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MARINE DISTRIBUTION AND BEHAVIOR OF JUVENILE AND ADULT MARBLED MURRELETS OFF SOUTHWEST VANCOUVER ISLAND, BRITISH COLUMBIA: APPLICATIONS FOR MONITORING

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Abstract. We examined the marine distribution and behavior of newly fledged juvenile (hatching year; HY) and adult (after hatching year; AHY) Marbled Murrelets (*Brachyramphus marmoratus*) off southwest Vancouver Island, British Columbia, to test whether assumptions associated with estimating productivity are met in this area. Productivity estimates for murrelets use HY:AHY ratios from marine surveys, which assume limited emigration and that juvenile and adult birds are similarly distributed. We examined observations from June–August, 1994–2005. Behavioral data were collected from land-based surveys via instantaneous scan sampling. Locations of murrelets at sea were mapped from cliff-top vantage points using a theodolite; Geographic Information Systems (GIS) was then used to compare the distances from shore of juveniles and adults. Data from boat surveys were analyzed using GIS kernel density analysis to compare adult and juvenile murrelet distributions at sea. At fine scales (1–100 m), juveniles were associated with adults; however, they were found significantly closer to shore than adults. At coarse scales (1–10 km), juvenile and adult distribution overlapped on a daily basis but showed less overlap with annually averaged distributions. Juveniles typically were solitary foragers, whereas adults often foraged in pairs or larger groups. Our results indicate that monitoring HY:AHY ratios using boat transects off southwest Vancouver Island as an indicator of breeding success need not take into account possible "nursery areas," although the proximity of juveniles to the shoreline means that monitoring must consistently include waters closest to the shore. Sequential ratios should be used to account for emigration of adults due to postbreeding dispersal.

Key words: *age ratios*, Brachyramphus marmoratus, *juveniles*, *Marbled Murrelet*, *marine distribution*, *monitoring*, *seabirds*.

Distribución Marina y Comportamiento de Aves Jóvenes y Adultas de *Brachyramphus marmoratus* al Suroeste de la Isla Vancouver, British Columbia: Aplicaciones para el Monitoreo

Resumen. Examinamos la distribución marina y el comportamiento de individuos jóvenes que recientemente habían emplumado (individuos en su año de eclosión, AE) e individuos adultos (de años posteriores al de eclosión, APE) de la especie *Brachyramphus marmoratus* al suroeste de la isla Vancouver, British Columbia. Nuestro objetivo fue determinar si algunas suposiciones asociadas con la estimación de la productividad se cumplen en esta área. Los estimados de la productividad de *B. marmoratus* emplean proporciones de AE:APE obtenidas a partir de censos marinos, suponiendo que la emigración es limitada y que las aves jóvenes y los adultos se distribuyen de modo simlar. Examinamos observaciones realizadas entre junio y agosto de 1994 a 2005. Los datos de comportamiento fueron obtenidos mediante censos realizados desde tierra, empleando muestreos instantáneos de barrido. Las ubicaciones de las aves en el mar fueron mapeadas desde puntos ubicados en las cimas de acantilados, utilizando un teodolito. Luego se utilizaron sistemas de información geográfica (SIG) para comparar las distancias medidas desde la costa a los individuos jóvenes y a los adultos. Los datos obtenidos mediante censos realizados desde botes fueron sometidos a análisis de densidad de *kernel* en un SIG para comparar las distribuciones de los jóvenes y de los adultos en el mar. A escalas finas (1–100 m), los jóvenes estuvieron asociados con los adultos, pero se encontraron significativamente más cerca de la costa que éstos. A escalas más gruesas (1–10 km), las distribuciones de los jóvenes y de los adultos se superpusieron diariamente, pero mostraron menos superposición al evaluar las distribuciones promediadas anualmente. Los jóvenes típicamente forrajearon en solitario, mientras que los adultos lo hicieron en parejas o grupos más grandes. Nuestros resultados indican que monitorear las proporciones de AE:APE utilizando transectos realizados desde botes al suroeste de la isla Vancouver como indicador del éxito reproductivo, no necesita tener en cuenta posibles "áreas de guardería," aunque la proximidad de las aves jóvenes a la costa significa que las aguas costeras deben ser monitoreadas con regularidad. Las proporciones secuenciales deben ser empleadas para tener en cuenta la emigración de los adultos causada por la dispersión posterior a la reproducción.

