MARBLED MURRELET GROUP SIZE AT SEA AS AN INDEX TO PRODUCTIVITY

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ABSTRACT—Population demographics of marbled murrelets (*Brachyramphus marmoratus*) are difficult to measure. Population size can be estimated from at-sea densities, and productivity indices are sometimes derived from ratios of hatch-year to after-hatch-year birds observed during systematic surveys on the ocean. However, one cannot determine from marine surveys alone what proportion of a marbled murrelet population sampled at sea is nesting in any given year, which would allow a more meaningful interpretation of productivity ratios. We hypothesized that group size (the number of murrelets occurring together on the water) could provide such an index if it could be demonstrated that single murrelets detected on the ocean during the incubation phase of the breeding season represent breeding birds. We monitored radio-tagged murrelets in Desolation Sound, British Columbia, from 29 May through 19 June 2001, using an incubating pair's distinct 24-h on-off occurrence on the water to determine nesting status. Of 160 murrelet groups comprised of at least 1 individual of known nesting status, there was a significantly greater percentage (37%) of single birds among incubating murrelets than among non-incubating birds (20%). Annual variation in the proportion of single murrelets recorded on marine surveys in Puget Sound during peak incubation corresponded with the annual productivity index in 4 of 5 y from 1997 to 2001. Our results suggest that group size, especially the proportion of single-bird groups, may help assess the proportion of murrelets that are nesting. Multiple-year comparisons of group size with nesting rates are needed to validate and interpret these results, and we need to continue to explore new methods to measure murrelet productivity.

Key words: *Brachyramphus marmoratus*, marbled murrelet, group size, marine surveys, telemetry, nesting status, productivity ratios, Desolation Sound, Puget Sound, British Columbia

Many seabirds, and most alcids, are colonial ground-nesters whose breeding sites can be monitored for such demographic parameters as population age structure, number of breeding attempts, and fecundity (Gaston and Jones 1998). The marbled murrelet (*Brachyramphus marmoratus*) poses a greater challenge because active nests in the forest canopy are dispersed and adult activity in the forest is more often at dawn or dusk, making nests difficult to locate and monitor. As a result, age structure is presumed from related species (Beissinger 1995) and fecundity is indexed by productivity, which is measured indirectly from counts at sea. Currently the most-frequently used index of productivity is obtained from the ratio of the number of juvenile to adult murrelets observed on the ocean (Beissinger 1995; Ralph and Long 1995; Kuletz and Kendall 1998). This measure is confounded by several factors. There is an unknown proportion of nonbreeders in murrelet populations observed at sea, which, based on other Pacific Alcidae, could range from 15 to >50% annually (Sealy 1975; Ewins 1993; Gaston 1994). Nonbreeders, likely consisting primarily of 1- to 3-y-old pre-breeders, are not reliably distinguished from adults as observed from a slowly moving survey vessel (but see Sealy 1975). Similarly, juveniles (hatch-year)

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become difficult to distinguish from molted after-hatch-year birds by early fall (Carter and Stein 1995), potentially resulting in underestimation of juvenile numbers. Detection probabilities may differ between juveniles and adults, due to behavior or differential habitat use (Kuletz and Piatt 1999), and movements of after-hatch-year and juvenile murrelets within the breeding season bias both components of the ratio. For example, there is a steady increase in numbers of marbled murrelets on the waters around the San Juan Islands, Washington, beginning in late July that exceeds what can be attributed to the appearance of fledged juveniles and reappearance of nesting adults that have completed incubation (Raphael and Evans 1997). Most of these birds are incorporated into the adult and not the juvenile component of the productivity ratio. If juvenile immigration was proportional and followed the same temporal pattern, the ratio might not be biased but wouldn't necessarily reflect local production.

Kuletz and Kendall (1998) proposed adjusting productivity ratios by using early-season counts of adults as the denominator (sequential vs. concurrent ratios), minimizing the bias of adult post-breeding movements. We explored this and other adjustments to marine survey data in Washington and found that our study population could be described as declining, stable, or increasing based solely on the method of calculating ratios (Raphael and Evans 1997). Ideally, the productivity index should be derived from known local breeders, but there has been no method to determine from marine surveys alone what proportion of the population sampled at sea is nesting in any given year. Here we consider group size (the number of murrelets occurring together on the ocean, see below for more complete definition) as a possible local index to breeding activity.

