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RESEARCH ARTICLE

# Declining Marbled Murrelet density, but not productivity, in the San Juan Islands, Washington, USA

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## ABSTRACT

The Marbled Murrelet (*Brachyramphus marmoratus*) is federally threatened in part of its range in western North America. Information on density and productivity is important for managing populations. Over an 18-yr period, we monitored murrelet density and productivity ratios during the breeding season along 170 km of shoreline of the San Juan Islands, Washington, USA. While murrelets occur throughout the coastal marine waters of Washington, the San Juan Islands support higher densities of murrelets during the breeding season than most other areas. From 1995 to 2012, the average density of adult murrelets declined significantly from 11.16 to 5.76 murrelets km$^{-2}$, a decline that mirrored large-scale at-sea surveys in Washington. Despite this consistent and ominous decline in overall murrelet density, the density of juvenile murrelets and murrelet productivity ratio (juveniles:adults) did not decline over this time period. Thus, the declining density of murrelets in the San Juan Islands was due to declines in adult murrelets only, not juveniles. Annual estimates of overall murrelet density were positively correlated with winter El Niño Southern Oscillation (ENSO) indices. We estimated that, on average, 6,605 ($\pm$ 2,531 SD) murrelets occurred during surveys annually, confirming that the San Juan Islands contain some of the most heavily used marine areas in the portion of the U.S. range in which murrelets are threatened. In ENSO years, numbers increased to $>$8,500 birds. Heavy use of the San Juan Islands in ENSO years suggests that this area may provide refugia marine habitat for murrelets when prey availability along the outer Pacific Coast is poorer than usual.

*Keywords: Brachyramphus marmoratus*, distance sampling, El Niño Southern Oscillation, productivity ratio, seabird, upwelling

## RESUMEN

*Brachyramphus marmoratus* es una especie de ave marina amenazada a nivel federal en parte de su rango en el oeste de América del Norte. La información sobre las tendencias de densidad y productividad son importantes para el manejo de las poblaciones. A lo largo de un período de 18 años, monitoreamos la densidad y los cocientes de productividad de *B. marmoratus* durante la estación reproductiva a lo largo de 170 km de costa de las Islas San Juan, Washington, EEUU. Mientras que los individuos de *B. marmoratus* estuvieron presentes en las aguas costeras marinas en Washington, las Islas San Juan albergaron densidades más altas de individuos durante la estación reproductiva que la mayoría de las otras áreas en Washington. De 1995 a 2012, las densidades promedio de adultos disminuyeron significativamente de 11.16 a 5.76 individuos /km$^2$, una disminución semejante a la de los muestreos a gran escala en el mar en Washington. A pesar de estas disminuciones consistentes y amenazadoras en las densidades generales de individuos de *B. marmoratus*, las densidades de juveniles y los cocientes de productividad (juveniles: adultos) no disminuyeron a lo largo de este periodo de tiempo. De este modo, la disminución en las densidades de *B. marmoratus* en las Islas San Juan se debieron a las disminuciones solo de los adultos, pero no de los juveniles. Las estimaciones anuales de densidad global de *B. marmoratus* estuvieron positivamente correlacionadas con los índices de invierno de la Oscilación del Sur El Niño (ENSO por sus siglas en inglés). Estimamos en promedio 6,605 ($\pm$2531) individuos presentes anualmente en los muestreos, confirmando que las Islas San Juan contienen algunas de las áreas marinas más usadas en la porción amenazada de su rango de EEUU. En los años ENSO, los números aumentaron a más de 8,500 aves. El gran uso de las Islas San Juan en los años ENSO sugiere que esta área puede brindar hábitat de refugio marino para los individuos de *B. marmoratus* cuando la disponibilidad de presas a lo largo de la costa externa del Pacífico es más pobre que lo usual.

*Palabras clave:* afloramiento, ave marina, *Brachyramphus marmoratus*, cociente de productividad, muestreo por distancia, Oscilación del Sur El Niño

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## INTRODUCTION

The Marbled Murrelet (*Brachyramphus marmoratus*) is a seabird that occurs from Alaska to California in North America. It typically forages in nearshore coastal waters within several kilometers of shore, but nests inland, often in coastal old-growth forests. It is listed as a threatened species from British Columbia, Canada, to California, USA, primarily because of harvesting and fragmentation of forested nesting habitat, and secondarily because of the threat of deteriorating marine conditions (e.g., oil spills, entanglement in fishing gear, depletion of prey from fisheries; USFWS 1997, Environment Canada 2014). Under the Northwest Forest Plan (NWFP), provisions were made to reduce the harvest of old forest on U.S. federal lands from Washington to California, while monitoring murrelet populations and nesting habitat (Madsen et al. 1999). A goal of the NWFP was to stabilize murrelet populations and nesting habitat in Washington, Oregon, and California, at which point the species could potentially be removed from the U.S. Endangered Species List.

Despite protections to nesting habitat on U.S. federal lands, Raphael et al. (2016) reported continued declines and fragmentation of murrelet nesting habitat from 1993 to 2012 in Washington, Oregon, and California. Most of the reported habitat declines were associated with timber harvest on nonfederal lands. These declines in nesting habitat were associated with declines in murrelet densities recorded during NWFP at-sea surveys in Washington State (Falxa et al. 2016). In adjacent waters to the north, Bertram et al. (2015) also reported declines in Marbled Murrelets from radar counts on southeastern Vancouver Island and the southern mainland British Columbia coast from 1995 to 2013. While rigorous tests of hypotheses have not been possible, circumstantial evidence suggests that declining nesting habitat in Washington and British Columbia has prevented many adults from breeding, resulting in decreased productivity, which has led to fewer murrelets during surveys (Bertram et al. 2015, Falxa et al. 2016). Other factors, such as nest predation, poor marine conditions, emigration, or reduced adult survival, may have contributed to these declines (Environment Canada 2014, Bertram et al. 2015). Assessing the contribution of productivity to murrelet population declines is important because the other causal factors require different management strategies. If declines are due to reduced adult survival or increased adult emigration associated with poor marine conditions, managing marine habitat may be as important as managing nesting habitat for sustaining murrelet populations.

For murrelets, productivity is best measured using counts of juveniles and adults on the water from late July through August (Peery et al. 2009). Murrelet productivity cannot be estimated from NWFP surveys because the survey period ends in late July, before most juveniles have fledged (Raphael et al. 2007). Radar cannot be used to estimate productivity because the ages of individuals passing radar stations cannot be determined. Beginning in 1995, and prior to the implementation of NWFP at-sea surveys in 2001, the U.S. Forest Service, Pacific Northwest Research Station, began surveys for Marbled Murrelets in nearshore waters of the San Juan Islands, Washington. Surveys were conducted from May through August until 2012. Observers counted all adult and juvenile murrelets observed from transect lines, enabling estimates of murrelet productivity. To our knowledge, this 18-yr dataset represents the longest-running consistent survey effort for murrelets of both age classes (adults and juveniles) in the region. While the San Juan Islands contain only a small proportion of the marine habitat used by murrelets in Washington and British Columbia, they consistently contain high densities of murrelets (Falxa et al. 2016) and are centrally located within the Salish Sea. Information on productivity ratios in the San Juan Islands may therefore provide insights into murrelet productivity and reproductive success in the region.

The main objective of our study was to test the hypothesis that murrelet density and productivity declined in the San Juan Islands from 1995 to 2012, following the trend reported from at-sea surveys. Incidentally, over the 18 yr of our surveys, we observed large among-year variation in murrelet abundance. Some of these changes were beyond the reproductive capacity of the species, indicating immigration from other regions, and were associated with known disruptive climatic events that influenced sea surface temperatures along the Pacific Coast (Schwing et al. 2006). Such events can indirectly affect seabirds by reducing foraging opportunities (e.g., Peterson et al. 2002, Black et al. 2010) and may lead to low breeding success or emigration (Bertram et al. 2005, Jones et al. 2008, Cubaynes et al. 2011). Therefore, another objective of our study was to assess whether changes in murrelet density and productivity in the San Juan Islands were associated with variation in spring upwelling or the El Niño Southern Oscillation in the Pacific.

## METHODS

### Study Area

We conducted surveys for Marbled Murrelets in nearshore waters of the San Juan Islands, Washington (~48°33′N, 122°57′W; Appendix Figure 5). The San Juan Islands are an archipelago in the northern portion of the U.S. part of the Salish Sea, centrally located when considering both the U.S. and Canadian portions of the Salish Sea. They lie between Vancouver Island, Canada, and the U.S. mainland, ~40 km south of the U.S.–Canada border and ~130 km from the Pacific Ocean. The U.S. Geological Survey

recognizes 124 islands within San Juan County (i.e. the San Juan Islands), although it is estimated that >400 islands and rock piles occur in the archipelago at mean high tide. Most of the larger islands have previously been logged and are used for agriculture, although small tracts of old-growth forest persist. While it is possible that murrelets nest in some of these old-growth tracts in the San Juan Islands, no nests have been documented there. The majority of murrelets observed offshore of the San Juan Islands are believed to nest on Vancouver Island or mainland USA and Canada. Movements of murrelets between these areas and the San Juan Islands have been confirmed with banding and radio-telemetry (Beauchamp et al. 1999, Lorenz et al. 2017).

The San Juan Islands have a maritime climate, with relatively warm, mild winters and mild summers. They are within the rain shadow of the Olympic Mountains and thus receive less rainfall than other parts the Salish Sea, averaging 50–70 cm annually. Compared with the outer coasts of Washington and Vancouver Island, they are buffered from oceanic influences by the ~100-km long Strait of Juan de Fuca. The western and northern boundaries of the San Juan Islands are formed by Haro Strait and Boundary Pass, both major shipping canals between the U.S.–Canada border that are >200 m deep (Appendix Figure 5). Relatively strong and complex tidal currents are common around the San Juan Islands (Mackas and Harrison 1997) and, overall, the marine environment is more influenced by tides and terrestrial runoff from land and rivers (e.g., the Fraser, Nooksack, and Skagit rivers; Wise et al. 2007) than marine areas along the Pacific coast of Washington and British Columbia.

## Field Methods

Observers surveyed murrelets from 16 line transects located 300 m offshore of the San Juan Islands during the murrelet breeding season from 1995 to 2012. Individual line transects were between 4 and 22 km long, but for some analyses we split each transect into 2-km long segments and considered segments the basic unit of measure (Appendix Table 3). We selected areas to survey that were relatively easy to access from our base station at Friday Harbor, Washington, or that were known to have consistently high densities of murrelets. Considered together, surveys covered 170 km of the shoreline of the San Juan Islands. We surveyed 300 m offshore because pilot surveys in our first year indicated that transects 300 m offshore resulted in higher detections of murrelets compared with transects 100 m, 500 m, and 800 m offshore (Ralph et al. 1996). Importantly, however, our estimates of density do not represent overall density or population size in the San Juan Islands because murrelets are known to occur in areas that we did not survey and transects were not selected randomly. Our inferences apply to the area on either side of our 300-m transects and not to the entire range of murrelets in the San Juan Islands.

Observers conducted surveys between May 12 and August 30 each year. Our goal was to repeatedly survey all transects once every 10 days, for a total of 11 repeat 'intervals' each year. For various reasons, however, not all 10-day intervals were surveyed each year (Appendix Table 4). In 1995 and 1996, 54% and 34% of segments were skipped because a definitive protocol had not been established during these initial years. In 2000, 55% of segments were skipped while effort was devoted to the implementation of NWFP at-sea surveys (Miller et al. 2006). In all other years, observers completed surveys on most or all segments (82–100%; Appendix Table 4). Observers rotated transects amongst each other among intervals, so that no one observer completed all transects. With the exception of a few transects that were surveyed on multiple days due to weather or equipment failure, observers completed transects within 1 day to minimize the double counting of murrelets that moved between segments along a transect in a day.

Surveys were conducted from small boats during daylight hours (between 06:00 and 21:00 hours). Observers maintained a distance of 300 m from shore using radar and GPS. They deviated from this 300-m distance only to avoid shallows or hazardous conditions. One observer scanned from 90° left to 90° right of the bow and recorded all murrelets detected (i.e. unlimited distance surveys). For each murrelet detection, the observer recorded group size, perpendicular distance to the transect line, and plumage class, following Carter and Stein (1995), Strong (1998), and Raphael et al. (2007). Prior to the survey season, surveyors completed a 2–3 week class in murrelet identification, murrelet plumage classes, and distance estimation (Raphael et al. 2007). During the survey season, observers were tested on their distance estimates every 3 survey days for calibration (Raphael et al. 2007).

Observers recorded sea conditions, including Beaufort sea state, at the beginning of each survey and when conditions changed (0 = calm, smooth sea surface; 1 = small ripples on sea surface; 2 = small wavelets, not breaking). They did not initiate surveys in conditions with Beaufort sea states >2 and when their ability to detect murrelets may have been compromised (Raphael et al. 2007). For a few surveys, however, sea state increased during a survey, and in these cases observers completed the survey despite a Beaufort sea state >2. Vessel speed was set at 14–23 km $hr^{-1}$, although surveys were paused when necessary to identify murrelets or murrelet plumage classes.