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INTRODUCTION

Measuring reproductive success of threatened or endangered species is fundamental to demographic analyses for population monitoring and management. Although the production of young may be easily measured for some species, for others, the task may be much more difficult. The Marbled Murrelet (*Brachyramphus marmoratus*) is a species quite secretive in its nesting behavior, and nest sites are extremely difficult to access. Because birds nest noncolonially, usually in the canopies of large old-growth conifers (Nelson 1997), their nesting ecology is difficult to study without expensive radio-telemetry and cannot be used for demographic analysis (Beissinger 1995, Cam et al. 2003). Consequently, productivity is estimated from counts of newly fledged juveniles, which are identifiable at sea during the summer months before the adults molt (Carter and Stein 1995). Both juvenile densities and at-sea ratios of juveniles (hatching-year; HY) to after-hatching-year (AHY) birds have been used to estimate the reproductive success of murrelets (Ralph and Long 1995, Kuletz and Kendall 1998, Lougheed et al. 2002), and these data are used to evaluate demographic models (Beissinger 1995). Four assumptions, however, in the quantification of HY:AHY ratios are that: (1) adults and juveniles are identified correctly at sea, (2) timing and degree of natural and anthropogenic mortality of HY and AHY is low when counts for HY:AHY ratios are made, (3) emigration or immigration rates are low, and (4) HY and AHY birds are similarly distributed at sea (Carter and Stein 1995, Peery et al. 2007). Knowledge of the emigration, distribution, and habitat associations of juvenile murrelets is therefore important for reliable surveys of juveniles and estimates of HY:AHY ratios (Ralph and Long 1995, Kuletz and Kendall 1998, Lougheed et al. 2002).

The transition from terrestrial nestling to independent marine juvenile is a critical phase in the life history of seabirds (Burger 1980, Ydenberg 1989). Nevertheless, habitat use and foraging behavior of newly fledged juveniles are poorly known for most seabirds. Among the alcids (Alcidae), newly fledged juveniles from the semiprecocial species (which make up the bulk of the alcid species) do not accompany their parents to sea and are therefore entirely independent from the moment of leaving the nest (Ydenberg 1989, Gaston and Jones 1998). It is therefore valuable to know whether newly fledged juveniles have similar habitats and foraging methods to those of adults.

The marine habitat use of murrelets has received some recent investigation (Carter and Sealy 1990, Lougheed 2000, Becker and Beissinger 2003, Day et al. 2003), yet little is known about the habitat use of juvenile murrelets. In some areas in Alaska, Kuletz and Piatt (1999) found that juvenile murrelets were clustered in "nursery areas" associated with kelp beds, which could result in skewed HY:AHY ratios if such nurseries were not identified. Other areas in Alaska did not show nursery areas (Kuletz and Kendall 1998). In Desolation Sound, British Columbia, Lougheed (2000) suggested that juveniles were found in different areas than were adults, and several studies observed that juveniles were more likely to be found in nearshore waters and were often associated with kelp (Sealy 1975, Carter 1984, Beissinger 1995, Carter and Stein 1995, Strachan et al. 1995). In California, however, juvenile and adult birds show similar at-sea distributions, creating little bias in the quantification of HY:AHY ratios (Peery et al. 2007).

British Columbia supports a large population of Marbled Murrelets, and some of the highest at-sea densities have been found off the southwest coast of Vancouver Island (Burger 1995). Some areas off southwestern Vancouver Island such as Clayoquot Sound (Kelson et al. 1995) and Barkley Sound (Burger 1995, 2000) showed declines in murrelet populations. In Pacific Rim National Park Reserve (PRNPR), juvenile murrelets were regularly sighted along the West Coast Trail, which may be linked to the large tracts of forested nesting habitat adjacent to that area (Burger 1995, 2002). Little is known about juvenile distribution in this area and whether it differs from that of adults. Because recruitment is generally low in this species, knowledge of juvenile marine habitat needs may be important to the conservation of this threatened species (Beissinger 1995).

In this study, we examined marine distribution and behavior of juvenile Marbled Murrelets in PRNPR. Our objectives were to: (1) test for differences in juvenile and adult distributions at multiple spatial and temporal scales, (2) test for emigration of juvenile and adult birds from the study area, and (3) examine potential mechanisms that may be influencing juvenile distributions. Specifically, two mechanisms tested included: (i) possible association of juveniles with shorelines and kelp beds, and (ii) foraging behavior of juveniles in association with adult murrelets. Our results provide information on marine distributions of juvenile murrelets, which is essential for management and long-term monitoring of reproductive performance, and to improve the application of the HY:AHY ratio currently used as an index of recruitment in this species.

METHODS

STUDY SITE

Surveys took place along the West Coast Trail (WCT) unit of Pacific Rim National Park Reserve (PRNPR) on the southwest coast of Vancouver Island between Cape Beale (48°47′N, 125°14′W) and Port San Juan (48°32′N, 124°29′W; Fig. 1). Hatching-year birds (hereafter juveniles) were distinguished from after-hatching-year birds (hereafter adults) by their plumages (Carter and Stein 1995). It is difficult to differentiate adults in basic plumage and juveniles at sea (Carter and Stein 1995); thus, only data collected between mid-June and mid-August (a period when adults would normally be in alternate plumage) were analyzed. Previous studies off southwestern Vancouver Island reported peak numbers of juveniles between mid-June to mid-August. The coastline of this study