Marbled murrelets occur as pairs and singles on the ocean more than any other group size (Carter and Sealy 1990; Strachan and others 1995; Collins 2000; Carten 2001). Studies in British Columbia have effectively demonstrated that groups of 2 marbled murrelets captured early in the breeding season are likely to be male-female pairs (Sealy 1975; Vanderkist 1999; McFarlane Tranquilla and others, In press), and McFarlane Tranquilla and others (In press) proposed that counts of pairs early in the breeding season could reflect breeding activity. Alternatively, the unique incubation pattern of nesting marbled murrelets, combined with our perception that the proportion of single birds observed from marine surveys changed seasonally, suggests that single birds may be a better indicator of breeding activity.

When incubating, a nesting marbled murrelet spends about 24 h on the nest, and then spends the next approximately 24 h on the ocean while its mate incubates the egg (Nelson 1997; Bradley 2002). Therefore, during the incubation phase of the nesting cycle a given bird will be on the ocean every other day. During chick rearing, both parents make feeding visits to the nest, but they resume a daily occurrence on the water. The daily on-off incubation pattern suggests that single birds should be more commonly observed on the ocean during the incubation period compared with the chick-rearing or post-breeding periods. Further, because many pairs of murrelets captured early in the breeding season are male-female pairs, it follows that these pairs would be separated during incubation, and the sightings of singles on the ocean would increase.

We suggest that group size could provide an alternative index to productivity if it could be demonstrated that single murrelets detected on the ocean during the incubation phase of the breeding season represent nesting birds. If true, this could lead to a simple way of estimating the proportion of breeding birds from populations sampled with marine surveys. Our objectives in this study were to (1) observe group size in a population of marked birds whose nesting status was known, and (2) retrospectively examine marine survey data to (a) determine if the frequency of single birds among murrelet groups detected on the water changed seasonally, (b) examine whether the proportion of single birds during the incubation period changed year to year, and (c) test whether the annual change in the proportion of singles during incubation corresponded to annual variation in productivity, as estimated from juvenile to adult ratios. For this test, we were primarily interested in concordance of directions of change from year to year in the proportion of singles and in the juvenile to adult ratio.

Study Areas and Methods

From an earlier assessment of marine surveys in the San Juan Islands (Fig. 1), we had ob-

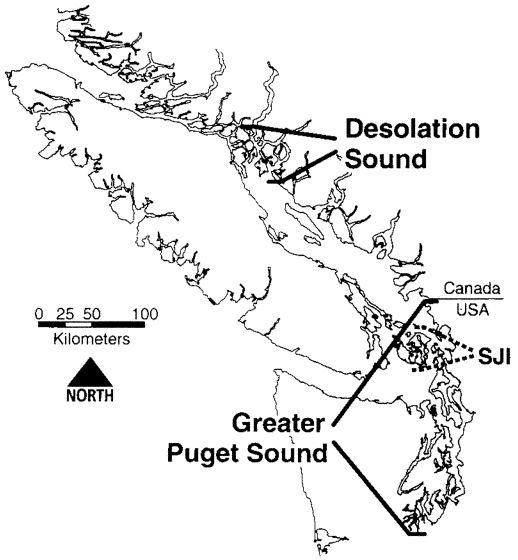

FIGURE 1. Puget Sound (including the San Juan Islands, 'SJI'), Washington, and Desolation Sound, British Columbia, study areas.

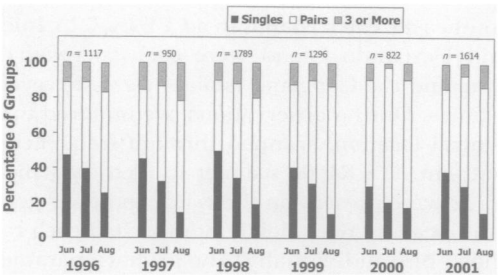

FIGURE 2. Seasonal variation in proportions of murrelet group sizes (1, 2, 3 or more individuals) from marine surveys in San Juan Islands, Washington, was consistent among years. Sample sizes (n) for the 3 months total are shown above bars for each year.

served a consistent annual pattern of decreasing proportion of single marbled murrelets over time from June to August compared with pairs or larger groups (Fig. 2). June, July, and August loosely corresponded to the latter part of incubation, chick-rearing, and the latter part of the breeding season, respectively, in Washington. This observation was based on data from a series of transects in the San Juan Islands, WA (Collins 2000; Carten 2001). Transects were surveyed during sequential 10-d intervals throughout the summer. Lengths of transects totaled 170 km. Observers recorded the number of murrelets in each group detected. Groups were defined as birds in close proximity (generally 1 to 2 m of each other) engaged in similar behavior and responding to disturbance in the same manner (for example, changing direction when swimming).

