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LOCAL SURVIVAL OF ADULT AND JUVENILE MARBLED MURRELETS AND THEIR IMPORTANCE FOR ESTIMATING REPRODUCTIVE SUCCESS

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Abstract. Juvenile ratios estimated using numbers of hatch year (HY) and after-hatch-year (AHY) Marbled Murrelets (*Brachyramphus marmoratus*) counted concurrently during at-sea surveys have been used to estimate fecundity in this species. These ''concurrent'' juvenile ratios assume that HY birds remain in an area, and are likely biased because they do not account for potential differences in emigration rate of HY and AHY birds. We studied the emigration rates of adult and juvenile Marbled Murrelets marked with radio-transmitters. Juveniles had a high emigration rate compared to adults. The weekly local survival rate (ϕ) of newly radio-tagged HY birds was 27%. AHY local survival was 95% during incubation and early chick rearing, suggesting a resident population during the breeding season. We calculated juvenile ratios from 1996–1998 using (1) HY counts corrected for emigration and mean AHY counts around the breeding season peak, and (2) HY and AHY counts from concurrent at-sea surveys. The average ''corrected'' juvenile ratio (0.13 $\pm$ 0.05 SE) was higher than the ''concurrent'' juvenile ratio (0.04 $\pm$ 0.02 SE) but lower than estimates of fecundity from nest monitoring (0.18–0.22). Low juvenile ratios from at-sea surveys could result either from an unknown proportion of nonbreeding birds in the population, or, more likely, from differences in the at-sea distribution of AHY and HY birds. Fluctuation in the timing of the peak number of AHY birds across years might result in an uncorrectable bias in the counts. Because of biases and potential problems, caution is needed when interpreting juvenile ratios from at-sea surveys.

Key words: Alcidae, Brachyramphus marmoratus, *British Columbia, juvenile ratio, local survival, Marbled Murrelet, radio-telemetry, seabird.*

Supervivencia Local de *Brachyramphus marmoratus* Adultos y Juveniles y su Importancia para Estimar Éxito Reproductivo

Resumen. Utilizamos los cocientes entre individuos juveniles (nacidos en un año) y adultos (nacidos en años anteriores) de *Brachyramphus marmoratus*, censados simultáneamente durante conteos en el mar, para estimar la fecundidad de esta especie. Estos cocientes ''simultáneos'' de individuos asumen que los juveniles permanecen en una misma área, y podrían estar sesgados ya que no toman en cuenta diferencias en las tasas de migración de juveniles y adultos. Estudiamos las tasas de emigración de individuos juveniles y adultos de *B. marmoratus* marcados con radio-transmisores. Los juveniles tuvieron una tasa alta de emigración comparada con los adultos. La tasa de supervivencia local semanal (ϕ) para juveniles fue del 27%. La tasa de supervivencia local para adultos durante la incubación e inicio de la cría de polluelos fue del 95%, sugiriendo que se trata de una población residente durante la estación reproductiva. Calculamos el cociente entre juveniles y adultos para 1996–1998 utilizando (1) conteos de juveniles corregidos por emigración y promedio de adultos contados durante el pico de la estación reproductiva, y (2) juveniles y adultos contados simultáneamente durante los censos. El cociente ''corregido'' promedio entre juveniles a adultos (0.13 $\pm$ 0.05 EE) fue mayor que el cociente ''simultáneo'' (0.04 $\pm$ 0.02 EE) pero menor que las estimaciones de fecundidad obtenidas por medio del monitoreo de nidos (0.18–0.22). Los bajos cocientes obtenidos de conteos en el mar podrían explicarse por la presencia de una proporción desconocida de aves no-reproductivas en la población, o, más probablemente, por diferencias existentes en la distribución de juveniles y adultos en el mar. Fluctuaciones anuales en la sincronización del período pico de la estación reproductiva

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podrían introducir error a los conteos de adultos. Debido a estos sesgos y problemas potenciales, es importante interpretar con cautela los cocientes entre juveniles y adultos obtenidos de conteos en el mar.