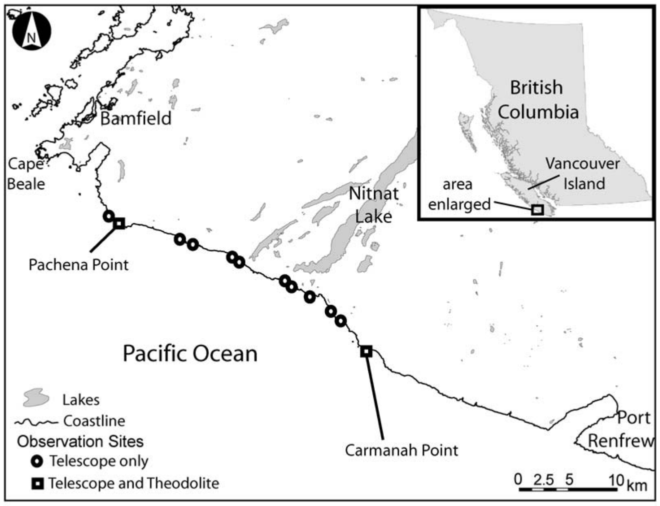

FIGURE 1. Study area investigating the distribution of Marbled Murrelets (*Brachyramphus marmoratus*) along the West Coast Trail, Pacific Rim National Park Reserve, Vancouver Island, British Columbia. Boat transects were conducted between Port Renfrew and Cape Beale (1994–1996 and 1998–2005). Shore-based observations were conducted from 12 sites between 14 May and 9 August 2004.

area is mainly straight and not indented with large estuaries or bays. In this simple marine habitat, surveys easily cover the entire study area and there are no places for juveniles or adults to be missed during surveys.

DATA COLLECTION

Boat transect surveys were conducted for most years between 1994 and 2005 along approximately 65 km of coastline between Port Renfrew and Cape Beale (Fig. 1). AEB and BH, along with PRNPR staff, conducted biweekly boat surveys from May through September in 1994–1996 and 1998–2005. The staff were trained by AEB or BH to identify and age murrelets at sea and had several years of experience conducting seabird surveys in PRNPR prior to undertaking these surveys. AEB conducted nearly all of the surveys between 1994 and 1996. Approximately 80% of the surveys between 1998 and 2005 were conducted by BH. The number of surveys varied each year due to weather and staff availability. Surveys were conducted from a 5 m inflatable boat or a rigid-hull 7 m inflatable, with a few surveys in 1994–1996 from a 10 m fiberglass vessel. Differences in vessel size should not affect the detectability of murrelets within the narrow transect strips used. Boats traveled between 15–22 km hr^{-1}, which was necessary to cover the transect distance within a survey day. Transects ran parallel to shore at a distance of approximately 300 m from the shore in 1999–2005, and 200 m in 1994–1996 and 1998, which is within the zone of highest density of murrelets along this coast (Burger et al. 2008). Surveys used a fixed-width transect method (Resources Inventory Committee 1997), recording the number, group size, and species of all birds within 150 m of either side of the boat (i.e., 300 m strip width) within 1-min time intervals. Although line transects (distance sampling) are thought to produce more accurate density estimates than strip transects (Becker et al. 1997), line transect data were not available for this long-term dataset. By using strip transects, we likely underestimated actual bird densities (Becker et al. 1997); however, there was likely no age-class ratio bias. In four of the survey years (1995, 1996, 2004, and 2005), a Global Positioning System (GPS) was used to track the boat positions in one minute intervals, thus providing geo-referenced bird counts in 1 min intervals for use in kernel density analysis (below). Although detectability of juveniles and adults may differ depending on sea and weather conditions, we made no corrections for detectability because we were interested only in *relative* distribution patterns between juvenile and adult murrelets rather than precise density quantification necessary for population estimates.

From cliff-top vantage points at Pachena and Carmanah Points (Fig. 1), we used a digital theodolite (Total Station Model NPL-332 Pulse Laser, Nikon-Trimble Co., Ltd., Tokyo, Japan) to map fine-scale distributions of murrelets on the water between 14 May and 9 August 2004. This technique is accurate to within 2 m up to 2 km from the observation site (Denardo et al. 2001). The theodolite had a built in scope (26× optical) to locate birds and measured angles to murrelet locations on the water (Ronconi and St. Clair 2002). These angles were used to calculate the positions of murrelets (northings and eastings) relative to the theodolite using basic trigonometric functions (Ronconi and St. Clair 2002). Mapping was conducted using sequential sweeping scans (up and down) from one side of the study area to the other. We mapped locations of individuals and groups of murrelets, recording group size and age class (juvenile or adult).

Foraging behavior of Marbled Murrelets was observed between 14 May and 9 August 2004 from 12 cliff-top vantage points along the WCT (Fig. 1). Instantaneous visual scan sampling techniques (Martin and Bateson 1986, Davoren and Burger 1999) were used to measure bird activities between 06:00 and 21:00 PST. Scan sampling, using a 20× spotting scope, consisted of 20 1-min observations over each hour of observation. During each 1-min interval, the scope was fixed in position, and the numbers of birds, group sizes, and activity state of individuals (resting, diving, bathing, preening, displaying, flying) within the field of view of the scope were recorded. This was repeated for 20 nonoverlapping fields of view (10 along an upper horizontal row and 10 along a parallel lower row). An observation period of 60 sec was chosen to ensure that any murrelets diving would be observed once surfacing from a dive; typical dive times for Marbled Murreletes are about 30 seconds (Jodice and Collopy 1999, Henkel et al. 2004). No observations were made in rain, fog, or when sea state was higher than 3 on the Beaufort Scale.