## Estimating Murrelet Density

We estimated murrelet densities using distance sampling in program Distance 7.0 (http://distancesampling.org/).

We used recommendations by Buckland et al. (2001:45) for modeling the distance function with uniform and half-normal key functions. We did not consider hazard-rate key functions based on recommendations by Raphael et al. (2007:45). We selected the model with the lowest Akaike's information criterion (AIC) as the best from among those we considered. We treated years as strata and intervals as samples, and estimated the detection function at the stratum level (annually). We truncated observations beyond 180 m because preliminary analyses indicated that including murrelets detected beyond this distance did not improve the detection function or density estimate.

To estimate murrelet density for individual transect segments within each interval where too few murrelets were detected for estimating segment-level detection functions directly in program Distance, we applied sample-level estimates of detection probability, modified from Raphael et al. (2007) using the following formula:

$$d_{\text{segment}} = \left(1,000 \times f(0) \times N\right) \Big/ 4, \qquad \text{(equation 1)}$$

where $d_{\text{segment}}$ is the estimate of murrelet density for each kilometer of survey within each interval within each year, 1,000 converts our density estimate from murrelets $m^{-2}$ to murrelets $km^{-2}$, $f(0)$ is the estimate of detection probability from program Distance, and $N$ is the number of murrelets on each segment. We divided the estimate by 4 to account for the 2-km long transects in our study and to account for surveying murrelets on 2 sides of our transect lines. We also estimated segment-level juvenile and adult density using this formula, where $N$ was the number of juveniles or adults detected on each segment.

We considered that the ability of observers to detect murrelets could have been affected by Beaufort sea state and compared support for models with and without sea state as a covariate. Prior to this analysis, we combined all surveys with Beaufort classes >1 into the class 2 sea state because few surveys (1.4%) were conducted in sea states above 2. We then treated Beaufort sea state as a factor-level covariate in program Distance (with 3 levels: 0, 1, and ≥2). We assessed the effects of Beaufort sea state for years 2001 to 2012 because sea state was not consistently recorded prior to 2001. Unlike Miller et al. (2012), we did not consider observer as a covariate because observers were rotated among transects within years. Differences in detection as a result of changes to observers among years were accounted for by estimating separate detection functions for each year, as described above.

## Productivity Ratios

For comparison with other studies, we computed several estimates of murrelet productivity. First, we computed uncorrected ratios of juveniles (HY, or hatch-year) to adults (AHY, or after-hatch-year) for direct comparison with the results of Kuletz and Piatt (1999) in Alaska and Lougheed et al. (2002) in British Columbia. For comparison with the findings of Kuletz and Piatt (1999), we averaged juvenile and adult numbers from August 7 to 24 only, which was the sample period for that study. Lougheed et al. (2002) used different start and end dates each year, so for comparison with their study we used mean start and end dates for computing productivity ratios in our study, or June 21 to August 10. We did not attempt to make direct comparisons with the results of Wong et al. (2008) or Kuletz and Kendall (1998) because, in those studies, either ratios were not computed or daily ratios were the basis of productivity ratios. Daily productivity ratios would have been biased in our study because only a subset of surveys were conducted each day.

We also computed corrected HY:AHY ratios using the methods of Peery et al. (2007) as a guide. We estimated ratios using the sums of juvenile and adult murrelets counted from survey intervals 9 to 13, which corresponded to surveys conducted between July 11 and August 19. These dates marked the period within which juveniles consistently occurred during surveys, but before adults began molting into basic plumage in large numbers, making them difficult to distinguish from juveniles during surveys. We used the equation devised by Peery et al. (2007:229) to estimate productivity ratios:

$$\hat{R}_t = \sum_{9}^{13} H_i \Big/ \sum_{9}^{13} A_i, \qquad \text{(equation 2)}$$

where $H_i$ and $A_i$ are the sum of corrected numbers of hatch-year and after-hatch-year murrelets (see below) counted during surveys in intervals 9 to 13 in year $t$. We computed 95% confidence intervals as:

$$\widehat{CI_t} \pm 1.96 \times \sqrt{\frac{\left(\frac{\bar{x}_{Ht}}{\bar{x}_{At}}\right)^2 \left\{ \left(\frac{\mathrm{SD}_{H_t}}{\bar{x}_{Ht}}\right)^2 + \left(\frac{\mathrm{SD}_{A_t}}{\bar{x}_{At}}\right)^2 - \frac{(2corrH_tA_t \times \mathrm{SD}_{H_t} \times \mathrm{SD}_{A_t})}{\bar{x}_{Ht} \times \bar{x}_{At}} \right\}}{n}}, \qquad \text{(equation 3)}$$

where $\bar{x}_{At}$ and $\bar{x}_{Ht}$ are the mean counts of adults and juveniles for year $t$, $\mathrm{SD}_{At}$ and $\mathrm{SD}_{Ht}$ are the standard deviations of adult and juvenile counts for year $t$, and $corrH_tA_t$ is the correlation coefficient for adult and juvenile counts for year $t$.

Similarly to Peery et al. (2007), we corrected raw counts of adults and juveniles by accounting for 2 potential biases in our survey data: missing birds that were not on the water and could not be counted due to (1) incubation (for adults during early surveys) or (2) late fledging events (for juveniles

that fledged after our survey season ended). To correct for missing adults during the incubation period, we estimated the proportion of incubating murrelets for each day using data from a sample of 157 radio-tagged murrelets tracked from 2004 to 2008 in Washington. We estimated the best-fit polynomial regression line for the proportion of tagged murrelets that were incubating each day using PROC GLM in SAS (Appendix Figure 6). For the midpoint ordinal date within each 10-day interval, we then computed the likely proportion of adult murrelets that were incubating at that time, and corrected our adult estimates for the corresponding interval using the following formula:

$$A_i = A_{observed} \Big/ \left[1 - \left(3.139 \times 10^{-5}(x^2) + 0.01036x - 0.7855\right)\right], \quad \text{(equation 4)}$$

where $A_i$ is the estimated number of adult murrelets counted during surveys corrected for incubating murrelets, $A_{observed}$ is the number of adult murrelets seen during each interval, and $x$ is the midpoint ordinal date for each interval. We computed corrected adult counts only for the time period during which adults were incubating (as estimated from our telemetry data), or ordinal dates 126 to 206 (May 6 to July 25). This analysis corrected our raw AHY counts for adults that may have been incubating during surveys.

We accounted for a second bias associated with juveniles that would not have fledged by the end of our survey period using fledging dates from Washington and British Columbia derived from 4 sources: breeding records (Hamer and Nelson 1995; $n = 35$ dates), telemetry data from British Columbia (Bradley 2002, Bradley et al. 2004; $n = 99$ dates), at-sea survey data from Washington (M. G. Raphael personal observation; $n = 4$ dates), and nests found in Washington and British Columbia (S. K. Nelson personal communication; $n = 29$ dates). We estimated the best fit line for the cumulative proportion of juveniles fledged ($H_i$) for 3 time periods: (1) early (ordinal date <180; $H_{early} = H_{observed}$ / $(0.204x - 32.11)$), (2) midseason (ordinal date 180–220; $H_{mid} = H_{observed}$ / $(2.133x - 384.477)$), and (3) late (ordinal date >220; $H_{late} = H_{observed}$ / $(0.44x - 7.977)$; Appendix Figure 7). This analysis corrected our raw HY counts for juveniles that fledged after the end of our surveys (August 30).

We assumed that our corrected productivity ratios most accurately reflected the true ratio of juveniles to adults in the San Juan Islands, compared with raw or uncorrected ratios. We therefore used corrected HY:AHY ratios for examining trends in productivity among years.

### Trends and Oceanographic Effects

We used linear regression to estimate trends in murrelet density and productivity around transects from 1995 to 2012. To estimate trends in the density of all murrelets, we used annual (stratum-level) density estimates from conventional distance sampling (no-covariates model) calculated in program Distance. To estimate trends in the densities of adult and juvenile murrelets separately, we used estimates of murrelet densities at the segment level because too few juvenile murrelets were seen to estimate separate age-specific detection functions in program Distance. Estimates of murrelet densities computed at the segment level were highly correlated with estimates at the stratum level ($r >$ 0.98). Following McShane et al. (2004) and Miller et al. (2006, 2012), we fit a linear regression line to the natural logarithm of density, where the annual rate of change was equal to the slope of the line (Falxa et al. 2016). To estimate trends in murrelet productivity, we used corrected productivity ratios, as noted above.

To assess whether temporal correlation affected estimates of standard errors in our trend analyses, we checked for correlations in our linear regression model residuals for lags of up to 5 yr. We also plotted murrelet density and productivity against lags of 1–12 yr to look for evidence of a linear relationship, indicative of autocorrelation. We found low correlations in both of these analyses. Correlations in model residuals averaged 0.27 (range: 0.18–0.41), and correlations in density and productivity lags averaged 0.13 (range: 0.01–0.35), indicating that temporal autocorrelation was not an issue with these data.

To assess the relationships between murrelet density and productivity and oceanographic conditions, we first obtained a monthly index of the state of the El Niño Southern Oscillation (ENSO) from the National Oceanic and Atmospheric Administration (NOAA 2017, Smith and Sardeshmukh 2000). We also characterized upwelling effects on murrelets using the annual date of physical spring transition. The annual date of physical spring transition is defined as the date of the lowest upwelling value in each year. Earlier dates are typically associated with higher marine productivity in the northern California Current (Logerwell et al. 2003, Emmett et al. 2006, Bograd et al. 2009) and increases in forage fish and other prey (Wells et al. 2008, Zador et al. 2009). We determined the date of spring transition from the Bakun Upwelling Index obtained from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory website (www.pfel.noaa.gov) for 125°W, 48°N, which is offshore northwestern Washington. This index is an estimate of the offshore Ekman transport derived from surface pressure fields (Pérez-Brunius et al. 2007) measured in $m^3\ s^{-1}\ 100\ m^{-1}$. We computed Pearson correlation coefficients between annual estimates of murrelet density and productivity and these 2 indices. For ENSO, we averaged the index within 2 seasons in the California Current, defined following Bograd et al. (2009): winter (January 1 to date of spring transition, on average January

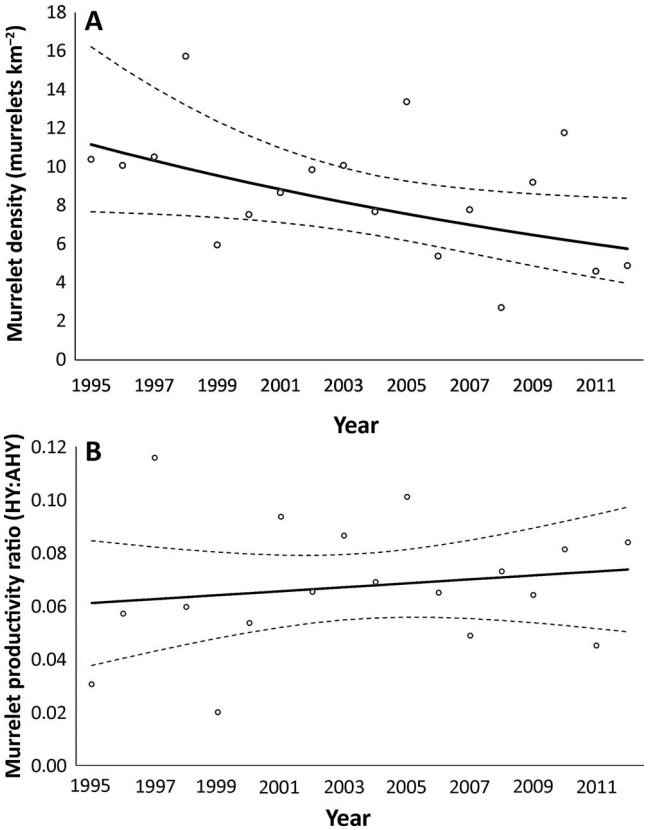


**FIGURE 1.** Fitted regression line with 95% confidence intervals of trend in (**A**) density and (**B**) productivity of Marbled Murrelets in the San Juan Islands, Washington, USA, 1995–2012. Open circles are annual estimates of the density (**A**) or productivity (**B**).

to April), and summer (the upwelling period, from spring transition to the peak cumulative upwelling for each year, or May to August).

