All statistical tests were run using Systat 9.0 (SPSS, Chicago, IL, USA), with alpha set at 0.05. For all comparisons using Marbled Murrelet survey data, line transect data (as opposed to strip transect data) were used as the boat-based data. We also compared line transect data to at-sea strip transect data for Marbled Murrelets.

Finally, for all taxa, we calculated the concordance correlation coefficient, $r_{\rm c}$ (Lin 1989), between density estimates from aerial data and boat-based data. This coefficient is similar to the Pearson correlation coefficient, but was derived specifically to test for concordance between paired measures of the same value. These calculations did not involve hypothesis testing; non-transformed data were used to allow direct comparisons between coefficients for various taxa. Mean values are presented in the text with ± 1 standard deviation.

RESULTS

Using iterative regression (see Methods), we found that, for some taxa, elapsed time between paired surveys affected the difference in density estimates from the two platforms. For all birds combined, and for the two most abundant taxa (all gulls combined and Western and Clark's Grebes), surveys separated by more than 155 minutes resulted in significant regressions. To avoid this potential source of bias, data from surveys separated by more than 155 minutes were therefore discarded. For all other taxa, all survey data were retained, with up to 219 minutes between surveys for Marbled Murrelet and Surf Scoter Melanitta perspicillata and up to 186 minutes between surveys for Brandt's Cormorant and all loons combined. After this truncation of data, analysis of variance revealed no significant interactions of date and platform for all birds combined (F = 0.38, df = 5, P = 0.86), or for Marbled Murrelets (F = 0.97, df = 5, P= 0.45), indicating that variable viewing conditions on different dates did not affect the relative differences between density estimates from the two platforms.

Mean species richness (the number of individual species or taxa identified on each survey) was significantly greater on boat-based surveys (8.9 \pm 3.2) than on aerial surveys (6.5 \pm 2.8; t = 4.7, df = 43, P < 0.001). This difference between platforms was expected, given the greater amount of time available to observers on the boat to identify individual birds, the ability to use binoculars if needed, and the 25% wider strip width from the boat.

Density estimates were significantly greater from aerial surveys than from boat-based surveys for all birds combined and for Western and Clark's Grebes (Table 1). Mean density estimates for all gulls and all loons were also substantially greater from the air than from the boat, but these differences were not significant. For all species combined, the relationship between aerial and boat-based surveys was driven primarily by the most abundant taxon, Western and Clark's Grebes. Indeed, after removing that taxon, density estimates for all species combined were not significantly different between the two platforms (t = 1.1, df = 38, P = 0.27; $r_c = 0.80$). Density estimates for Brandt's Cormorants were somewhat

TABLE 1
Mean density estimates (birds $^{\circ}$ km $^{-2}$) for selected taxa from paired boat-based surveys and aerial surveys (non-transformed data in parentheses), number of surveys used in analyses (n), results of t-tests, and correspondence coefficients (r_c)

Taxon	Density		n	t	P	r _c
	Boat-based	Air-based				
All birds	112.3 (121.7)	178.4 (285.2)	39	2.2	0.03	0.70
MAMU	15.2 (12.7)	17.6 (19.8)	37	1.0	0.31	0.82
WEGR	33.8 (99.0)	105.5 (274.2)	28	3.2	0.003	0.56
All gulls	46.0 (50.9)	68.5 (97.8)	39	1.7	0.10	0.63
BRCO	8.3 (9.3)	5.0 (4.8)	41	1.4	0.18	0.43
All loons	3.3 (2.6)	6.3 (7.6)	33	1.1	0.30	0.33

MAMU = Marbled Murrelet *Brachyramphus marmoratus*; WEGR = Western and Clark's Grebes *Aechmophorus* occidentalis/clarkia; BRCO = Brandt's Cormorant *Phalacrocorax penicillatus*. greater from boat-based surveys, but not significantly so (Table 1). Density estimates for Marbled Murrelets were similar from the two platforms (boat line transect compared with aerial strip transect), more so than for any other taxon. In addition, mean boat-based density estimates for Marbled Murrelets from line transects (15.2 \pm 12.7) and 100-m strip transects (15.3 \pm 14.0) were remarkably similar (t = 0.09, df = 36, P = 0.93).