STATISTICAL ANALYSES

At-sea distribution. We examined spatial distributions of adults and juveniles daily, annually, and across years (four-year averaged distributions) using kernel density estimation methods (O'Sullivan and Unwin 2003) to map hotspots of bird densities. Kernel densities convert point data (i.e., bird counts per 1 min transect segment), into a continuous surface grid (raster layer) showing relative bird densities per grid cell. Kernel densities take into account both location of groups and group size to calculate relative densities of birds. In spatial analyses, it is important to select appropriate scales (Wiens 1989), which may be identified by spatial autocorrelation (Jelinski and Wu 1996). Kernel size (grid cell size) was set at 275 m, which was the average distance traveled per minute of transect. The kernel smoothing function was set at 825 m, because we found murrelets are spatially autocorrelated up to this distance. Density raster layers were created for adult murrelets on each survey day with GPS positions. The mean murrelet density was calculated for each raster layer, and grid cells were classified as either low density (lower than average murrelet density) or high density (higher than average murrelet density).

To investigate daily distributions of juveniles relative to adults, we mapped locations of individual juveniles with respect to adult kernel densities on each day. Counts were made of juveniles found in each category (low- and high-density adult areas). To investigate annual patterns of juvenile distribution, we mapped juvenile densities with the kernel method (above). Few juveniles were sighted on most survey days; therefore, all sightings of juveniles were pooled for transect surveys in each of four years: 1995, 1996, 2004, and 2005. Because juveniles were sparsely distributed compared to adults, kernel cell size and smoothing function were increased to 500 m and 1500 m, respectively, to produce a more generalized density distribution than for adult distributions (Seaman and Powell 1996). The use of small kernels for high density adults and large kernels for low density juveniles is similar to the adaptive kernel method, which uses more smoothing in areas of low density observations (Silverman 1986). We overlaid juvenile and adult kernel densities in each year to compare percentage overlap between adult and juvenile distributions. Finally, to investigate long-term differences in juvenile and adult distribution, density layers from these four years were averaged, creating a single four-year overlaid density distribution for juvenile and adult birds.

Emigration of juvenile and adult birds. To test for emigration of juvenile and adult birds from the study area (we assumed no appreciable immigration; Burger et al. 2008), we calculated juvenile and adult densities (birds per km^2) for each survey day in each year. Although this calculation does not take into account detectability issues between juvenile and adult birds, it provides a relative density estimate that can be used to compare general trends throughout the season. We regressed density estimates against day of year to quantify seasonal changes in numbers and potential emigration of juvenile and adult birds.

Juvenile associations with shorelines and kelp beds. Northing and easting positions were imported to a geographical information system (GIS). Shorelines and areas of kelp beds were also mapped with the theodolite, and the GIS was used to calculate the nearest distances of the birds from these features. Mann-Whitney U tests were used to compare distances of juveniles and adults from shorelines and kelp beds. Juveniles were typically alone or in groups of two; therefore, to make suitable comparisons with adults, we used only those adult observations in groups of one or two individuals. Murrelets typically forage singly or in pairs (Strachan et al. 1995), and juveniles also occur in larger flocks with adults when not feeding (Carter 1984, Carter and Stein 1995). In our study, we never observed juveniles in large groups; therefore, by focusing solely on small groups of adults, we were not introducing biases in distribution that might be associated with activity (i.e., foraging versus not foraging).

Juvenile foraging behavior observations. Foraging activity budgets of adults and juveniles were determined as percentages of individuals engaged in diving. We also tested for changes in juvenile foraging activity (counts of birds diving and resting) as influenced by adult association (with or without an adult in their group) using chi-square tests. Fine-scale distributional associations between juvenile and adult birds were tested from boat transect data by comparing counts of adults during 1 min transect segments with juveniles to adjacent 1 min segments without juveniles. Both georeferenced and nongeoreferenced data were used for this analysis. All tests were two tailed and were significant at $P < 0.05$. Statistical analyses were conducted using SPSS 15.0 (SPSS, Inc., Chicago, Illinois). GIS analysis was conducted using ArcGIS 9.0 (ESRI, Redlands, California). Values reported are means ± SD.