To determine if these observed patterns in group sizes were reflective of nesting behavior, we monitored a marked population of marbled murrelets in Desolation Sound, British Columbia, in 2001 (Fig. 1). Murrelets were captured at night with dip nets (Whitworth and others 1997) from 20 April through 26 May 2001. Capture methods are detailed in Vanderkist and others (1999) and Lougheed and others (1998). Radio transmitters were attached to 75 birds. Beginning 25 April, telemetry monitoring flights were conducted daily by helicopter, with the flight path passing over the main waters of Desolation Sound and, on routes alternating by day, over the main drainages within the study area (see Hull and others 2001 for a detailed map of this study area). Part of each day's flight included a stop on a centrally located ridge, and all extant frequencies were scanned from this location. We used the distinct 24-h on-off pattern to identify nesting status (Bradley 2002). For our study, murrelets detected consistently on alternating days on the water were assumed to be in the incubating phase of their breeding cycle, and locations of birds at inland nest sites confirmed nesting status. To identify the beginning of the chick-rearing period, we used a 30-d incubation period (Nelson 1997) in combination with daily detections of the radio-tagged adult on the water. A cessation of the 24-h on-off pattern in <30 d identified failed nesters (unless, for birds tagged after they initiated incubation, continued inland visitation suggested chick-rearing [Bradley 2002]), and birds that never initiated a consistent on-off pattern were classified as nonnesters.

To assess the relationship between group size on the ocean and nesting status, we visually located the radio-tagged birds from a small boat during 29 May through 19 June 2001. Observations were concentrated in the central portion of Desolation Sound, from the west and south ends of Homfray and Waddington channels, respectively, to the area between the northwest tip of the Malaspina Peninsula and

southeast Cortes Island. In addition, Toba Inlet and Hernando Island were each surveyed 1 time and the Copeland Islands were surveyed 3 times. During observations, we motored to a central location, scanned through frequencies with an ATS R4000 scanner to identify which birds were present on the water and their general location, then slowly approached each radioed bird individually. The primary parameter of interest was group size at the point when the radioed bird was located visually (initial group size). We also recorded behavior (foraging, swimming, taking flight, avoidance dive), map location, GPS location, and ending group size. For example, if the group responded to the approach of the boat and reconfigured itself (for example, if some or all birds dove or flew or the group separated), we recorded the group size for the target murrelet after reconfiguration ('ending group size'). If conditions allowed and the group could be observed from a distance, we observed for 5 to 10 min to determine if the target murrelet remained in the group. Repeat observations of the same individual on 1 d were separated by several hours to avoid autocorrelation and didn't exceed 2 observations per day per individual. Nesting status was assigned for each individual for each day it was visually observed on the water.

Following the breeding-status study, we returned to marine survey data for a more detailed retrospective analysis, including a better definition of the breeding season. To make inferences from group sizes recorded on marine surveys during incubation compared with the rest of the nesting season, we 1st defined a peak incubation period. The known nesting chronology in Washington, from a limited sample of nests and grounded young (Hamer and Nelson 1995), is similar to the incubation period identified for Desolation Sound (Lougheed 2000). Assuming similar nesting chronologies for the 2 areas, we used estimated nest start dates from Desolation Sound telemetry data from 1998 through 2001 to delineate a peak incubation period for each of these 4 y. We projected a 30-d incubation from each estimated nest start date, and from a frequency histogram identified the range of days that encompassed the incubation period of the middle 75% of the nests. Because telemetry data will not always be available to define the incubation period each year, we averaged the peak incubation dates from 1998 through 2001 to define a peak incubation period that could apply generally to all years (Fig. 3). We divided the remainder of the calendar year into 3 additional seasons.