## RESULTS

### Murrelet Density

We completed 30,168 km of surveys for Marbled Murrelets in the San Juan Islands from 1995 to 2012. Most surveys (85%) were conducted in Beaufort states 0 or 1. Beaufort sea state was not a strong factor influencing density estimation; on average, >97% of the uncertainty in the estimate of density was due to encounter rate, rather than parameter estimates of the detection function (~2%). Based on AIC, neither the Beaufort nor the no-covariates model was consistently ranked higher. The Beaufort model was top ranked in 9 yr, and the no-covariates model was top ranked in 3 yr. There was also little difference in murrelet density estimates obtained from the top-ranked Beaufort sea state model and no-covariates model (average difference in murrelet density = 0.701), and confidence intervals from both models overlapped in all years (Appendix Figure 8). For parsimony, we therefore used the no-covariate model to examine trends in murrelet density for the 1995–2012 survey period.

From conventional distance sampling in program Distance, we estimated that, on average, 6,605 (± 2,531 SD) murrelets occurred during surveys annually. Murrelet density averaged 8.67 birds km$^{-2}$ (± 3.27 SD) annually and varied by year, transect, and interval (Figures 1, 2, and 3, Appendix Table 5). In most years, densities on transects increased seasonally (Figure 3). Increases corresponded with the completion of incubation by adult murrelets (beginning ~May 17 and peaking ~June 16; Figure 3, Appendix Figure 6) and fledging by juvenile murrelets (typically beginning July 1 and peaking ~July 29; Figure 3, Appendix Figure 7).

Annual estimates of the numbers of murrelets varied by an order of magnitude. A low of 2,067 birds was estimated for 2008, compared with a high of 12,523 following the strong El Niño winter of 1998 (Table 1). Numbers of adults and juveniles did not peak in the same years. Highest counts of adults occurred in 1998 and 2005 following El Niño or delayed upwelling conditions (see below), when we estimated >8,500 adults (95% CI: 8,661–14,646; Table 1). In contrast, juvenile counts peaked in 2002 and 2004 (Table 1).

### Productivity

On average, we first observed juveniles on July 1 (± 18 days SD). Juveniles were seen much less frequently on transects than adults. We estimated that 256 (± 122 SD) juveniles occurred during surveys. Mean group size for juveniles was 2.7 (± 3.3 SD), and 47% of these groups contained at least 1 adult, compared with mean group size of 2.2 (± 1.6 SD) for adults. Juveniles were observed singly (group size = 1) in 43% of cases, compared with 22% of cases for adults.

Uncorrected productivity ratios for our monitoring period (July 11–August 19) averaged 0.044 (± 0.016 SD). When computing ratios for the time period between August 7 and 24 for comparison with the findings of Kuletz and Piatt (1999), uncorrected productivity ratios averaged 0.054 (± 0.034 SD, range: 0.008–0.167) across all years. For the time period of June 21 to August 10 (for comparison with the results of Lougheed et al. (2002), uncorrected productivity ratios averaged 0.042 (± 0.022 SD, range: 0.013–0.113). Corrected juvenile productivity ratios were considerably higher, averaging 0.07 (± 0.02 SD). Corrected ratios were variable among years (Appendix Figure 9), ranging from 0.02 (95% CI: –0.01 to 0.05) to 0.12 (95% CI: 0.05 to 0.18).

### Trends and Oceanographic Effects

There was a significant declining trend in murrelet density over the 18-yr period of our surveys ($F_{1,16} = 4.81$, $P = 0.04$, $\beta = -0.039$; Figure 1), and the 95% confidence interval for

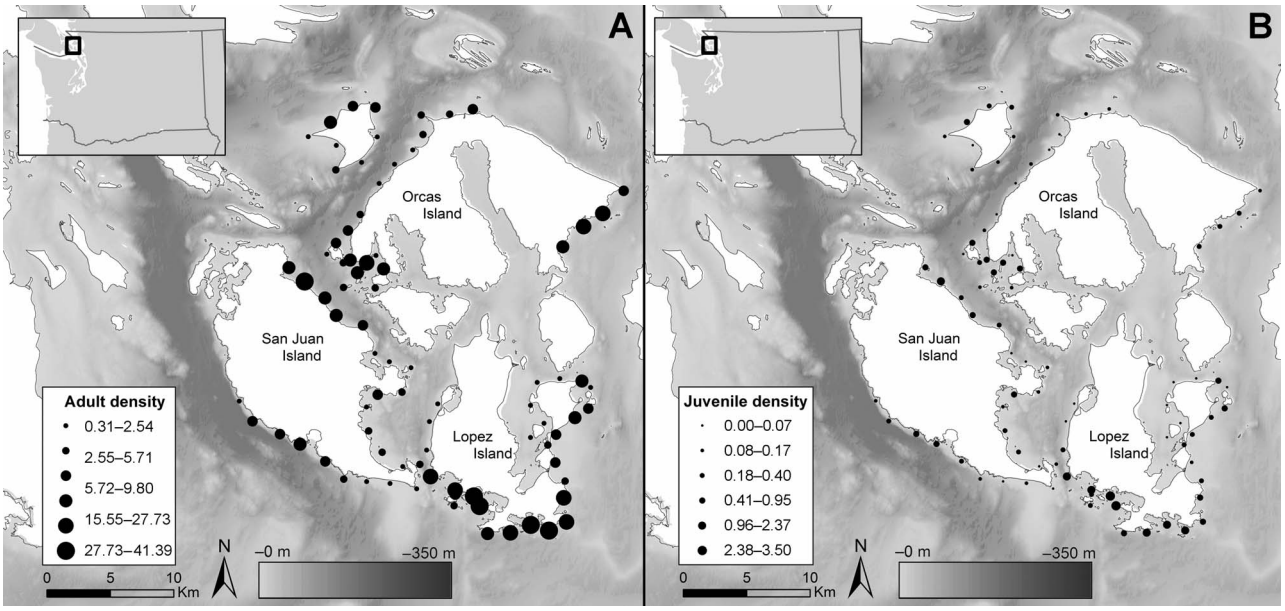


**FIGURE 2.** Density (murrelets km$^{-2}$) of (**A**) adult and (**B**) juvenile Marbled Murrelets along 2-km segments of 16 transects in the San Juan Islands, Washington, USA, 1995–2012, with bathymetry.

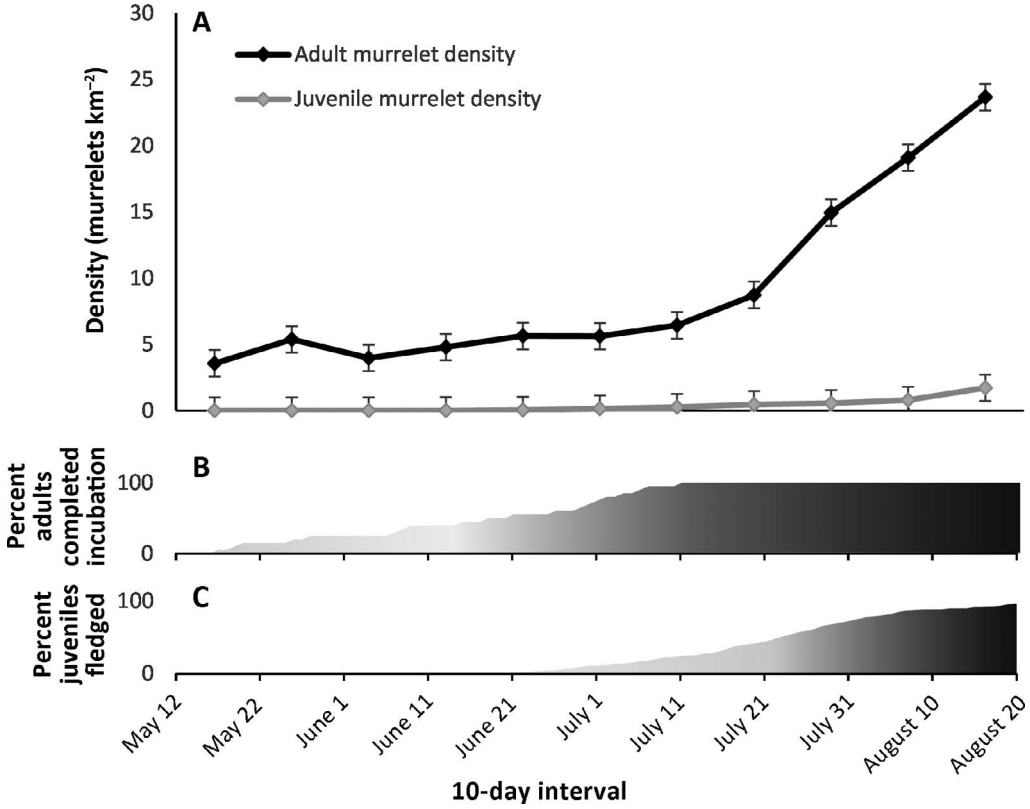


**FIGURE 3.** (**A**) Mean density of adult (black line) and juvenile (gray line) Marbled Murrelets for each 10-day interval from May 12 to August 30, averaged across 1995–2012, in the San Juan Islands, Washington, USA, and the estimated cumulative percentage of (**B**) breeding adults that had completed incubation and (**C**) juveniles that had fledged for this same time period.

**TABLE 1.** Annual estimates of juvenile and adult Marbled Murrelet density and abundance (with 95% confidence intervals) in the San Juan Islands, Washington, USA, 1995–2012.

| Year | Adult density (murrelets km$^{-2}$) | Adult abundance (95% CI) | Juvenile density (murrelets km$^{-2}$) | Juvenile abundance (95% CI) |
|---|---|---|---|---|
| 1995 | 13.03 | 8,771 (6,858–10,684) | 0.18 | 121 (54–187) |
| 1996 | 12.14 | 8,173 (6,588–9,757) | 0.19 | 125 (77–173) |
| 1997 | 10.71 | 7,209 (5,635–8,783) | 0.53 | 357 (202–512) |
| 1998 | 18.22 | 12,263 (9,881–14,646) | 0.39 | 260 (176–345) |
| 1999 | 7.33 | 4,938 (3,954–5,921) | 0.08 | 52 (28–77) |
| 2000 | 9.31 | 6,271 (4,671–7,871) | 0.37 | 247 (139–356) |
| 2001 | 9.65 | 6,497 (5,428–7,566) | 0.42 | 286 (196–375) |
| 2002 | 10.86 | 7,312 (5,937–8,687) | 0.64 | 434 (178–690) |
| 2003 | 10.74 | 7,233 (6,030–8,436) | 0.54 | 362 (249–476) |
| 2004 | 9.60 | 6,461 (5,209–7,712) | 0.62 | 418 (263–572) |
| 2005 | 14.87 | 10,008 (8,661–11,354) | 0.39 | 264 (185–344) |
| 2006 | 5.79 | 3,895 (2,871–4,920) | 0.40 | 268 (157–379) |
| 2007 | 8.52 | 5,733 (4,717–6,748) | 0.15 | 101 (64–137) |
| 2008 | 3.01 | 2,025 (1,433–2,616) | 0.06 | 42 (20–63) |
| 2009 | 9.83 | 6,616 (5,386–7,846) | 0.37 | 249 (164–335) |
| 2010 | 12.90 | 8,685 (7,292–10,078) | 0.52 | 353 (256–450) |
| 2011 | 4.91 | 3,303 (2,502–4,104) | 0.42 | 279 (109–450) |
| 2012 | 5.19 | 3,494 (2,646–4,342) | 0.58 | 392 (192–592) |

this estimate did not overlap zero (–0.004 to –0.057). This declining trend was due to significant declines in adults on transects ($F_{1,16} = 6.84$, $P = 0.02$, $\beta = -0.045$); there was no significant trend in the density of juveniles ($F_{1,16} = 0.47$, $P = 0.50$, $\beta = 0.022$). There was also no significant linear trend in the productivity ratio from 1995 to 2012 ($F_{1,16} = 0.45$, $P = 0.51$) and the slope of the line was near zero ($\beta = 0.001$; Figure 1).

Murrelet density and productivity were not correlated ($r = 0.256$, $P = 0.31$), and years of the highest overall densities (1998, 2005, and 2010) were not associated with the highest productivity ratios (Figure 1, Appendix Figure 9). Murrelet densities around transects were strongly correlated with winter ENSO conditions ($r = 0.849$, $P < 0.001$; Table 2, Figure 4). Murrelet densities peaked in years with a high ENSO index, including 1998 (strong winter El Niño), 2005 (year of delayed upwelling and high winter ENSO index), and 2010 (strong winter El Niño; Figure 4). The years of 1998 and 2005 were particularly notable. Our estimates of average murrelet abundance in both of these years exceeded 10,000 birds, approximately double the mean across years (Table 1). Murrelet productivity was not as strongly correlated with oceanographic conditions. We observed weaker, but nevertheless significant, positive correlations with the date of spring transition ($r = 0.611$, $P = 0.007$) and the summer ENSO index ($r = 0.515$, $P = 0.03$; Table 2). However, these correlations were largely due to high productivity in 2 yr of delayed upwelling (1997 and 2005; Figure 4). If we removed these years from analysis, the correlations were nonsignificant ($r = 0.177$, $P = 0.51$ for the spring transition, and $r = 0.251$, $P = 0.35$ for the ENSO index), suggesting that there was no apparent relationship between productivity and the oceanographic factors that we considered.