RESULTS

AT-SEA DISTRIBUTION

Data from at-sea surveys were used to examine the daily and annual distributions of juveniles with respect to adults. Juveniles were sighted on a total of ten days (with GPS locations) from 1995–1996 and 2004–2005 during boat transect surveys (Table 1). For daily distribution maps, juveniles were rarely found in areas without adults (2% of cases), and the greatest proportion (78%) of juveniles was found in the adult high-use areas (Table 1). Comparison of annual distributions between juveniles and adults showed considerable interannual variability in overlap (Fig. 2). This overlap is not influenced by nesting area locations, as the distribution of murrelets at sea off the WCT is not affected by the proximity to forested nesting habitat inland (Burger et al. 2008). On average, more than half (58% ± 14%, range: 44%–76%) of the high juvenile density areas overlapped with high adult density areas, but fewer

TABLE 1. The daily distribution of juvenile Marbled Murrelets relative to adults along 10 boat transect surveys of the West Coast Trail, Vancouver Island, British Columbia (1995–1996 and 2004–2005). Densities were determined from 300-m wide strip-transects (i.e., 150 m on either side of boat). Adult low-density (<mean density) and high-density (>mean density) areas were determined from kernel density analysis (Fig. 2).

Date	Density (birds km^{-2}) Adults	Density (birds km^{-2}) Juveniles	Number of juveniles	Juvenile distribution (numbers): In areas not used by adults	In low-density areas	In high-density areas
3 August 1995	8.4	1.5	29	0	3	26
25 June 1996	95.9	0.8	16	0	4	12
8 July 2004	43.9	0.3	6	0	3	3
25 July 2004	9.4	0.6	13	0	2	11
4 August 2004	6.4	0.9	7	1	2	4
17 August 2004	2.9	0.6	12	1	3	8
23 June 2005	28.5	0.2	3	0	1	2
04 July 2005	44.0	0.2	3	0	0	3
17 July 2005	45.8	0.5	4	0	1	3
13 August 2005	6.3	0.5	6	0	1	5
Mean	29.1	0.6				
Total (%)			99	2 (2)	20 (20)	77 (78)

than half (47% ± 9%, range 35%–58%) of the high adult density areas contained high densities of HY birds. Four-year averaged distribution maps (Fig. 3), however, showed considerable (91%) overlap between juvenile and adult high-density areas. Therefore, over the long term, high densities of juvenile murrelets can be expected to overlap with high densities of adults, yet there may be considerable inter- and intra-annual variability in this overlap. It seems that areas where high juvenile densities do not overlap with high adult densities occur primarily at the margins of the adult distributions (Fig. 2).

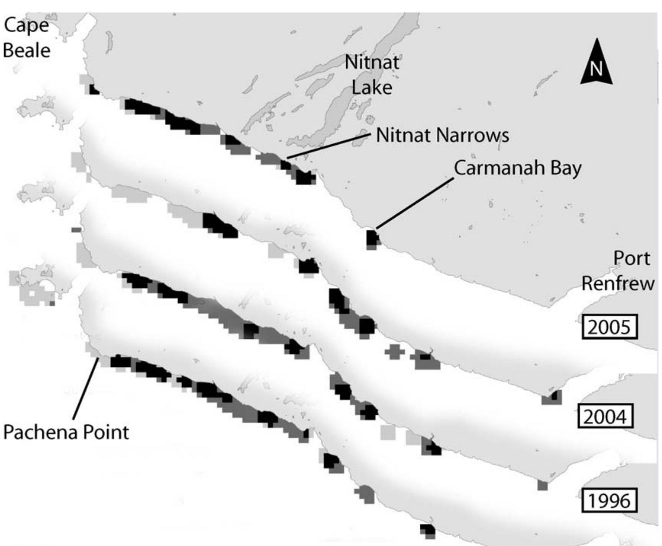

FIGURE 2. Yearly (1995, 1996, 2004, 2005) averaged distribution of juvenile and adult Marbled Murrelets along the West Coast Trail, Vancouver Island, British Columbia, showing considerable interannual variability in overlap between juvenile and adult high-density areas. Adult and juvenile densities were determined by kernel density analysis. High-density grid cells were all cells with higher densities than the mean. Table 1 contains transect dates used in kernel analysis.

Given the variability in overlap between juvenile and adult distributions, it is important to understand if juvenile and adult densities occur in predictable regions from one year to the next. By overlaying high-density areas for juvenile and

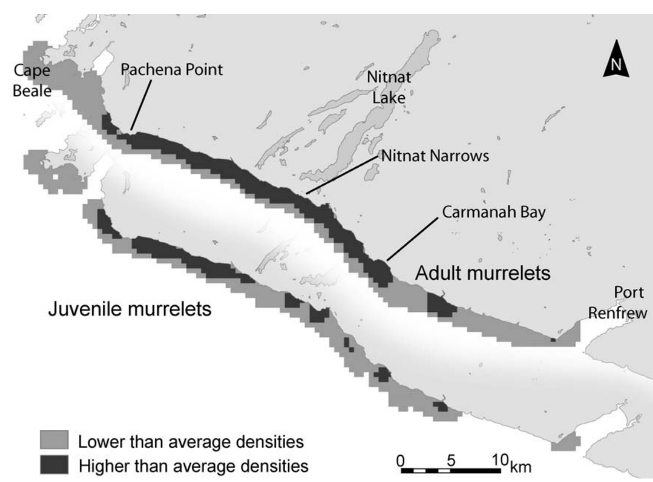

FIGURE 3. Marine distribution of juvenile and adult Marbled Murrelets along the West Coast Trail, Vancouver Island, British Columbia, averaged over four years (1995, 1996, 2005, 2006), showing considerable (91%) overlap between juvenile and adult high-density areas. Densities were calculated using kernel density analysis.

adult birds across all four years, it seems that high-adult-density areas may be more predictable than high-juvenile-density areas. For adult birds, 31% of high-density kernels were used in one year, 21% in two years, and 48% in three or more years. By contrast, even though they were less abundant, juvenile birds showed less consistent aggregations, using 53% of high-density kernels used in only one year, 24% in two years, and only 23% in three or more years.