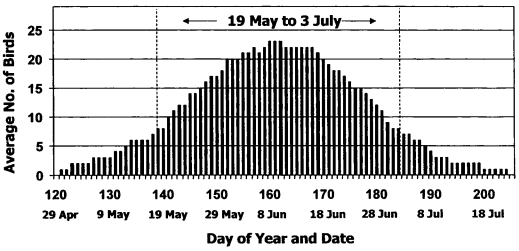

FIGURE 3. Frequency histogram of the average number of murrelets incubating on any single date and day of the year in Desolation Sound, 1998 to 2001, calculated from nest start dates from telemetry data and assuming a 30-d incubation period. Dates within brackets define the middle 75% of nests.

We used 1997 to 2001 marine survey data from Puget Sound (of which the previously referenced San Juan Island data was a subset) to examine seasonal changes in the proportion of single murrelets detected on the water, and we compared annual differences in the proportion of singles during peak incubation to annual estimates of productivity. Because larger groups could potentially have higher detection probabilities at equivalent distances, resulting in an underestimate of single birds, we examined the relationship between group size and detectability using 2001 long-term monitoring survey data in Puget Sound. Results from program DISTANCE (Buckland and others 1993) showed a weak, nonsignificant relationship (MGR and DEM, unpubl. data).

The productivity index was calculated from juvenile to adult ratios adjusted for time of year of survey following the methods of Beissinger (1995), but including only Washington and British Columbia fledge dates from Hamer and Nelson (1995), augmented by fledge dates from British Columbia telemetry data and at-sea surveys in Puget Sound, per the methods in Hamer and Nelson (1995). Specifically, counts of juveniles were adjusted upward by the proportion of young that would have fledged by the end of the survey period, based on a cumulative frequency of fledge dates from Washington and British Columbia. Because the data were asymptotic, we divided the cumulative frequency curve into 3 time periods and calculat-

ed a regression for each period separately. The adjustment factors (cumulative proportion of nests fledged) were (0.00204 × day of year) − 0.3212 for dates before day 180; (0.02133 × day of year) − 3.8448 for days 180 to 220; and (0.0044 × day of year) − 0.0798 for days > 220. Standard errors for the adjusted ratios were calculated from a standard formula for the variance of a ratio (Manley and others 1993). Although we used the adjusted ratio in an attempt to compensate for weaknesses in the simple calculation of total juvenile to total adults observed, we were more interested in changes in the trend from year to year than in the absolute value of the index.

We used Chi-square tests to compare (1) proportions of initial group size by nesting status, and (2) proportions of single murrelets among seasons. For nesting status, chick-rearing birds and failed nesters were included with non-nesters to represent non-incubating birds. Non-parametric post hoc multiple comparisons were conducted on the 6 possible pairings of seasons (Marascuilo and McSweeney 1977). We used SPSS v 10.0.5 (SPSS Inc. 1999) for statistical analyses, with a significance level (α) of 0.05.

RESULTS

During the nest-status study, we visually located 43 of the 75 radioed marbled murrelets on the water at least 1 time, recording 160 observations of initial group size. These included 84 observations of nesting birds in the incubating phase of their breeding cycle (hereafter referred to as 'incubating birds', even though their mate was presumably incubating when they were observed on the water), 17 observations of birds in the chick-rearing phase, 4 of failed nesters, and 55 of non-nesters. Pairs (54 observations) and singles (46 observations) comprised 63% of the total sample. Comparing single birds (group size = 1) to all other group sizes combined, there was a greater proportion of singles among incubating birds (37%) than among non-incubating birds (20%; $n = 160$, $\chi^2 = 5.74$, $P = 0.02$; Fig. 4). Neither group was biased by a small sample of individual murrelets; 29 murrelets comprised the incubating group compared with 24 non-incubators. The relationship was strengthened when we combined chick-rearing and failed nesters along with incubating birds as breeding birds; singles comprised 37% of this group compared with 13% non-breeders ($\chi^2 = 10.50$, $P < 0.01$).

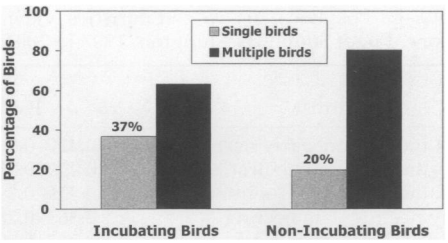

FIGURE 4. Proportions of single and multiple murrelets among incubating birds ($n = 84$) compared with non-incubating birds ($n = 76$) in Desolation Sound, British Columbia, 2001.