**TABLE 2.** Correlation coefficients (with corresponding *P*-values) between Marbled Murrelet density and productivity and averaged seasonal El Niño Southern Oscillation (ENSO) and date of physical spring transition in the upwelling season from 1995 to 2012 in the San Juan Islands, Washington, USA.

| | January–April | May–August |
|---|---|---|
| ENSO | | |
| Murrelet density | 0.849 ($P < 0.001$) | −0.002 ($P = 0.99$) |
| Murrelet productivity | 0.246 ($P = 0.33$) | 0.515 ($P = 0.03$) |
| Date of physical spring transition | | |
| Murrelet density | 0.320 ($P = 0.20$) | |
| Murrelet productivity | 0.611 ($P = 0.007$) | |

## DISCUSSION

### Murrelet Density

Annually, murrelet density on our transects in the San Juan Islands averaged 8 murrelets km$^{-2}$ and was as high as 28 murrelets km$^{-2}$ for some of the more heavily used areas, such as the southern portion of Lopez Island. Density estimates from our study are within the range of those reported by Falxa et al. (2016) for the San Juan Islands for NWFP at-sea surveys in Washington ($\bar{x} = 3.8$, range: 0.0–47.2 murrelets km$^{-2}$). With the exception of high murrelet densities along the central Oregon coast ($\bar{x} = 22.2$, range: 0.8–51.7 murrelets km$^{-2}$) and Strait of Juan de Fuca, Washington ($\bar{x} = 12.9$, range: 0.4–36.0 murrelets km$^{-2}$), the densities that we report are among the highest reported from Washington to California. This confirms that

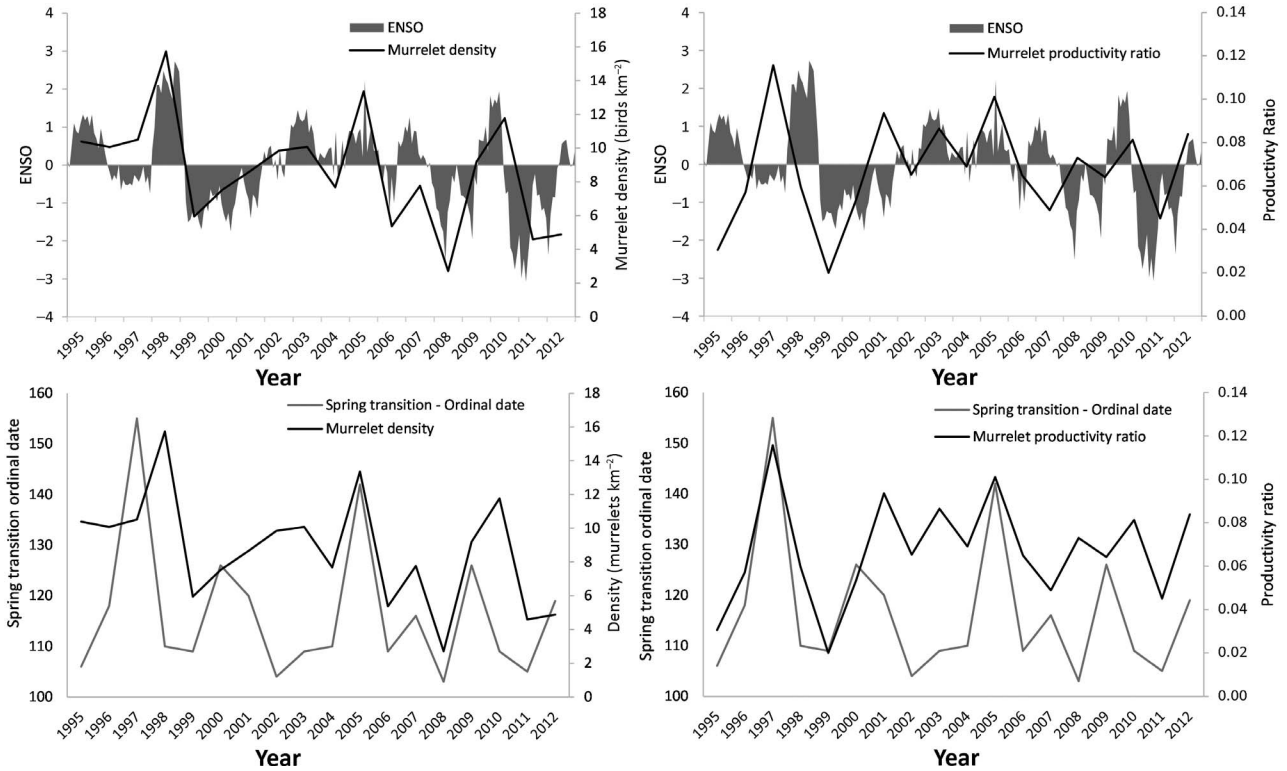


**FIGURE 4.** Relationships between Marbled Murrelet density (left) and productivity (right) and the El Niño Southern Oscillation (ENSO; top) and date of physical spring transition (ordinal date; bottom) in the San Juan Islands, Washington, USA, 1995 to 2012. Ordinal date 100 = April 10 and ordinal date 160 = June 9 (except in leap years).

portions of the San Juan Islands provide valuable marine habitat for Marbled Murrelets in the threatened portion of their U.S. range.

Within years, murrelet densities during our surveys in the San Juan Islands typically increased from May through August, likely due to 3 factors: (1) cessation of incubation by breeding adults, (2) fledging of juveniles, and (3) postbreeding immigration of adults and juveniles, presumably from British Columbia and other parts of Washington. The timing of incubation and fledging in this region is relatively well documented, based on observations at nest sites and radio-telemetry. Most incubation in Washington and British Columbia is completed by early July and most juveniles fledge by mid-August, which corresponds to the increases in density that we observed from mid-July onward. The timing and rates of immigration are not well understood and likely vary among years. While rates of immigration have not been quantified, murrelet immigration to and from the San Juan Islands has been documented by banding and telemetry studies. Beauchamp et al. (1999) noted a banded murrelet that traveled to and from the San Juan Islands and Desolation Sound, British Columbia (~200 km distant), though the exact timing of the immigration and emigration events for this individual were unknown. Lorenz et al. (2017) described the use of the San Juan Islands by radio-tagged murrelets captured along Washington's mainland coastline. Murrelets captured from multiple locations used the San Juan Islands, including birds captured in the Pacific Ocean (~200 km distant via water), Strait of Juan de Fuca (30–120 km distant), and Hood Canal–Admiralty Inlet (20–100 km distant). In that study, breeding murrelets also used the San Juan Islands, although no nests were found on the San Juan Islands themselves. Murrelets nesting on Vancouver Island, British Columbia, and the Olympic Peninsula, Washington, visited the San Juan Islands during the daytime, presumably to forage. This underscores the value of the San Juan Islands to providing marine foraging habitat for breeding murrelets in Washington.

The pattern of increasing murrelet density from May to August was consistent year-to-year; we observed it in all years except 2005. In 2005, murrelet densities were high in May and did not change appreciably from May to August (Appendix Table 4), resulting in a high density estimate for that year (13.4 murrelets km$^{-2}$) compared with other years (8.7 murrelets km$^{-2}$). Productivity ratios in 2005 were also relatively high, perhaps due to higher-than-average immigration of juveniles into the region. Years 1998 and 2010 also had high overall densities of murrelets (15.7 and 11.7 murrelets km$^{-2}$, respectively), although within those years

density increased following the usual pattern from May to August and productivity ratios were not especially high.

The 3 yr with the highest murrelet densities overall (1998, 2005, and 2010) also had anomalous oceanic conditions that may have affected murrelet use of the San Juan Islands. The winters preceding the 1998 and 2010 breeding seasons were strong El Niño years and in the spring of 2005 there was delayed upwelling. All 3 of these events (1998 and 2010 El Niño events and 2005 delayed upwelling) caused disruptions in marine systems throughout the California Current and affected a range of taxa, including seabirds (cormorants: Jones et al. 2008; auklets: Bertram et al. 2005, Wilson 2005; boobies: Cubaynes et al. 2011). For example, following the 1998 El Niño event, Bertram et al. (2005) observed reduced burrow occupancy and survival rates of Cassin's Auklets (*Ptychoramphus aleuticus*) in British Columbia, and Wilson (2005) noted reduced chick growth rates in Rhinoceros Auklets (*Cerorhinca monocerata*) in Washington. Reductions or changes in zooplankton and fish prey during El Niño events (Peterson et al. 2002, Black et al. 2010) are thought to cause poor seabird reproduction in these years. For Marbled Murrelets, we suspect that densities in the San Juan Islands increased in 1998, 2005, and 2010 because of emigration of murrelets from the Pacific Ocean. This is supported by telemetry data from 2004 to 2008 in this region. Lorenz et al. (2017) reported that 58% of 40 radio-tagged murrelets used the San Juan Islands in 2005, while none were captured there (compared with 29% of 117 tagged murrelets that used the islands across other years). Unfortunately, our murrelet surveys in the San Juan Islands ended in 2012, precluding analyses of murrelet responses to anomalous oceanic conditions in 2014 and 2016.

In addition to the peaks in murrelet densities that we observed in 1998, 2005, and 2010, in general we saw a strong correlation between murrelet densities and winter ENSO conditions; murrelet densities increased in years of stronger ENSO events and decreased in years with weaker ENSO indices. Strong ENSO events typically cause warm water to accumulate along the western coast of North America, which is considered poor for marine productivity. These conditions may force murrelets to search elsewhere for food and may bring large numbers of birds into inland waters that are less affected by oceanic conditions. The San Juan Islands are buffered somewhat from the Pacific Ocean by the ~100-km long Strait of Juan de Fuca. They are close in proximity to multiple large rivers that drain from the Cascade Range or Rocky Mountains, including the Fraser, Nooksack, and Skagit rivers. The islands are also surrounded by relatively strong and complex tidal currents compared with many marine areas along the Pacific coast of Washington and British Columbia (Mackas and Harrison 1997). Overall, marine conditions in the San Juan Islands differ from those along the outer coast and may provide alternative habitat for murrelets in years when prey is reduced by strong winter ENSO conditions or delayed upwellings. This should be examined in future studies of murrelet diet and prey in the San Juan Islands vs. along the Pacific coast, and it may change in the future if foraging conditions in the Salish Sea are altered by climate change (Ruckelshaus and McClure 2007).

### Temporal Trends in Density and Productivity

Over our 18 yr of surveys, we documented an overall declining trend in murrelet density, with an annual rate of decline of ~3.9% (95% CI: –5.7% to –0.4%). This rate of decline is numerically close to rates of decline estimated for this region from NWFP at-sea surveys, and within the 95% confidence interval of those estimates. Falxa et al. (2016) reported a decline of 3.9% (95% CI: –7.6% to 0.0%) between 2001 and 2013 for conservation zone 1 in Washington, which includes the San Juan Islands and the Strait of Juan de Fuca, and a decline of 4.6% (95% CI: –7.5% to –1.5%) for all of Washington State, including the outer coast. These estimates were obtained from at-sea surveys, although they used slightly different survey methodology than that used in our study. Surveys reported by Falxa et al. (2016) were conducted using a more complicated design, with inshore and offshore units (ranging from 100 m to 2,000 m offshore from the San Juan Islands; Miller et al. 2006), and covered a different portion of the shoreline of the San Juan Islands (Miller et al. 2006). Their estimates were also derived from surveys completed in different time intervals: May 15 to July 31, 2001–2013 (Falxa et al. 2016), compared with May 12 to August 31, 1995–2012 (this study). Thus, these 2 datasets complement, but do not duplicate, each other. The nearly identical declining trend from these 2 survey efforts is striking and ominous; 2 independent datasets show a numerically equivalent and significant decline, despite protections for Marbled Murrelets enacted in the NWFP. It is also notable that our estimated decline is within the 95% credibility interval of declines reported by Bertram et al. (2015) in southern British Columbia using radar counts. Bertram et al. (2015) estimated declines in Marbled Murrelets for the southern mainland coast of British Columbia of between –0.058 and –0.005 for the years 1996–2013. These regional declines may be due to many factors that have been discussed elsewhere (e.g., COSEWIC 2012, Miller et al. 2012, Bertram et al. 2015), including continued declines in nesting habitat (Raphael et al. 2016), nest predation (Nelson and Hamer 1995, Hébert and Golightly 2007), declines in higher trophic-level prey (Norris et al. 2007, Gutowsky et al. 2009), fisheries bycatch (Smith and Morgan 2005, Piatt et al. 2007), or a combination of these factors.