EMIGRATION OF JUVENILE AND ADULT BIRDS

Postbreeding emigration of adult birds after mid-July is well documented for this area (Carter 1984, Burger 1995, Burger et al. 2008). To test whether there were differences in adult and juvenile emigration or immigration along the study area, we examined the relationship between day-of-year and the density of adults and juveniles per survey, as well as changes in HY:AHY ratio. We found a significant negative linear relationship between the adult density and day of year ($r^2 = 0.35$, $P < 0.001$, $n = 50$), whereby adult densities decreased between June and August (Fig. 4). No significant relationship existed between juvenile densities and day of year, though a quadratic equation was the best fit ($r^2 = 0.11$, $P = 0.07$, $n = 50$), suggesting a peak in juvenile numbers in mid to late July (Fig. 4). As a result of the differences in emigration between juveniles and adults, the HY:AHY ratio increased significantly throughout the season ($r^2 = 0.15$ $P = 0.005$, $n = 50$; Fig. 4).

SHORELINE AND KELP BED ASSOCIATIONS

In 2004, 31 juveniles and 1824 adults were mapped using a theodolite. Mean distance to shore for juveniles was 449 m (± 296) and for adults was 575 m (± 318), and the distance from shore was significantly less for juveniles than adults (Mann-Whitney *U* Test: $Z = 2.9$, $P = 0.004$; Fig. 5). Mean distances to kelp were 384 m (± 383) for juveniles and 390 m (± 288) for adults, which were not significantly different (Mann-Whitney *U* test: $Z = -1.0$, $P = 0.30$; Fig. 5). Thus, fine scale segregation between juveniles and adults appears to be influenced by distance to shore but not distance to kelp beds.

BEHAVIOR AND ASSOCIATIONS WITH ADULTS

A total of 417 hours of scan sampling observations were conducted in 2004, and 40 juveniles were observed between 28 June and 6 August. The overall foraging activity budget for juvenile and adult ($n = 17\,816$) murrelets was nearly identical: 25% and 26% diving, respectively. Diving activity of the 40 juveniles observed was dependent on associations with adults (chi-square test: $\chi^2_1 = 7.2$, $P = 0.01$), whereby 38% of juveniles were diving without adults present ($n = 26$), but juveniles were never observed diving when in groups with adults ($n = 14$).

During boat transect surveys, juveniles ($n = 132$) were observed alone in 66% of the sightings. Adult densities were significantly higher in the 1 min segments with juveniles than in the adjacent segments without juveniles (paired *t*-test: $t_{131} = 3.1$, $P = 0.002$). These results suggest that juveniles are usually solitary but at fine scales (~200–300 m), are associated with higher adult densities.

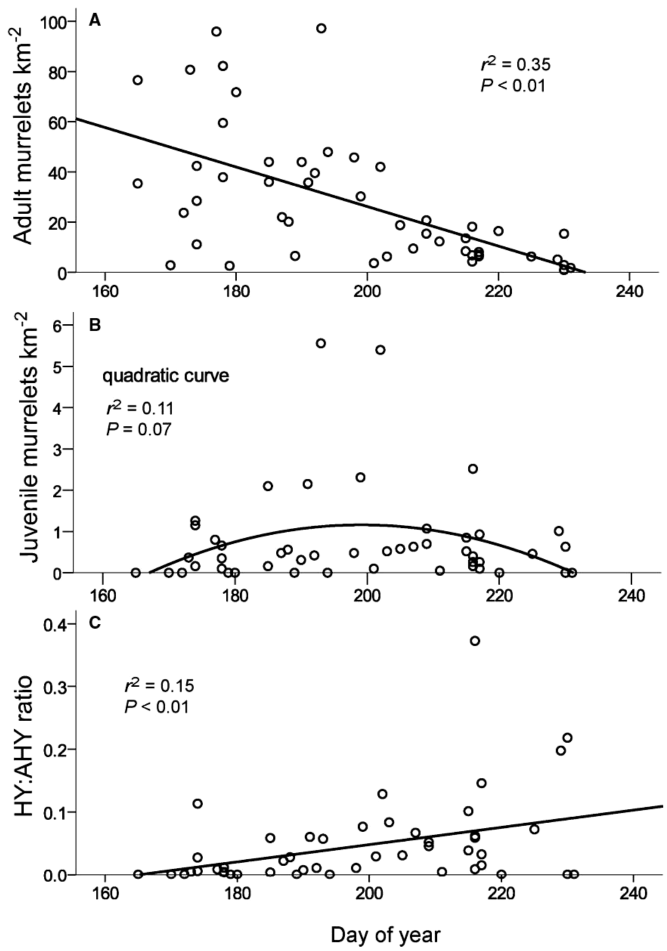

FIGURE 4. Emigration and immigration of adult and juvenile Marbled Murrelets along the West Coast Trail, Vancouver Island, British Columbia (1994–1996 and 1998–2005). Seasonal (day of year) changes in (A) adult densities, (B) juvenile densities, and (C) HY: AHY ratio. Day of year 160 = 9 June.