Incubating murrelets also were encountered in pairs (25% of observations) and in larger groups of 3 to 17 birds (38%), demonstrating that members of an incubating pair will join other birds when their mate is incubating. Exclusive of chick-rearing and failed nesters, 49% of non-nesting murrelets occurred in pairs, 12% as singles, and the remaining in groups of 3 to 11. Among incubating murrelets, 16 groups (of 84) reconfigured during the observation, resulting in a different group size by the end of the observation. None of these reconfigured groups were singles that joined other groups, and 4 of the 6 incubating birds initially observed in a group of 2 ended up as a single. In comparison, a similar proportion (8 of 55) of groups containing non-nesters reconfigured during the observation, with only 3 ending up as singles and none as pairs. None of the 21 groups containing chick-rearing and failed nesters reconfigured during approach.

The peak incubation periods from Desolation Sound telemetry data for 1998 through 2001, respectively, were 20 May to 30 June, inclusive (days 140 to 181), 22 May to 3 July (days 142 to 184), 16 May to 7 July (days 137 to 189), and 13 May to 30 June (days 133 to 181). The average of these periods was 19 May though 3 July (days 139 to 184; Fig. 3). From these dates we defined an early breeding season of April 20 through 18 May, a late breeding season from 4 July through 15 August, and a fall-winter season from 16 August through 28 February.

From our retrospective analysis of marine survey data in Puget Sound, singles and pairs of murrelets represented 88% of all groups encountered. The proportion of single birds dif-

TABLE 1. Post hoc pairwise comparisons of the proportion of single murrelets detected on the water among seasons, Puget Sound, Washington, 1997 to 2001. Significant differences ($P \leq 0.05$) are marked with (*).

Contrast	Estimate	Estimated variance	95% confidence interval
Peak incubation–early nesting	0.429–0.363 = 0.066	0.0008	−0.0149 to 0.1469
Peak incubation–late nesting	0.429–0.288 = 0.141	0.0001	0.1080 to 0.1740*
Peak incubation–fall-winter	0.429–0.195 = 0.234	0.0002	0.1990 to 0.2690*
Early nesting–late nesting	0.363–0.288 = 0.075	0.0008	−0.0028 to 0.1528
Early nesting–fall-winter	0.363–0.195 = 0.168	0.0008	0.0893 to 0.2467*
Late nesting–fall-winter	0.288–0.195 = 0.093	0.0001	0.0657 to 0.1203*

fered among seasons ($\chi^2 = 347.17$, $P < 0.001$), with the highest proportion during peak incubation and lowest proportion during fall and winter (Table 1, Fig. 5). The change in proportion of pairs was the reverse of the change in singles—the proportion of pairs was highest in fall-winter when the proportion of singles was lowest, was lowest during peak incubation when the proportion of singles was highest, and was intermediate during early and late nesting (Fig. 5). The shift in proportion of larger groups among seasons was variable.

The proportion of single marbled murrelets during peak incubation varied among years, and this variation generally tracked changes in the annual productivity index (Fig. 6). Both were high in 1997, decreasing to a low in 1999, and then increasing again in 2000. Only in 2001 did the 2 measures diverge, when the productivity index increased substantially but the percent of singles decreased.

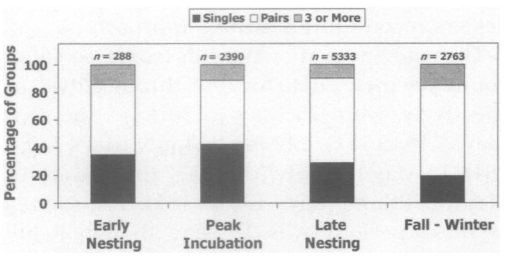

FIGURE 5. Seasonal change in proportions of marbled murrelet group sizes (1, 2, 3 or more individuals) during marine surveys in Puget Sound, Washington, 1997 to 2001. Early breeding season: 20 April to 18 May; peak incubation: 19 May to 3 July; late breeding season: 4 July to 15 August; fall-winter: 16 August to 28 February (no surveys conducted from 1 March to 19 April). Sample sizes (n) for each season are shown above bars.