Concordance correlation coefficients varied among species, from a low of 0.33 for all loons to a high of 0.82 for Marbled Murrelets (Table 1). If aerial and boat-based surveys resulted in similar density estimates, we would expect a 1:1 correspondence of data (dashed lines, Fig. 2). For all gulls and for Western and Clark's Grebes (and as a result, for all birds), density estimates varied to a greater degree when abundance was greater (Fig. 2). For those taxa, greater abundance resulted in relatively higher density estimates from aerial surveys than from boat-based surveys. For example, density estimates for Western and Clark's Grebes were 2–4 times greater in aerial surveys than in boat-based surveys when mean density from the boat was more than 100 birds •km⁻².

DISCUSSION

We initially predicted that smaller birds, such as Marbled Murrelets, would be difficult to detect from a fast-moving airplane and that, by collecting more accurate data from boat-based surveys, we would be able to develop models to calibrate aerial survey data to account for missed birds. The only previous study to compare simultaneous aerial and boat-based surveys (Briggs et al. 1985b) found that density estimates from aerial surveys were much greater than those from boatbased surveys with a combined strip width of 800 m for large birds and 300 m for less conspicuous birds. Densities from the boat-based surveys may have been underestimated if birds were not detected in the outer portions of the relatively wide transects. We used a narrow strip corridor (100 m) for boat-based surveys and distance sampling for boat-based surveys of Marbled Murrelets in an effort to improve survey accuracy. Contrary to our expectations, however, we found that density estimates for all birds combined and for Western and Clark's Grebes were greater from the air and that densities of other taxa, including Marbled Murrelets, were not significantly different between the two platforms. Lower mean density estimates from aerial surveys were seen only for Brandt's Cormorant.

Higher density estimates for all birds combined and for Western and Clark's Grebes from aerial surveys were presumably the result of boat avoidance, inaccurate abundance estimates of birds within the 100-m strip for boat-based surveys, or overestimation of abundance from aerial strip transects. We think that overestimation on aerial surveys was unlikely, given the experience of the observers. Boat avoidance has been previously noted for some seabird species (Bailey & Bourne 1972, Clarke et al. 2003, Borberg et al. 2006), and Briggs et al. (1985b) noted that loons avoided the research vessel in their study. However, data are lacking on boat avoidance for most seabird species. We noted that Western and Clark's Grebes often dove in response to the boat up to several hundred meters ahead, and that loons often took flight from the transect route when the boat was several hundred meters away. Although observers attempted to estimate the number of birds that were present before the boat arrived at a given location, some birds may have been missed. It is possible that many or all taxa exhibited some boat avoidance, although our distance sampling for Marbled Murrelets indicated no substantial boat avoidance by this species within 50 m (Fig. 1). In contrast, avoidance of the fast-moving airplane was unlikely, although others have noted avoidance (e.g. diving murrelets) from larger or louder aircraft (Nysewander *et al.* 2005; M. Kirchoff, Alaska Department of Fish and Game, pers. comm.).

It is also possible that density estimates from boat-based surveys were inaccurate because birds in the outer portion of the strip transect were not detected or because larger flocks were underestimated. Density estimates for Marbled Murrelets were almost identical based on distance sampling and a 100-m strip transect from the boat, and no decline in detectability was noted within 50 m. There is no reason to expect that Marbled Murrelets would be easier to detect at 50 m than any other species in this study, but it would be useful to have data on detectability of other species. Although conducting distance sampling for all species simultaneously when abundances are high (as in the nearshore environment of the California Current) is not feasible, we suggest that, during at-sea surveys from boats, observers use distance sampling methods on one species per survey to provide data on potential boat avoidance by all species surveyed.

We suspect that, if abundance was underestimated within the boat-based strip transects, those underestimates were likely related to inaccurate estimation of larger flock sizes rather than poor detectability within the transect. It may be easier to accurately estimate the size of larger flocks (e.g. more than 20 birds) from the air, looking down on the flock, than at an oblique angle from a boat. We found that for Western and Clark's Grebes, and for all gulls combined, when abundance was greater, the differences between density estimates from the two platforms increased, with aerial density estimates becoming relatively larger as compared with estimates from the boat-based surveys (Fig. 2). In the case of the Western and Clark's Grebes, the difference may have been related to boat avoidance, but observers did not notice any obvious boat avoidance by gulls.