DISCUSSION

Issues of scale are important to consider when examining the distribution patterns of organisms. Hunt and Schneider (1987) reviewed the effects of scale-dependent oceanographic processes on marine birds and suggested scales of importance to ornithologists, including the following: meso-scale processes (100–1000 km), which affect foraging distributions, coarse-scale processes (1–100 km), which affect local foraging opportunities, and fine-scale processes (meters to hundreds of meters), which affect social interactions and foraging behavior. Moreover, to gain a complete understanding of distributions and processes,

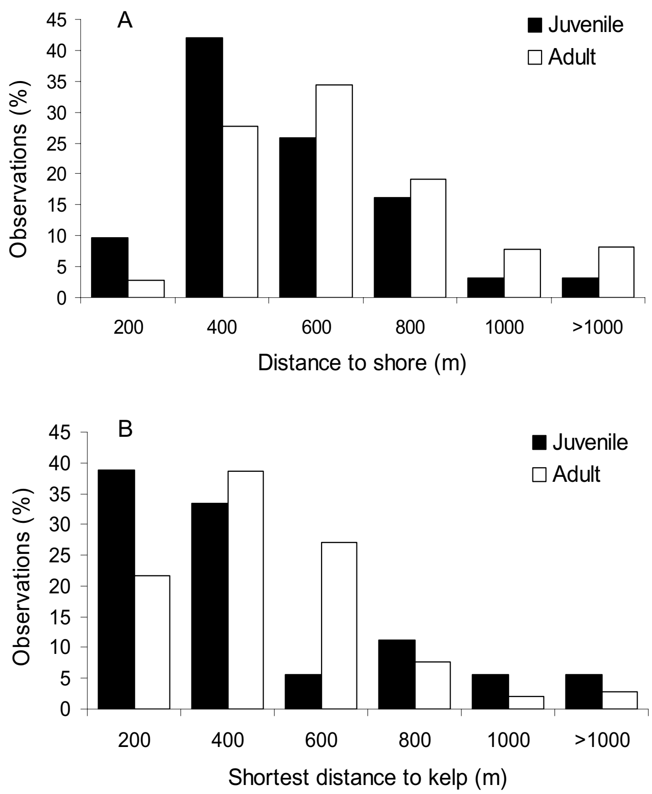

FIGURE 5. Juvenile and adult Marbled Murrelet distance to (A) shore and (B) the distance to nearest kelp bed, measured from fine-scale theodolite mapping along the West Coast Trail, Vancouver Island, British Columbia from 14 May to 9 August 2004. Results include solitary or paired adults to reflect the group size of juvenile observations. Total sample size for juveniles = 31 and adults = 1824.

we need to study organisms at multiple spatial and temporal scales because general ecological patterns are best studied at coarse scales, whereas mechanistic understandings are better determined from fine-scale studies (Wiens 1989). Using kernel density analysis, our study examined the distribution of juveniles and adults at various temporal scales: (1) daily distributions, (2) annual distributions, and (3) multiyear averaged distribution. While we did not explicitly test our data at each spatial scale mentioned above, we used different approaches to examine our data at two spatial scales. Fine-scale distribution was examined using the theodolite distribution mapping and the juvenile-adult associations in 1 min (275 m) vessel transect segments. Coarse-scale distribution was examined using kernel density mapping along the entire study area.

At fine scales, our study found a fairly close association between juveniles and adults, whereby adult densities were significantly higher in 1 min survey segments with juveniles than in the adjacent segments without juveniles. However, juveniles were significantly closer to shore than were adults. At coarse scales, we found a close association between juveniles and adults on a daily basis but not annually. Thus, on a daily microhabitat level, juvenile and adult murrelet distribution was similar, but over longer temporal and coarser spatial scales, juveniles and adults may have different habitat requirements. Some studies found no significant differences in distribution between adults and juveniles (Ralph and Long 1995, Mason et al. 2002), while others reported juveniles closer to shore (typically <200m) and near kelp beds (Sealy 1975) or small channels (Carter 1984).