While our surveys were less extensive than NWFP and radar surveys, which cover most of Washington, Oregon, and California (Raphael et al. 2007) and British Columbia

(Bertram et al. 2015), respectively, our surveys are valuable for providing estimates of murrelet productivity, which are not available from these other efforts. This can provide insight into the extent to which declines in murrelet reproduction are driving declining trends. We observed no evidence of a decline in murrelet productivity ratios from 1995 to 2012 and no evidence of a decline in juvenile densities; declines in overall murrelet densities from 1995 to 2012 were due to declines in adult densities only. Thus, productivity ratios and juvenile densities appear stable around transects in the San Juan Islands.

Corrected annual productivity ratios from our surveys averaged 0.067, which was generally higher than those reported for Oregon (annual means of 0.015–0.045; Strong 2015, 2016) and California (annual mean of 0.032 reported by Peery et al. (2007) for central California, 0.043 reported by Strong (2014) for southern Oregon–northern California). Uncorrected productivity ratios ranged from 0.042 to 0.054 in our study, depending on the dates used to estimate the ratio. These uncorrected ratios were lower than those reported for Alaska by Kuletz and Piatt (1999; 0.16) but similar to those for Alaska reported by Kuletz and Kendall (1998; 0.054) and for British Columbia by Lougheed et al. (2002; 0.04). This indicates relatively high productivity ratios for murrelets using the San Juan Islands compared with more southerly populations. This result was surprising. In a concurrent telemetry study, we observed low rates of murrelet breeding propensity (proportion of adults that attempted to nest) compared with rates in other studies from California to Alaska (Lorenz et al. 2017). Thus, we expected low productivity ratios in the San Juan Islands compared with ratios in California, Oregon, and British Columbia. We suggest 4 potential explanations for our higher-than-expected productivity ratios: (1) juveniles are immigrating to the San Juan Islands from British Columbia or other parts of Washington at higher rates than adults; (2) estimates of breeding propensity from Lorenz et al. (2017) are biased; (3) breeding propensity is low, but breeding success is high for breeders that attempt to nest; or (4) the number of breeding adults has not declined in the region, while nonbreeding adults have declined.

If juveniles are immigrating into the San Juan Islands from other populations and inflating our productivity ratios, the most likely major source populations are in British Columbia or on the Olympic Peninsula of Washington. While immigration of adults from both of these areas has been observed, juvenile immigration has not been specifically documented and would be extremely difficult to quantify, given the difficulty of finding and accessing nests (for banding and/or radio-tagging juveniles). Telemetry studies with juveniles captured on the water (presumably near natal sites) provide evidence for postfledging dispersal in young murrelets (Lougheed et al. 2002, Parker et al 2003), but these studies have not attempted to track juveniles over long distances and have not documented juvenile movements to the San Juan Islands. Therefore, while juvenile immigration is likely (given current information on the species' natural history) and adult immigration has been documented, we have no estimates of immigration rates to the San Juan Islands for either juveniles or adults.

A second possibility is that reproduction in Washington is not compromised and the low breeding propensity reported by Lorenz et al. (2017) was due to transmitters negatively affecting reproduction. However, other studies estimating murrelet breeding propensity have used similar tracking devices (e.g., Hull et al. 2001, Bradley et al. 2004, McFarlane Tranquilla et al. 2005, Hébert and Golightly 2008, Peery et al. 2009, Barbaree et al. 2014). Thus, while transmitters may affect breeding, comparisons of breeding propensity among these studies should not be biased because all studies have used transmitters, with slight variation in transmitter attachment methods, capture methods, and transmitter weight. The possibility that breeding success in our region is high is difficult to assess because of extremely small sample sizes of nests, but seems unlikely given the available information. In the study of Lorenz et al. (2017), only 4 of 20 breeders successfully fledged young (2.5% of 157 tagged murrelets). With this in mind, we suggest that the most likely explanations for stable productivity ratios in our surveys (and stable juvenile densities, 1995–2012) are that juveniles are immigrating into the San Juan Islands from other areas of Washington or from British Columbia at higher rates than adults, or that nonbreeding adults are declining in the region (while breeding adult numbers are stable). We hasten to add that these hypotheses should be tested with future studies before they are considered definitive explanations.

These uncertainties, and the large confidence intervals associated with our estimates of productivity and density, underscore the challenges of studying Marbled Murrelets. Numerous attributes of their life history are difficult to observe and quantify. While at sea, individuals move throughout the nearshore environment, and in a single breeding season may range over hundreds of square kilometers of shoreline (McFarlane Tranquilla et al. 2005, Hébert and Golightly 2008, Peery et al. 2009, Barbaree et al. 2015), presumably tracking prey availability, but contributing to large variation in at-sea counts. Unlike many seabirds, nests are widely dispersed and cryptic. Nests are also extremely difficult to access, being high in the canopy of large trees, making robust estimates of nest success nearly impossible with current technology. Given these challenges, as new data and survey methods become available, our estimates of productivity and density in the San Juan Islands should be revised. Moreover, assessments

of trends should be made with an understanding of the challenges of monitoring murrelets. For more accurately monitoring trends in density, larger-scale survey efforts that simultaneously track murrelet abundances throughout their range (i.e. from Alaska to California) are needed. For monitoring productivity, at-sea surveys of productivity are necessary because studies of breeding success using monitored nests are not realistic at this time. Studies of juvenile movements would be ideal (assuming that they are not detrimental to survival) and would shed light on whether productivity ratios in the San Juan Islands are high due to juvenile immigration. Without such information, there will be a high degree of uncertainty when assessing whether observed declines in Washington are due to poor local reproduction or other factors such as emigration or mortality of adults. Thus, while a simplistic interpretation of our study results indicates that reproductive output is stable for murrelets using the San Juan Islands, we do not have a high level of confidence in this interpretation.

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**Ethics statement:** Wild birds were not handled in this study and no formal ethical procedures or permissions were needed.

**Author contributions:** M.G.R. conceived the idea and design for the study and developed the methods. T.J.L. analyzed the data and wrote the paper.

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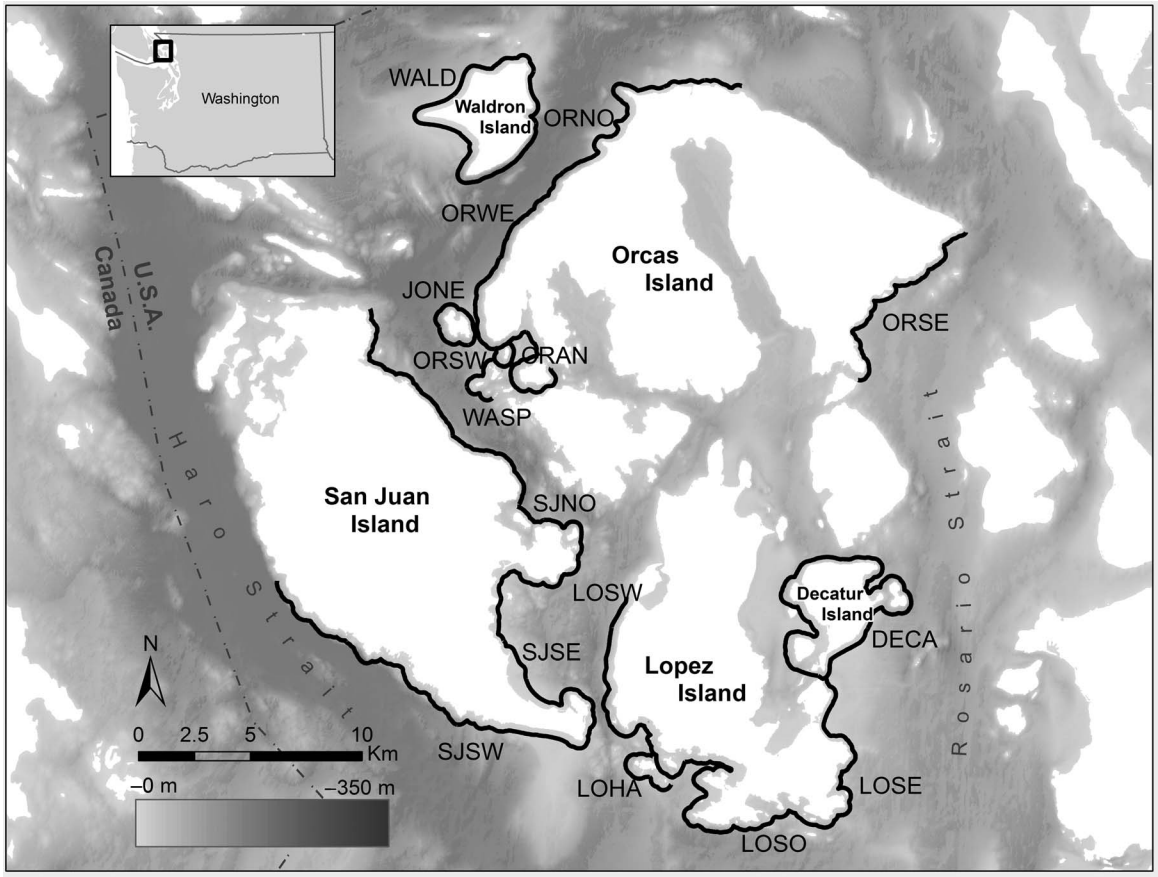
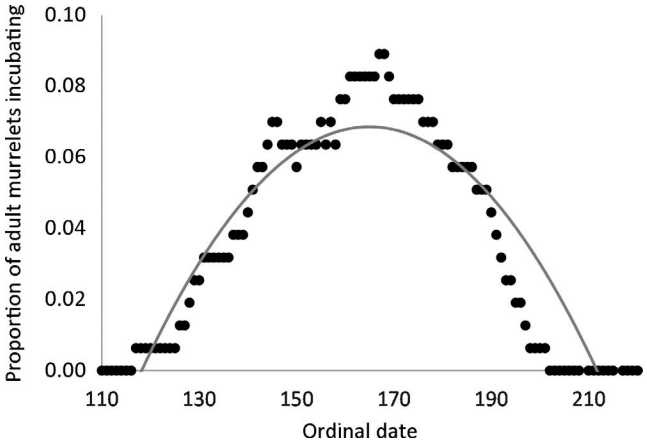


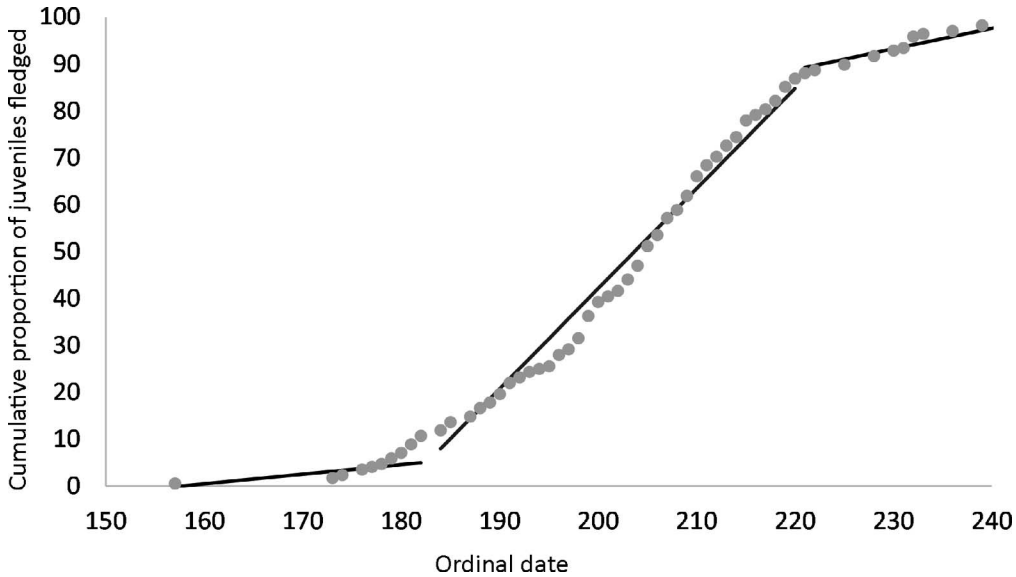

**APPENDIX FIGURE 5.** Layout of 16 transects (solid black lines and 4-letter codes) surveyed for Marbled Murrelets in the San Juan Islands, Washington, USA, 1995 to 2012, with bathymetry. Transect length varied from 4 km (CRAN, LOHA, and ORSW) to 22 km (DECA) and is summarized in Appendix Table 3.

**APPENDIX TABLE 3.** Lengths of the 16 transects surveyed for Marbled Murrelets in our study in the San Juan Islands, Washington, USA, 1995–2012, and number of 2-km segments associated with each transect.