We observed considerable variance in the degree of correlation between densities on paired surveys for most species (Fig. 2); concordance correlation coefficients ranged from 0.33 to 0.82. The lack of strong concordance for most species indicated some turnover (movement into and out of the survey area) between paired surveys. We found, for all birds, for all gulls, and for Western and Clark's Grebes in paired surveys conducted more than 155 minutes apart, a significant relationship between time difference and density difference (positive or negative), indicating that substantial movement of those taxa had occurred. Although we corrected the data by eliminating surveys more than 155 minutes apart, less substantial movements may explain much of the variation

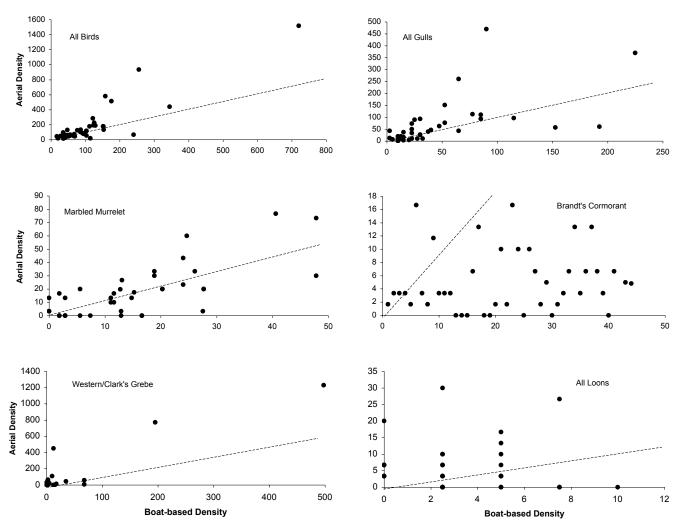


Fig. 2. Scatter plots of density estimates (birds•km⁻²) from aerial surveys versus density from boat-based surveys for all birds combined and for five individual taxa. Dashed lines represent a hypothetical 1:1 correspondence of paired data.

in correlation of paired surveys. Stronger correlations suggested that some taxa were more stable in their distribution over time; the strong correlation for Marbled Murrelets indicates that this species was quite stable. Spatial stability of various species over time is a topic that has received little research attention, but it has important implications for interpretation of at-sea survey data (Henkel et al. 2004). Spatial stability of a given taxon over time is likely related to its propensity for patchy versus random distribution. For some abundant taxa such as gulls and grebes, movements of large flocks in or out of a transect corridor would have large effects on density estimates. For species such as the Marbled Murrelet, movement of more evenly dispersed small groups (typically pairs) would have a relatively small effect on density estimates. Also, because aerial and boat-based transects did not precisely overlap because of their different strip widths, density estimates of clumped taxa in which a clump spanned the edge of the transect corridor would be less similar than estimates for taxa with more uniform spatial distributions.

Transect width will affect density estimates if birds are not detected in the outer portion of the transect. Thus, results of this study are not necessarily applicable to all at-sea survey studies. Most pelagic boat-based surveys have been conducted from large vessels, with typical transect widths of 300 m (e.g. Briggs et al. 1985b, Spear et al. 2004). Single observers counting birds in a wide (e.g. 300-m) transect are likely to miss a substantial proportion of birds present, although many observers bin sightings in 100-m increments, allowing for analyses of decreasing detectability with increasing distance (Dixon 1977, Briggs et al. 1985a, Van der Meer & Camphuysen 1996, Spear et al. 2004). In nearshore waters, surveys are often conducted from small boats, with transect widths of 100 m (e.g. Becker et al. 1997, Henkel 2004). These narrower transects may be better for detecting all birds within the transect, but boat avoidance is also likely scale dependent. Boat avoidance may occur to a greater degree with larger vessels, but given the wider transects typically used on larger boats, boat avoidance may have little effect on density estimates (i.e. birds may move away from the boat, but stay within the 300-m strip). Ship attraction may also occur more frequently with larger vessels. Thus, accuracy of boat-based density estimates is influenced by the size of the research vessel, transect width and behavior of species surveyed. Density estimates from aerial surveys may be less biased with respect to avoidance, but additional studies using simultaneous aerial and boat-based surveys would help in determining the relationship between survey density estimates from a variety of boat-based and aerial survey designs.

Given the potential variability of density estimates from different vessels with different strip widths, it is difficult to assess whether estimates from the two platforms produce comparable results. As others have proposed (Briggs *et al.* 1985b, Ford *et al.* 2004), variability from different survey platforms may be relatively unimportant compared with variability from the naturally patchy distribution of most seabirds. However, if aerial surveys consistently record higher densities than boat-based surveys do (in this case, an average of 1.6 times greater density for all species combined), analysis of heterogeneous datasets may be affected by survey platform. However, in the present study, we found that density estimates for Marbled Murrelets during winter from aerial surveys were similar to those from boat-based line transects.

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