Several mechanisms have been proposed that might explain differences between juvenile and adult marine distributions. Previous observations found that juveniles preferred nearshore waters and were often associated with kelp. Strachan et al. (1995) found that juveniles were most commonly found within 100 m of the shoreline, especially in the presence of bull kelp (*Nereocystis luetkeana*). Similarly, Speckman et al. (2003) observed most juveniles within 10 m of the water's edge. Ralph and Long (1995) found 15% of juveniles but only 5.7% of adults within 200 m of shore. Surveys through kelp beds in Clayoquot Sound, British Columbia, had greater juvenile-to-adult ratios than total at-sea counts (I. Manley and J. Kelson, Conservation International, unpubl. data; cited in Beissinger 1995). Juveniles are known to feed in kelp beds, which may also provide inexperienced juveniles with some protection from avian predators (Kuletz and Piatt 1999). Our results suggest that juveniles along the WCT have a greater affinity for nearshore waters than do adults, but there were no differences in associations with kelp beds between juveniles and adults.

Foraging behavior may be another explanation for the variability in juvenile distribution. Previous work found that juveniles usually forage separately from adults (Strachan et al. 1995). This suggests that juveniles do not learn to forage from adults but may be using adults as indicators of good foraging locations, as has been suggested for other seabirds (Drury and Smith 1968, Porter and Sealy 1982). We found little difference between juveniles and adults in the proportion of time spent diving. Juveniles were solitary foragers and were never seen diving when in groups with adults. Our data comparing adult densities in 1 min segments with juveniles to adjacent 1 min segments without juveniles similarly suggest that juvenile murrelets were associated with areas of higher murrelet densities. Moreover, kernel density analysis showed that daily juvenile distributions were most often associated with high adult densities. Thus, juveniles may be attracted to foraging areas used by adults, even if they are not foraging in groups with adults. This suggests that juveniles may use local enhancement (Wittenberger and Hunt 1985) to find suitable foraging locations.

Another possible explanation for differences in distribution between juveniles and adults is difference in food preferences. Diets of juvenile murrelets have been studied in only two locations, both in British Columbia (Sealy 1975, Carter

1984). Off Langara Island, newly fledged murrelets selected more sea perch (*Cymatogaster aggregata*) than did adults, though sand lance (*Ammodytes hexapterus*) were still the dominant prey for both age classes (Sealy 1975). However, Burkett (1995) cautioned that these differences in dietary composition were partially a result of seasonal changes in prey abundance or local changes in prey distribution. In Barkley Sound, bordering our study area, Carter (1984) found similar diets between juvenile and adult birds, though juveniles showed slightly higher proportions of juvenile herring (*Clupea harengus*) and lower proportions of sand lance. Therefore, it is unlikely that dietary differences may account for longer temporal and coarser scale differences in juvenile and adult distribution, though few data are available to corroborate.

Peery et al. (2007) suggested that several assumptions must be met when using HY:AHY ratios to monitor reproductive success. The first is that juvenile and adult marine distribution should be similar, and if not, the sampling design should account for this. Along the WCT, we found that this assumption was met, and juveniles were generally found in the same areas as adults. Kuletz and Piatt (1999) found distinct nursery areas in some places in Alaska, which consisted of shallow, semiprotected seas, the presence of kelp, and locally productive waters. We found no evidence for distinct nurseries of juveniles along the West Coast Trail; thus, it is unlikely that juveniles from our study area were aggregating in nursery areas outside our sampling range. At coarse scales, we identified marine areas that were used repeatedly across years, but these were also regularly used by adult birds. However, the proximity of juveniles to the shoreline means that monitoring must consistently include the shallow waters closest to the shore. Although the mean difference in distance to shore between juveniles and adults was potentially not biologically significant (only 125 m), this distance may cause significant underestimates of juveniles during 150 m wide strip-transect surveys typically conducted 300 to 400 m from shore. More complex coastlines may require additional care to ensure accurate counting of juveniles close to shore.

Extensive immigration or emigration by adults could be an important source of bias in estimating productivity using HY:AHY ratios (Kuletz and Kendall 1998, Lougheed et al. 2002, Peery et al. 2007). Adult murrelet densities declined as a result of postbreeding dispersal in nearby Desolation Sound, British Columbia (Lougheed et al. 2002). We found similar results in southwestern Vancouver Island whereby there was a decrease in the number of adults from June to August that resulted in inflated HY:AHY ratios. These inflated ratios must be accounted for; thus, a "sequential" ratio, proposed by Kuletz and Kendall (1998), should be used in this area, which calculates HY:AHY ratios using HY abundance during peak fledging period and AHY abundance during early incubation. Given the uncertainties of local movements and migrations in Marbled Murrelets, these ratios are rough estimates of breeding productivity, but they remain the only known method for tracking this parameter in this species.

At fine scales and on a daily basis at coarse scales, we found that juvenile and adult distribution was similar, thereby meeting one of the assumptions associated with using HY:AHY ratios to estimate and monitor productivity of Marbled Murrelets. A "sequential" ratio (Kuletz and Kendall 1998) should be used, however, due to the extensive emigration of adults during the month of August, which results in inflated HY:AHY ratios. The apparent overlap between adult and juvenile fine-scale habitat is perhaps good news from a management perspective. Because juvenile murrelets are difficult to study because of their naturally low abundance, understanding the fine-scale habitat requirements of adults may provide insight into the habitat requirements of juveniles. Moreover, the identification and protection of important adult marine habitats will likely enhance the protection of juvenile habitat as well.

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