INTRODUCTION

The conservation of Marbled Murrelet (*Brachyramphus marmoratus*) populations is a concern over most of the species' range, including Oregon, Washington, and British Columbia, where the species has been designated threatened (Rodway 1990, Rodway et al. 1992, U.S. Fish and Wildlife Service 1992) and California, where the species is listed as endangered (U.S. Fish and Wildlife Service 1997). All changes in population size result from changes in vital rates (births, deaths, emigration, or immigration; Caswell 1989). Conservation measures are usually more effective and reliable with knowledge of the demography of a population, especially the vital rates (Caughley 1994). Although none of these rates are known with any certainty for any Marbled Murrelet population, monitoring of fecundity (births) has been identified as a priority, because it is thought to be low (Beissinger 1995).

Accurate estimates of fecundity are essential for demographic population modeling (Caswell 1989). Fecundity is defined as the number of female offspring per breeding-age female (Caswell 1989), but is commonly measured as some form of general reproductive success, such as the number of fledglings per breeding adult or per nest, a measure better described as productivity.

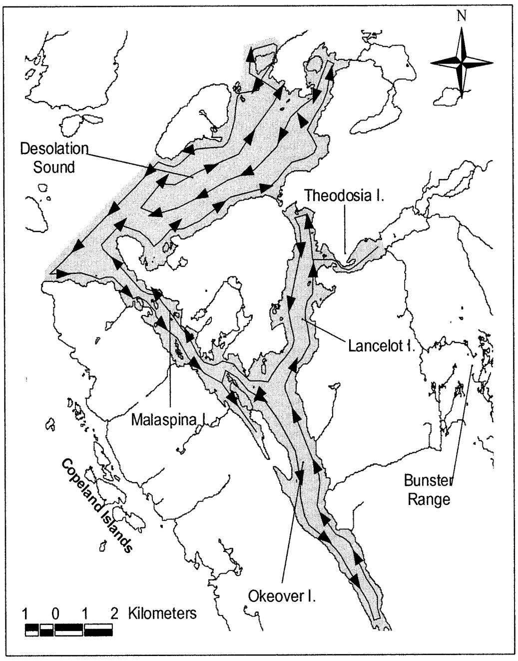
Marbled Murrelets are atypical members of the family Alcidae in that their nests are relatively widely dispersed and usually found high in trees in old-growth, coastal forests (Nelson and Hamer 1995, Nelson 1997). The inaccessibility of their nests and their cryptic behavior make unbiased measurements of Marbled Murrelet reproductive success from nest observations very difficult and expensive at best (Nelson and Hamer 1995). Monitoring reproductive success of this species is important; therefore, alternate indices of fecundity are needed. The most commonly used method is a calculation of the proportion of hatch year (HY) to after-hatch-year (AHY) birds counted concurrently during surveys at sea, usually called either ''juvenile to adult'' or ''juvenile'' ratios (Beissinger 1995, Ralph and Long 1995, Strong et al. 1995, Kuletz and Kendall 1998). Juvenile ratios have been assumed to be an index of fecundity because they approximate the proportion of juveniles per adult. Subadult AHY birds (birds too young to breed) have the same plumage as breeding-age AHY birds, and they cannot be separated in counts at sea; therefore, juvenile ratios are not true fecundity (as required in demographic models) but an index of productivity.

Juvenile ratios from concurrent at-sea surveys are likely biased (Beissinger 1995, Kuletz and Kendall 1998) because they do not account for immigration or emigration rates of HY and AHY birds. Pilot work at our study site in 1997 suggested that juveniles move out of the survey area at a high rate, and that adults emigrate as the end of the breeding season approaches (CL, unpubl. data). Differential turnover of the two age classes (AHY and HY) could lead to biases in the observed juvenile ratio (Beissinger 1995, Kuletz and Kendall 1998).

The objectives of this study were (1) to estimate the local survival of HY birds after fledging and AHY birds during incubation and early chick rearing; (2) to calculate juvenile ratios (as productivity indices) using HY counts corrected for juvenile emigration, and AHY counts at the peak of the breeding season; and (3) to compare these ''corrected'' ratios to traditional ''concurrent'' ratios and other independent measures of fecundity. We examined the assumptions and potential biases of using these methods.