DISCUSSION

Our results support our hypothesis that the seasonal change in proportion of marbled murrelet groups of different sizes could be a direct reflection of nesting activity. The proportion of single birds encountered on the water was highest during incubation, and single birds observed during this time of year were more likely to be incubating birds than nonnesters. This fits well with the marbled murrelet's distinctive 24-h incubation pattern, as breeding pairs would be separated during incubation and the bird not actively attending the egg would occur on the water without its mate. However, incubating murrelets in Desolation Sound also were observed in pairs and in larger groups during their stint away from the nest. It is this dynamic that requires further investigation and interpretation. We also recognize that our observations of telemetered murrelets were from 1 location during 1 y, but suggest that factors influencing grouping behavior are not site-specific.

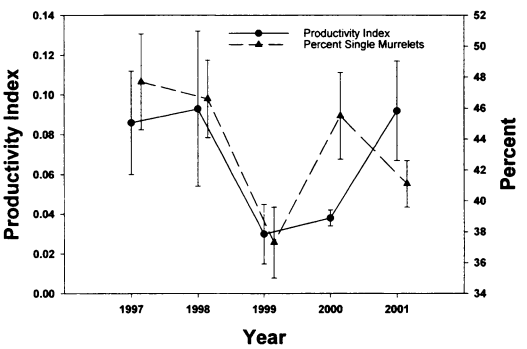

FIGURE 6. Annual change in proportion of single marbled murrelets during peak incubation compared with annual productivity index, Puget Sound, Washington, 1997 to 2001. Error bars represent 1 $s_{\bar{x}}$.

We used initial group size of the radioed murrelets as our parameter for analysis because it reflected conditions on a marine survey, whereby an observer encounters a murrelet group at a random, brief point in time as the vessel continues along a transect. Ending group size, although less characteristic of a marine survey, offered additional insight into the behavior of incubating and non-nesting birds. None of the 31 incubating birds 1st encountered as a single on the water joined another group during the short observation period. Additionally, an incubating bird paired with another murrelet, presumably not its mate, ended up more often than not as a single when the pair was approached or disturbed, causing the birds to move. The fact that an incubating bird often separated from the other murrelet contrasts with the relatively strong bond displayed by many other pairs that may be 'mated', as evidenced by repeated (and increasingly strenuous) vocalizations upon surfacing to locate each other after becoming separated during a dive, then swimming to rejoin the other bird (DEM pers. obs.; Laura McFarlane Tranquilla, Simon Fraser University, Burnaby, BC, pers. comm.). Our observations suggest that incubating birds will behave in a solitary manner more than birds not incubating, but this distinction would not be consistently apparent from a boat-based population survey, as some incubating birds would appear with other birds.

Our results would be biased if group size was predominantly behavioral (for example, if some murrelets were 'loners' with a greater propensity to occur as singles). Sample sizes for individuals observed more than once were too small to perform statistical tests. We identified 1 murrelet (of the 9 incubating individuals that were observed 4 or more times) that might have been exhibiting a propensity to be alone (4 of 6 observations). However, none of the 6 non-incubating birds observed 4 or more times showed the same propensity, suggesting that occurrence as singles vs. in a group was more reflective of breeding status. We did not assess territoriality (singles repeatedly observed in the same places) in either our marine surveys or our observations of telemetered murrelets. Additional studies of murrelet behavior on the water would help clarify these issues.

The occurrence of incubating murrelets with 1 or more other murrelets in Desolation Sound could be a function of relatively high murrelet density in this region. Although we lacked direct comparisons, average densities in Desolation Sound proper during 1996 to 1998 (excluding inlets and weighted by the number of polygons; Lougheed 2000) were up to 4 times higher than in Puget Sound in 2000 and 2001 (Bentivoglio and others 2002; Jodice 2002), depending on year and strata compared (for example, 6.5 birds/km^2 in Desolation Sound in 1996 compared with 1.6 birds/km^2 for Puget Sound in 2000). An incubating bird leaving the nest for the water would be more likely to encounter other murrelets when bird density on the water is high than in regions where murrelets are less dense and thus more dispersed. In addition, group sizes encountered along random transects in Desolation Sound in 2001 during observations of telemetered birds were larger compared with the same time period in Puget Sound ($\bar{x} = 2.43$, $s = 1.98$ vs. $\bar{x} = 1.93$, $s = 1.22$, respectively; $t = -4.94$, df = 904, $P < 0.01$). Larger groups could be correlated with higher densities, such as was found during morning surveys (but not at other times of day) in Barkley Sound, BC (Carter and Sealy 1990). More study of murrelet grouping behavior is needed to determine if incubating birds have a similar affiliation with other birds when the population is more dispersed. For example, a repeat telemetry study (that includes visual observations of known nesters) in areas of lower murrelet densities would provide a good comparison.