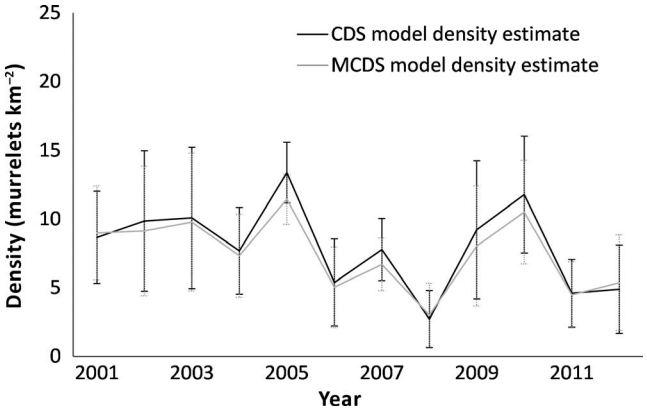
| Survey area | Transect name | Distance surveyed (km) | Number of 2-km segments |
|---|---|---|---|
| Crane Island | CRAN | 4 | 2 |
| Jones Island | JONE | 6 | 3 |
| Decatur Island | DECA | 22 | 11 |
| Long and Hat islands | LOHA | 4 | 2 |
| Lopez Island southeast | LOSE | 8 | 4 |
| Lopez Island south | LOSO | 10 | 5 |
| Lopez Island southwest | LOSW | 14 | 7 |
| Orcas Island north | ORNO | 6 | 3 |
| Orcas Island southeast | ORSE | 8 | 4 |
| Orcas Island southwest | ORSW | 4 | 2 |
| Orcas Island west | ORWE | 14 | 7 |
| San Juan Island north | SJNO | 12 | 6 |
| San Juan Island southeast | SJSE | 18 | 9 |
| San Juan Island southwest | SJSW | 18 | 9 |
| Waldron Island | WALD | 16 | 8 |
| Wasp Islands | WASP | 6 | 3 |
| Total | 16 | 170 | 85 |



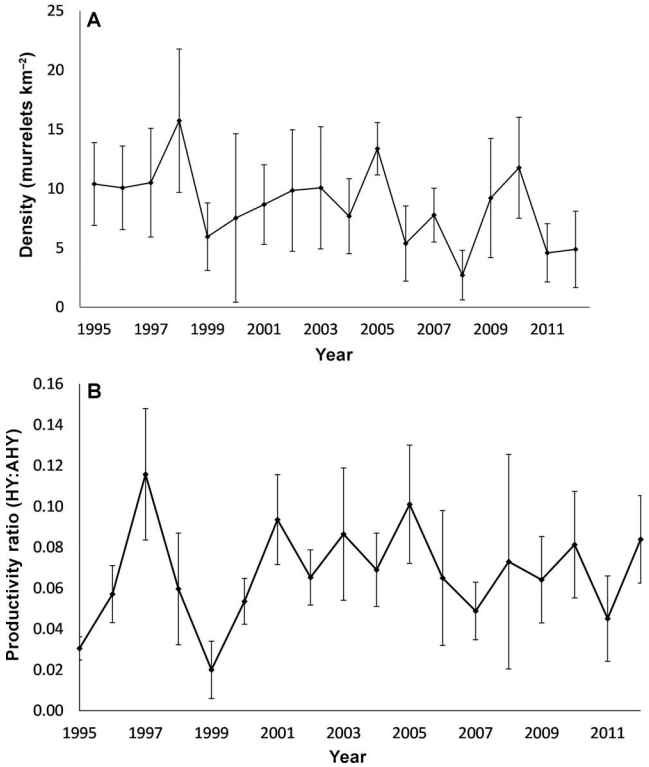

**APPENDIX FIGURE 6.** To correct our productivity ratios to account for adult Marbled Murrelets missing from at-sea surveys during the incubation period, we estimated the proportion of incubating murrelets within our study population each day using data from a sample of radio-tagged murrelets tracked from 2004 to 2008 in Washington, USA (Lorenz et al. 2017). This figure shows the proportion of radio-tagged Marbled Murrelets ($n = 157$) incubating on each ordinal date during our survey period (black circles), and best-fit regression line for the proportion of incubating murrelets by ordinal date (gray line; proportion of incubating murrelets $= -3.139 \times 10^{-5}(x^2) + 0.01036x - 0.7855$). Ordinal date 110 = April 20 and ordinal date 220 = August 8 (except in leap years).




**APPENDIX FIGURE 7.** To correct our productivity ratios to account for juvenile Marbled Murrelets that had not yet fledged by the end of our survey period each year (August 29), we computed the cumulative proportion of juvenile murrelets fledged for each ordinal date using known fledging dates ($n = 167$) from 4 other sources: (1) breeding records (Hamer and Nelson 1995; $n = 35$ dates), (2) telemetry data from British Columbia, Canada (Bradley 2002, Bradley et al. 2004; $n = 99$ dates), (3) at-sea survey data for Washington, USA (M. G. Raphael personal observation; $n = 4$ dates), and (4) nests found in Washington and British Columbia (S. K. Nelson personal communication; $n = 29$ dates). This figures shows the cumulative proportion of juvenile murrelets fledged for each ordinal date in our study (gray circles) and the best-fit regression line for the cumulative proportion of murrelets fledged for 3 time periods: (1) early (ordinal date $< 180$; $0.204x - 32.11$), (2) mid (ordinal date = 180–220; $2.133x - 384.477$), and (3) late (ordinal date $>$ 220; $0.44x - 7.977$). Ordinal date 150 = May 30 and ordinal date 240 = August 28 (except in leap years).




**APPENDIX FIGURE 8.** Comparison of Marbled Murrelet density estimates (juveniles and adults combined) and 95% confidence intervals generated from program Distance from a model that included Beaufort sea state (gray line; MCDS model density estimate) and from a model that did not include Beaufort sea state (black line; CDS model density estimate) as a covariate. Data are densities of murrelets from at-sea surveys conducted in the San Juan Islands, Washington, USA, 2001 to 2012. We restricted this analysis to the years 2001 to 2012 because Beaufort sea state was not consistently recorded during our surveys before 2001.




**APPENDIX FIGURE 9.** Annual estimates with 95% confidence intervals of Marbled Murrelet (**A**) density (juveniles and adults combined) and (**B**) productivity (ratio estimated using the methods of Peery et al. [2007]) calculated from at-sea surveys in the San Juan Islands, Washington, USA, 1995–2012.

**APPENDIX TABLE 4.** Summary of densities of adult and juvenile Marbled Murrelets (mean and standard deviation) during each 10-day interval in the San Juan Islands, Washington, USA, 1995–2012, and total area surveyed in each interval and year. Our goal was to repeatedly survey all transects once every 10 days, for a total of 11 repeat 'intervals' each year. For various reasons, however, not all 10-day intervals were surveyed each year. For example, in 1995 and 1996, 54% and 34% of segments were skipped because a definitive protocol had not been established for these initial years. In 2000, 55% of segments were skipped while effort was devoted to the implementation of Northwest Forest Plan (NWFP) at-sea surveys (Miller et al. 2006). In 2012, surveys were skipped in interval 8 because of mechanical problems with one of the survey boats. In most other years, observers completed surveys on all segments.

| Year | Interval | Dates | Mean adult density | SD adult density | Mean juvenile density | SD juvenile density | Mean murrelet density | SD murrelet density | Area surveyed ($km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| 1995 | 7 | June 21 to June 30 | 16.11 | 39.03 | 0.00 | 0.00 | 16.11 | 39.03 | 54.00 |
| | 8 | July 1 to July 10 | 7.58 | 21.70 | 0.00 | 0.00 | 7.58 | 21.70 | 34.56 |
| | 9 | July 11 to July 20 | 5.82 | 13.48 | 0.00 | 0.00 | 5.82 | 13.48 | 51.12 |
| | 10 | July 21 to July 30 | 8.88 | 16.58 | 0.21 | 1.18 | 9.09 | 17.07 | 52.56 |
| | 11 | July 31 to August 9 | 15.29 | 23.08 | 0.32 | 1.38 | 15.61 | 23.54 | 41.04 |
| | 12 | August 10 to August 19 | 21.98 | 41.33 | 0.67 | 1.97 | 22.65 | 42.30 | 42.48 |
| | 13 | August 20 to August 29 | 17.31 | 41.28 | 0.07 | 0.46 | 17.38 | 41.57 | 31.68 |
| 1995 total | | | 13.03 | 29.96 | 0.18 | 1.04 | 13.21 | 30.31 | 307.44 |
| 1996 | 7 | June 21 to June 30 | 6.10 | 14.00 | 0.00 | 0.00 | 6.10 | 14.00 | 61.20 |
| | 8 | July 1 to July 10 | 4.66 | 11.37 | 0.00 | 0.00 | 4.66 | 11.37 | 61.20 |
| | 9 | July 11 to July 20 | 7.14 | 16.16 | 0.07 | 0.47 | 7.22 | 16.17 | 61.20 |
| | 10 | July 21 to July 30 | 6.60 | 10.92 | 0.36 | 1.20 | 6.96 | 11.51 | 61.20 |
| | 11 | July 31 to August 9 | 15.55 | 26.82 | 0.47 | 1.30 | 16.02 | 27.49 | 61.20 |
| | 12 | August 10 to August 19 | 19.20 | 41.67 | 0.25 | 1.08 | 19.45 | 41.81 | 61.20 |
| | 13 | August 20 to August 29 | 25.73 | 50.08 | 0.14 | 0.94 | 25.87 | 50.14 | 61.20 |
| 1996 total | | | 12.14 | 29.29 | 0.19 | 0.89 | 12.33 | 29.47 | 428.40 |
| 1997 | 5 | June 1 to June 10 | 4.27 | 11.62 | 0.00 | 0.00 | 4.27 | 11.62 | 61.20 |
| | 6 | June 11 to June 20 | 5.40 | 23.07 | 0.00 | 0.00 | 5.40 | 23.07 | 61.20 |
| | 7 | June 21 to June 30 | 5.40 | 23.11 | 0.00 | 0.00 | 5.40 | 23.11 | 61.20 |
| | 8 | July 1 to July 10 | 3.46 | 10.32 | 0.00 | 0.00 | 3.46 | 10.32 | 61.20 |
| | 9 | July 11 to July 20 | 4.23 | 9.48 | 0.49 | 2.42 | 4.72 | 10.57 | 61.20 |
| | 10 | July 21 to July 30 | 8.86 | 21.76 | 0.45 | 1.99 | 9.31 | 23.02 | 61.20 |
| | 11 | July 31 to August 9 | 17.59 | 49.91 | 1.17 | 4.00 | 18.76 | 51.29 | 61.20 |
| | 12 | August 10 to August 19 | 18.22 | 39.10 | 1.62 | 6.03 | 19.84 | 44.19 | 61.20 |
| | 13 | August 20 to August 29 | 28.93 | 58.09 | 1.03 | 5.55 | 29.97 | 61.94 | 61.20 |
| 1997 total | | | 10.71 | 33.00 | 0.53 | 3.25 | 11.24 | 34.91 | 550.80 |
| 1998 | 5 | June 1 to June 10 | 2.76 | 7.19 | 0.00 | 0.00 | 2.76 | 7.19 | 61.20 |
| | 6 | June 11 to June 20 | 4.76 | 12.46 | 0.00 | 0.00 | 4.76 | 12.46 | 61.20 |
| | 7 | June 21 to June 30 | 9.30 | 23.11 | 0.04 | 0.39 | 9.34 | 23.11 | 61.20 |
| | 8 | July 1 to July 10 | 13.93 | 26.21 | 0.47 | 1.34 | 14.39 | 27.07 | 61.20 |
| | 9 | July 11 to July 20 | 16.65 | 27.65 | 0.38 | 1.12 | 17.03 | 28.07 | 61.20 |
| | 10 | July 21 to July 30 | 15.37 | 29.21 | 1.27 | 4.00 | 16.65 | 32.34 | 61.20 |
| | 11 | July 31 to August 9 | 20.81 | 36.40 | 0.89 | 2.08 | 21.70 | 37.46 | 61.20 |
| | 12 | August 10 to August 19 | 33.42 | 76.31 | 0.42 | 1.80 | 33.84 | 77.31 | 61.20 |
| | 13 | August 20 to August 29 | 46.96 | 104.31 | 0.00 | 0.00 | 46.96 | 104.31 | 61.20 |
| 1998 total | | | 18.22 | 49.94 | 0.39 | 1.77 | 18.60 | 50.49 | 550.80 |
| 1999 | 3 | May 12 to May 21 | 0.52 | 2.34 | 0.00 | 0.00 | 0.52 | 2.34 | 61.20 |
| | 4 | May 22 to May 31 | 5.25 | 20.52 | 0.00 | 0.00 | 5.25 | 20.52 | 61.20 |
| | 5 | June 1 to June 10 | 3.76 | 11.15 | 0.00 | 0.00 | 3.76 | 11.15 | 54.72 |
| | 6 | June 11 to June 20 | 3.09 | 6.80 | 0.00 | 0.00 | 3.09 | 6.80 | 61.20 |
| | 7 | June 21 to June 30 | 3.91 | 11.27 | 0.03 | 0.25 | 3.94 | 11.29 | 61.20 |
| | 8 | July 1 to July 10 | 2.60 | 6.84 | 0.00 | 0.00 | 2.60 | 6.84 | 61.20 |
| | 9 | July 11 to July 20 | 3.48 | 11.25 | 0.11 | 0.61 | 3.58 | 11.61 | 61.20 |
| | 10 | July 21 to July 30 | 8.10 | 17.14 | 0.22 | 0.99 | 8.32 | 17.53 | 61.20 |
| | 11 | July 31 to August 9 | 14.56 | 25.32 | 0.03 | 0.25 | 14.59 | 25.33 | 61.20 |
| | 12 | August 10 to August 19 | 15.84 | 30.60 | 0.05 | 0.35 | 15.90 | 30.74 | 61.20 |
| | 13 | August 20 to August 29 | 19.18 | 50.10 | 0.41 | 1.30 | 19.59 | 50.70 | 61.20 |
| 1999 total | | | 7.33 | 22.68 | 0.08 | 0.56 | 7.41 | 22.89 | 666.72 |