The proportion of single birds increased when failed nesters and chick-rearing birds were combined with known incubating birds. On the surface this seems contradictory, as failed nesters and chick-rearing birds could join with their mate on the water once nest attendance was no longer necessary. However, given that a chick-rearing pair staggers its fish deliveries to the nest, the adults would occur on the water at different times for at least some portion of the nestling period. Known pairs monitored with telemetry in Desolation Sound did occur together occasionally during chick-rearing, but not as often as during pre-incubation (McFarlane Tranquilla and others, In press).

Our sample of failed nesters was very small

(4 groups, 2 of which occurred as singles), and interpretation of their occurrence as singles is much more speculative. Death of 1 member of the pair could certainly cause nest failure and separation of the birds on the water, but whether this was the case among our marked population is unknown.

Our analysis of the proportions of group sizes encountered throughout the year in Puget Sound was based on the assumption of similar breeding chronology in Washington and British Columbia, allowing us to define the breeding season for Puget Sound from Desolation Sound telemetry data. Estimates from marbled murrelet nests and grounded chicks summarized in Hamer and Nelson (1995) were similar to those derived by Lougheed (2000) from several different methods. The sample of known fledging dates in Washington was relatively small, which limited our comparison. However, ongoing telemetry studies in Desolation Sound and Clayoquot Sound, BC, have demonstrated up to a 30-d difference in the chronologies of these 2 populations sharing the same latitude (Russell Bradley, Point Reyes Bird Observatory, Stinson Beach, CA, pers. comm.), suggesting variation within geographic areas and caution in our assumption of similar chronologies between British Columbia and Washington.

Our use of telemetry data, exclusively, to define a period of peak incubation allowed a 1:1 temporal correspondence of marine survey data with telemetry data for 4 of the 5 y analyzed (1998 to 2001), while also increasing the sample size of nest start dates 3-fold from that previously published (36 nest start dates from Hamer and Nelson [1995] for Washington and British Columbia compared with 125 from telemetry data). We defined 'peak incubation' as the period when the middle 75% of nests were being incubated, eliminating the earliest and latest nests. Lougheed (2000) defined a 'core incubation' period from the middle 50% of dates. Both approaches attempt to deal with the prolonged, asynchronous breeding season. Because we used these dates to interpret group size on the water during marine surveys and not to distinguish incubation from chick rearing per se, our less conservative 75% provided a broader window to capture more birds that might be incubating while excluding the more extreme ends of the spectrum. Finally, we averaged the dates from 1998 to 2001 to arrive at a general peak incubation period. We maintain that this average was a reasonable reflection of the general incubation activity in Washington, as these 4 y included a range of marine conditions (warmer and cooler sea surface temperatures) that might influence breeding.

Marbled murrelet productivity indices show annual variation (Beissinger 1995; Strong 1995). Productivity of seabirds can vary in response to oceanic conditions, through effects on prey and its availability. For example, seabird responses to El Niño events have been documented, although the influence of these events in the Strait of Georgia and Puget Sound are less clear than in other marine systems. In years of low productivity, we might expect fewer nesting attempts, and, if group size is a reflection of nesting, fewer single murrelets on the water during incubation. We found this pattern in 4 of the 5 y we compared. We expected that the variation in the productivity index might be greater than in the proportion of singles detected at sea because lower nesting effort should result in lower juvenile to adult ratios and vice versa, whereas group size didn't always indicate breeding status and could reflect a more consistent influence such as foraging strategy. However, the magnitude of change was similar for each variable. We found no obvious biological or environmental explanation for the divergence of the 2 measures in 2001.

In summary, group size on the water, and specifically the proportion of single-bird groups, may provide an index of nesting attempts, but the relationship is not precise and needs refinement. The breeding chronology within the study area needs to be well documented, which could require extensive telemetry or physiological studies. If data are available, one could redefine the incubation period each year from nest start dates to correspond directly with productivity in that year. As mentioned above, the extent to which group dynamics and group sizes are a function of density should be explored. Lastly, we need to continue to explore new methods to measure murrelet productivity.

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