**APPENDIX TABLE 4.** Continued.

| Year | Interval | Dates | Mean adult density | SD adult density | Mean juvenile density | SD juvenile density | Mean murrelet density | SD murrelet density | Area surveyed ($km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| 2000 | 5 | June 1 to June 10 | 0.89 | 3.55 | 0.00 | 0.00 | 0.89 | 3.55 | 61.20 |
| | 7 | June 21 to June 30 | 3.19 | 9.89 | 0.00 | 0.00 | 3.19 | 9.89 | 61.20 |
| | 9 | July 11 to July 20 | 2.38 | 7.22 | 0.00 | 0.00 | 2.38 | 7.22 | 61.20 |
| | 11 | July 31 to August 9 | 16.77 | 32.99 | 0.52 | 1.56 | 17.29 | 33.99 | 61.20 |
| | 12 | August 10 to August 19 | 23.34 | 38.61 | 1.32 | 3.27 | 24.67 | 40.91 | 61.20 |
| 2000 total | | | 9.31 | 25.00 | 0.37 | 1.69 | 9.68 | 26.15 | 306.00 |
| 2001 | 3 | May 12 to May 21 | 4.56 | 16.31 | 0.00 | 0.00 | 4.56 | 16.31 | 61.20 |
| | 4 | May 22 to May 31 | 6.02 | 22.42 | 0.00 | 0.00 | 6.02 | 22.42 | 61.20 |
| | 5 | June 1 to June 10 | 5.33 | 15.54 | 0.00 | 0.00 | 5.33 | 15.54 | 61.20 |
| | 6 | June 11 to June 20 | 3.41 | 13.15 | 0.00 | 0.00 | 3.41 | 13.15 | 58.32 |
| | 7 | June 21 to June 30 | 4.95 | 12.44 | 0.06 | 0.39 | 5.01 | 12.48 | 61.20 |
| | 8 | July 1 to July 10 | 5.45 | 14.35 | 0.15 | 0.82 | 5.60 | 14.87 | 61.20 |
| | 9 | July 11 to July 20 | 7.00 | 15.42 | 0.30 | 1.20 | 7.30 | 16.07 | 61.20 |
| | 10 | July 21 to July 30 | 7.87 | 16.80 | 0.77 | 2.76 | 8.64 | 18.67 | 61.20 |
| | 11 | July 31 to August 9 | 19.40 | 29.33 | 1.16 | 3.96 | 20.56 | 31.25 | 61.20 |
| | 12 | August 10 to August 19 | 21.96 | 36.49 | 1.16 | 3.28 | 23.13 | 38.84 | 61.20 |
| | 13 | August 20 to August 29 | 19.91 | 44.90 | 1.04 | 2.93 | 20.95 | 46.20 | 61.20 |
| 2001 total | | | 9.65 | 24.72 | 0.42 | 2.07 | 10.08 | 25.77 | 670.32 |
| 2002 | 3 | May 12 to May 21 | 2.92 | 8.88 | 0.00 | 0.00 | 2.92 | 8.88 | 61.20 |
| | 4 | May 22 to May 31 | 6.10 | 19.64 | 0.00 | 0.00 | 6.10 | 19.64 | 61.20 |
| | 5 | June 1 to June 10 | 2.62 | 8.75 | 0.00 | 0.00 | 2.62 | 8.75 | 61.20 |
| | 6 | June 11 to June 20 | 3.73 | 9.49 | 0.00 | 0.00 | 3.73 | 9.49 | 61.20 |
| | 7 | June 21 to June 30 | 3.58 | 11.50 | 0.00 | 0.00 | 3.58 | 11.50 | 61.20 |
| | 8 | July 1 to July 10 | 5.65 | 19.16 | 0.15 | 0.67 | 5.80 | 19.66 | 61.20 |
| | 9 | July 11 to July 20 | 8.61 | 20.07 | 0.33 | 1.19 | 8.94 | 20.77 | 61.20 |
| | 10 | July 21 to July 30 | 8.16 | 19.55 | 0.44 | 2.01 | 8.61 | 20.90 | 61.20 |
| | 11 | July 31 to August 9 | 25.45 | 45.20 | 1.03 | 3.26 | 26.49 | 47.34 | 61.20 |
| | 12 | August 10 to August 19 | 18.36 | 44.49 | 0.70 | 1.96 | 19.06 | 45.60 | 61.20 |
| | 13 | August 20 to August 29 | 34.28 | 64.94 | 4.43 | 18.80 | 38.72 | 75.86 | 61.20 |
| 2002 total | | | 10.86 | 31.86 | 0.64 | 5.93 | 11.51 | 34.82 | 673.20 |
| 2003 | 3 | May 12 to May 21 | 1.53 | 3.94 | 0.03 | 0.27 | 1.56 | 4.07 | 61.20 |
| | 4 | May 22 to May 31 | 3.06 | 6.92 | 0.03 | 0.27 | 3.09 | 7.00 | 61.20 |
| | 5 | June 1 to June 10 | 2.59 | 6.54 | 0.00 | 0.00 | 2.59 | 6.54 | 61.20 |
| | 6 | June 11 to June 20 | 1.02 | 2.56 | 0.00 | 0.00 | 1.02 | 2.56 | 51.12 |
| | 7 | June 21 to June 30 | 4.83 | 10.45 | 0.06 | 0.54 | 4.89 | 10.71 | 61.20 |
| | 8 | July 1 to July 10 | 5.19 | 11.83 | 0.21 | 0.79 | 5.39 | 12.32 | 61.20 |
| | 9 | July 11 to July 20 | 9.40 | 16.13 | 0.77 | 2.59 | 10.17 | 17.95 | 61.20 |
| | 10 | July 21 to July 30 | 15.94 | 37.94 | 0.85 | 3.22 | 16.79 | 38.97 | 61.20 |
| | 11 | July 31 to August 9 | 17.91 | 38.03 | 0.80 | 1.90 | 18.71 | 39.05 | 61.20 |
| | 12 | August 10 to August 19 | 24.16 | 42.71 | 0.88 | 1.67 | 25.05 | 43.64 | 61.20 |
| | 13 | August 20 to August 29 | 30.94 | 44.95 | 2.21 | 6.70 | 33.15 | 49.26 | 61.20 |
| 2003 total | | | 10.74 | 27.67 | 0.54 | 2.60 | 11.28 | 29.05 | 663.12 |
| 2004 | 3 | May 12 to May 21 | 0.83 | 2.55 | 0.00 | 0.00 | 0.83 | 2.55 | 61.20 |
| | 4 | May 22 to May 31 | 1.77 | 8.41 | 0.00 | 0.00 | 1.77 | 8.41 | 61.20 |
| | 5 | June 1 to June 10 | 2.06 | 7.01 | 0.00 | 0.00 | 2.06 | 7.01 | 61.20 |
| | 6 | June 11 to June 20 | 1.97 | 6.75 | 0.00 | 0.00 | 1.97 | 6.75 | 61.20 |
| | 7 | June 21 to June 30 | 8.48 | 22.39 | 0.00 | 0.00 | 8.48 | 22.39 | 61.20 |
| | 8 | July 1 to July 10 | 12.56 | 29.58 | 0.34 | 1.13 | 12.90 | 29.95 | 61.20 |
| | 9 | July 11 to July 20 | 7.62 | 15.56 | 0.40 | 1.98 | 8.02 | 16.89 | 61.20 |
| | 10 | July 21 to July 30 | 11.88 | 21.61 | 0.26 | 0.99 | 12.13 | 21.87 | 61.20 |
| | 11 | July 31 to August 9 | 13.42 | 27.06 | 0.51 | 1.72 | 13.93 | 27.98 | 61.20 |
| | 12 | August 10 to August 19 | 17.78 | 33.29 | 0.94 | 2.49 | 18.73 | 35.06 | 61.20 |
| | 13 | August 20 to August 29 | 27.20 | 67.74 | 4.37 | 10.54 | 31.57 | 75.09 | 61.20 |
| 2004 total | | | 9.60 | 29.01 | 0.62 | 3.58 | 10.22 | 31.24 | 673.20 |

**APPENDIX TABLE 4.** Continued.

| Year | Interval | Dates | Mean adult density | SD adult density | Mean juvenile density | SD juvenile density | Mean murrelet density | SD murrelet density | Area surveyed ($km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| 2005 | 3 | May 12 to May 21 | 13.82 | 31.38 | 0.00 | 0.00 | 13.82 | 31.38 | 61.20 |
| | 4 | May 22 to May 31 | 15.38 | 35.29 | 0.00 | 0.00 | 15.38 | 35.29 | 61.20 |
| | 5 | June 1 to June 10 | 16.16 | 33.27 | 0.00 | 0.00 | 16.16 | 33.27 | 61.20 |
| | 6 | June 11 to June 20 | 24.59 | 53.35 | 0.08 | 0.53 | 24.67 | 53.47 | 61.20 |
| | 7 | June 21 to June 30 | 19.90 | 29.87 | 0.41 | 1.37 | 20.31 | 30.54 | 61.20 |
| | 8 | July 1 to July 10 | 12.66 | 21.60 | 0.37 | 1.21 | 13.03 | 22.33 | 61.20 |
| | 9 | July 11 to July 20 | 15.99 | 25.45 | 0.70 | 2.28 | 16.69 | 26.69 | 61.20 |
| | 10 | July 21 to July 30 | 6.46 | 12.98 | 0.62 | 2.54 | 7.07 | 14.57 | 61.20 |
| | 11 | July 31 to August 9 | 11.02 | 25.55 | 0.29 | 1.23 | 11.31 | 26.43 | 61.20 |
| | 12 | August 10 to August 19 | 10.03 | 22.63 | 0.62 | 2.54 | 10.65 | 24.67 | 61.20 |
| | 13 | August 20 to August 29 | 17.52 | 32.57 | 1.23 | 3.61 | 18.75 | 34.90 | 61.20 |
| 2005 total | | | 14.87 | 31.21 | 0.39 | 1.84 | 15.26 | 31.91 | 673.20 |
| 2006 | 3 | May 12 to May 21 | 2.05 | 5.38 | 0.00 | 0.00 | 2.05 | 5.38 | 61.20 |
| | 4 | May 22 to May 31 | 1.11 | 3.49 | 0.00 | 0.00 | 1.11 | 3.49 | 61.20 |
| | 5 | June 1 to June 10 | 1.62 | 4.80 | 0.00 | 0.00 | 1.62 | 4.80 | 61.20 |
| | 6 | June 11 to June 20 | 2.62 | 5.62 | 0.00 | 0.00 | 2.62 | 5.62 | 61.20 |
| | 7 | June 21 to June 30 | 2.05 | 6.19 | 0.00 | 0.00 | 2.05 | 6.19 | 61.20 |
| | 8 | July 1 to July 10 | 0.68 | 2.64 | 0.11 | 0.74 | 0.79 | 2.99 | 61.20 |
| | 9 | July 11 to July 20 | 1.15 | 3.71 | 0.04 | 0.33 | 1.19 | 3.83 | 61.20 |
| | 10 | July 21 to July 30 | 5.17 | 15.85 | 0.04 | 0.33 | 5.21 | 15.84 | 61.20 |
| | 11 | July 31 to August 9 | 15.84 | 32.55 | 0.32 | 1.33 | 16.16 | 33.11 | 61.20 |
| | 12 | August 10 to August 19 | 15.01 | 47.88 | 1.58 | 4.18 | 16.60 | 48.67 | 61.20 |
| | 13 | August 20 to August 29 | 16.34 | 45.68 | 2.30 | 6.87 | 18.64 | 52.02 | 61.20 |
| 2006 total | | | 5.79 | 23.75 | 0.40 | 2.57 | 6.18 | 25.26 | 673.20 |
| 2007 | 3 | May 12 to May 21 | 10.25 | 35.09 | 0.00 | 0.00 | 10.25 | 35.09 | 61.20 |
| | 4 | May 22 to May 31 | 13.80 | 49.27 | 0.00 | 0.00 | 13.80 | 49.27 | 61.20 |
| | 5 | June 1 to June 10 | 4.54 | 13.24 | 0.00 | 0.00 | 4.54 | 13.24 | 61.20 |
| | 6 | June 11 to June 20 | 4.63 | 12.87 | 0.00 | 0.00 | 4.63 | 12.87 | 61.20 |
| | 7 | June 21 to June 30 | 4.32 | 12.05 | 0.00 | 0.00 | 4.32 | 12.05 | 61.20 |
| | 8 | July 1 to July 10 | 2.85 | 7.00 | 0.04 | 0.40 | 2.90 | 7.11 | 61.20 |
| | 9 | July 11 to July 20 | 3.68 | 9.64 | 0.13 | 0.89 | 3.81 | 10.07 | 61.20 |
| | 10 | July 21 to July 30 | 9.64 | 16.37 | 0.17 | 0.78 | 9.82 | 16.85 | 61.20 |
| | 11 | July 31 to August 9 | 8.13 | 11.90 | 0.43 | 1.54 | 8.56 | 12.42 | 61.20 |
| | 12 | August 10 to August 19 | 15.14 | 24.77 | 0.39 | 1.27 | 15.53 | 25.56 | 61.20 |
| | 13 | August 20 to August 29 | 16.69 | 24.49 | 0.48 | 1.48 | 17.17 | 24.69 | 61.20 |
| 2007 total | | | 8.52 | 23.54 | 0.15 | 0.85 | 8.67 | 23.73 | 673.20 |
| 2008 | 3 | May 12 to May 21 | 0.36 | 1.98 | 0.00 | 0.00 | 0.36 | 1.98 | 61.20 |
| | 4 | May 22 to May 31 | 1.29 | 4.93 | 0.00 | 0.00 | 1.29 | 4.93 | 61.20 |
| | 5 | June 1 to June 10 | 0.45 | 1.89 | 0.00 | 0.00 | 0.45 | 1.89 | 61.20 |
| | 6 | June 11 to June 20 | 0.42 | 2.34 | 0.00 | 0.00 | 0.42 | 2.34 | 61.20 |
| | 7 | June 21 to June 30 | 0.58 | 2.21 | 0.00 | 0.00 | 0.58 | 2.21 | 61.20 |
| | 8 | July 1 to July 10 | 0.23 | 0.87 | 0.03 | 0.30 | 0.26 | 0.91 | 61.20 |
| | 9 | July 11 to July 20 | 1.00 | 3.17 | 0.19 | 0.93 | 1.20 | 3.76 | 61.20 |
| | 10 | July 21 to July 30 | 1.91 | 5.79 | 0.10 | 0.66 | 2.01 | 5.80 | 61.20 |
| | 11 | July 31 to August 9 | 3.53 | 10.34 | 0.10 | 0.66 | 3.63 | 10.39 | 61.20 |
| | 12 | August 10 to August 19 | 8.00 | 21.37 | 0.16 | 0.78 | 8.16 | 21.41 | 61.20 |
| | 13 | August 20 to August 29 | 15.31 | 34.89 | 0.10 | 0.51 | 15.41 | 35.00 | 61.20 |
| 2008 total | | | 3.01 | 13.71 | 0.06 | 0.50 | 3.07 | 13.76 | 673.20 |

**APPENDIX TABLE 4.** Continued.

| Year | Interval | Dates | Mean adult density | SD adult density | Mean juvenile density | SD juvenile density | Mean murrelet density | SD murrelet density | Area surveyed ($km^2$) |
|---|---|---|---|---|---|---|---|---|---|
| 2009 | 3 | May 12 to May 21 | 1.94 | 7.32 | 0.00 | 0.00 | 1.94 | 7.32 | 61.20 |
| | 4 | May 22 to May 31 | 3.88 | 13.15 | 0.00 | 0.00 | 3.88 | 13.15 | 61.20 |
| | 5 | June 1 to June 10 | 8.04 | 32.38 | 0.00 | 0.00 | 8.04 | 32.38 | 61.20 |
| | 6 | June 11 to June 20 | 6.30 | 22.20 | 0.10 | 0.63 | 6.40 | 22.22 | 61.20 |
| | 7 | June 21 to June 30 | 2.28 | 9.07 | 0.10 | 0.89 | 2.37 | 9.77 | 61.20 |
| | 8 | July 1 to July 10 | 4.51 | 19.06 | 0.15 | 1.34 | 4.65 | 19.45 | 61.20 |
| | 9 | July 11 to July 20 | 5.57 | 23.15 | 0.29 | 1.66 | 5.86 | 23.98 | 61.20 |
| | 10 | July 21 to July 30 | 8.63 | 16.47 | 0.53 | 2.18 | 9.16 | 16.89 | 61.20 |
| | 11 | July 31 to August 9 | 9.84 | 25.50 | 0.34 | 1.71 | 10.18 | 26.53 | 61.20 |
| | 12 | August 10 to August 19 | 29.51 | 48.29 | 1.07 | 2.92 | 30.58 | 49.53 | 61.20 |
| | 13 | August 20 to August 29 | 27.62 | 45.87 | 1.50 | 4.40 | 29.12 | 47.42 | 61.20 |
| 2009 total | | | 9.83 | 28.51 | 0.37 | 1.98 | 10.20 | 29.28 | 673.20 |
| 2010 | 3 | May 12 to May 21 | 4.86 | 14.10 | 0.00 | 0.00 | 4.86 | 14.10 | 61.20 |
| | 4 | May 22 to May 31 | 7.56 | 28.07 | 0.00 | 0.00 | 7.56 | 28.07 | 61.20 |
| | 5 | June 1 to June 10 | 6.19 | 18.06 | 0.00 | 0.00 | 6.19 | 18.06 | 61.20 |
| | 6 | June 11 to June 20 | 6.64 | 20.34 | 0.04 | 0.38 | 6.69 | 20.59 | 61.20 |
| | 7 | June 21 to June 30 | 4.82 | 15.51 | 0.17 | 0.75 | 4.98 | 15.73 | 61.20 |
| | 8 | July 1 to July 10 | 10.22 | 26.40 | 0.37 | 1.72 | 10.59 | 27.34 | 61.20 |
| | 9 | July 11 to July 20 | 10.51 | 21.76 | 0.37 | 1.09 | 10.88 | 22.38 | 61.20 |
| | 10 | July 21 to July 30 | 15.95 | 27.00 | 1.37 | 3.41 | 17.32 | 29.17 | 61.20 |
| | 11 | July 31 to August 9 | 26.00 | 39.44 | 1.16 | 2.95 | 27.16 | 41.07 | 61.20 |
| | 12 | August 10 to August 19 | 23.17 | 43.72 | 0.83 | 2.70 | 24.00 | 45.47 | 61.20 |
| | 13 | August 20 to August 29 | 26.00 | 59.44 | 1.45 | 4.50 | 27.45 | 62.10 | 61.20 |
| 2010 total | | | 12.90 | 32.28 | 0.52 | 2.25 | 13.43 | 33.54 | 673.20 |
| 2011 | 3 | May 12 to May 21 | 1.33 | 4.94 | 0.00 | 0.00 | 1.33 | 4.94 | 61.20 |
| | 4 | May 22 to May 31 | 2.24 | 7.35 | 0.00 | 0.00 | 2.24 | 7.35 | 61.20 |
| | 5 | June 1 to June 10 | 2.00 | 7.27 | 0.09 | 0.81 | 2.09 | 7.85 | 61.20 |
| | 6 | June 11 to June 20 | 1.38 | 3.17 | 0.00 | 0.00 | 1.38 | 3.17 | 61.20 |
| | 7 | June 21 to June 30 | 2.27 | 7.23 | 0.00 | 0.00 | 2.27 | 7.23 | 61.20 |
| | 8 | July 1 to July 10 | 2.42 | 8.25 | 0.06 | 0.38 | 2.47 | 8.48 | 61.20 |
| | 9 | July 11 to July 20 | 2.00 | 5.72 | 0.12 | 0.66 | 2.12 | 6.08 | 61.20 |
| | 10 | July 21 to July 30 | 3.89 | 7.71 | 0.21 | 1.11 | 4.10 | 8.14 | 61.20 |
| | 11 | July 31 to August 9 | 8.28 | 15.80 | 0.18 | 0.85 | 8.46 | 16.18 | 61.20 |
| | 12 | August 10 to August 19 | 12.43 | 39.41 | 0.21 | 0.96 | 12.64 | 40.01 | 61.20 |
| | 13 | August 20 to August 29 | 15.73 | 37.75 | 3.71 | 12.57 | 19.44 | 48.54 | 61.20 |
| 2011 total | | | 4.91 | 18.57 | 0.42 | 3.96 | 5.32 | 21.09 | 673.20 |
| 2012 | 3 | May 12 to May 21 | 1.49 | 6.42 | 0.00 | 0.00 | 1.49 | 6.42 | 61.20 |
| | 4 | May 22 to May 31 | 2.51 | 9.84 | 0.03 | 0.25 | 2.53 | 9.93 | 61.20 |
| | 5 | June 1 to June 10 | 0.35 | 1.38 | 0.00 | 0.00 | 0.35 | 1.38 | 61.20 |
| | 6 | June 11 to June 20 | 1.41 | 4.81 | 0.05 | 0.49 | 1.47 | 5.20 | 61.20 |
| | 7 | June 21 to June 30 | 0.69 | 2.24 | 0.00 | 0.00 | 0.69 | 2.24 | 61.20 |
| | 8 | July 1 to July 10 | 0.53 | 2.20 | 0.04 | 0.28 | 0.57 | 2.46 | 46.08 |
| | 9 | July 11 to July 20 | 3.54 | 7.82 | 0.21 | 0.83 | 3.76 | 8.18 | 61.20 |
| | 10 | July 21 to July 30 | 5.06 | 11.80 | 0.19 | 0.63 | 5.25 | 11.86 | 61.20 |
| | 11 | July 31 to August 9 | 9.73 | 34.22 | 0.24 | 0.78 | 9.97 | 34.35 | 61.20 |
| | 12 | August 10 to August 19 | 17.03 | 34.91 | 1.47 | 5.23 | 18.50 | 39.34 | 61.20 |
| | 13 | August 20 to August 29 | 13.59 | 31.80 | 4.05 | 13.52 | 17.64 | 40.86 | 61.20 |
| 2012 total | | | 5.19 | 19.44 | 0.58 | 4.57 | 5.77 | 21.95 | 658.08 |
| Overall total | | | 9.57 | 28.34 | 0.39 | 2.83 | 9.96 | 29.54 | 10,860.48 |

**APPENDIX TABLE 5.** Transect-level estimates of juvenile and adult Marbled Murrelet densities and numbers (with 95% confidence intervals) in the San Juan Islands, Washington, USA, 1995–2012, in order of increasing adult densities.

| Transect | Adult density (murrelets km$^{-2}$) | Juvenile density (murrelets km$^{-2}$) | Adult numbers (95% CI) | Juvenile numbers (95% CI) |
|---|---|---|---|---|
| SJSE | 2.56 | 0.11 | 182 (149–216) | 8 (5–11) |
| ORSW | 3.76 | 0.03 | 60 (43–76) | 0 (0–1) |
| SJSW | 4.64 | 0.15 | 331 (278–384) | 10 (7–13) |
| DECA | 4.86 | 0.18 | 424 (357–491) | 15 (11–20) |
| ORWE | 5.24 | 0.13 | 290 (233–348) | 7 (4–10) |
| WALD | 5.34 | 0.23 | 339 (277–400) | 15 (9–21) |
| LOHA | 5.67 | 0.25 | 90 (68–111) | 4 (2–6) |
| JONE | 5.99 | 0.21 | 142 (105–180) | 5 (2–8) |
| ORNO | 7.22 | 0.23 | 172 (127–216) | 5 (0–11) |
| CRAN | 9.61 | 0.18 | 152 (92–213) | 3 (1–4) |
| LOSE | 12.20 | 0.95 | 387 (319–454) | 30 (14–46) |
| ORSE | 13.62 | 0.14 | 432 (375–488) | 5 (3–6) |
| WASP | 13.63 | 0.36 | 324 (261–387) | 9 (4–13) |
| SJNO | 18.13 | 0.77 | 861 (710–1,013) | 37 (22–51) |
| LOSW | 21.51 | 1.12 | 1,193 (1,058–1,328) | 62 (51–74) |
| LOSO | 26.86 | 1.20 | 1,064 (962–1,166) | 47 (36–59) |
| All transects | 9.57 | 0.39 | 6,442 (6,138–6,746) | 263 (232–293) |