METHODS

Fieldwork was conducted in Desolation Sound, British Columbia (50°06′N, 124°47′W; Fig. 1). AHY and HY Marbled Murrelets were counted in Desolation Sound and the adjacent glacial fjords (Malaspina, Lancelot, Okeover, and Theodosia Inlets) with at-sea surveys that followed standardized strip transect protocols (Resources Inventory Committee 1995). At-sea surveys were conducted from a 4.5-m hard-shell inflatable boat in 1996 and 1997, and from a comparable 5.2-m fiberglass boat in 1998, with one driver and two observers, one on each side of the vessel. The transect was 92 km long and 600 m wide, covering 50.2 km^2 of water. The crew was the same in 1996 and 1997, and one mem-



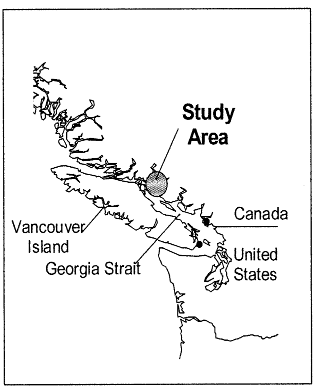


FIGURE 1. Study area (shaded) in Desolation Sound, British Columbia.

ber changed in 1998. At-sea surveys were replicated 24 times in 1996, 23 times in 1997, and 17 times in 1998 at average intervals of 4, 4, and 6 days respectively (range 1–12) between May and mid-August. Surveys were cancelled during rain or wind-wave conditions beyond 2 on the Beaufort scale. At-sea surveys ended after mid-August when HY birds could not be accurately differentiated from AHY birds as a result of AHY birds molting into basic plumage (Carter and Stein 1995). Surveys were estimated to cover 76% of the fledging period in Desolation Sound (Lougheed et al. 2002).

ESTIMATION OF JUVENILE MOVEMENT

We defined ''local survival'' as the probability of a bird staying alive and remaining in the survey area. To estimate the daily rate of juvenile local survival, radio-transmitters were attached to 16 recently fledged Marbled Murrelets captured by nightlighting (Whitworth et al. 1997) in the survey area from 10 July to 10 August 1998. Identification of HY birds during capture was based on plumage characteristics, egg-tooth presence, and weight (Carter and Stein 1995), although the exact age in days at first capture was unknown. Radio-transmitters were ATS Model 394 (Advanced Telemetry Systems, Isanti, Minnesota), weighing 2.0 g and with a battery life of 45 days. Transmitters were attached on each bird's back, between the scapulars, using epoxy glue (Bird Adhesive, Titan Corporation, Washington) and fiberglass insect screen. The birds were tracked during daylight from a 5.2-m Boston Whaler using a 4-element directional antenna mounted 3 m above the waterline, coupled with an ATS R4000 programmable receiver. Monitoring of the radio-tagged birds was done by boat at seven fixed at-sea locations within the survey area, 22 times from 11 July to 13 August (every 1.5 days on average, range 1–4 days). Movement of juveniles out of the survey area was confirmed by sporadic boat telemetry at 3 stations outside the survey area and by aerial telemetry over a wider area using a fixed-wing Cessna 172 airplane. Aerial telemetry was done on 10 August and 19 August following the coastline from Vancouver to Desolation Sound and the northern portion of the Strait of Georgia.

Program MARK (White 1999) was used to estimate the daily local survival of radio-tagged HY birds, using standard Cormack-Jolly-Seber open population models. We examined several models with different assumptions about the constancy of survival rate and recapture rate (detection) between intervals, and discriminated between models using Akaike's Information Criterion (AIC) as described in Lebreton et al. (1992). We tested whether survival rate (ϕ) and recapture rate (P) varied over time with likelihood ratio tests (LRT, Cooch and White 1999) by (1) comparing the fit of the time-dependent model of survival [$\phi(t)P(.)$] with that of the model with constant survival [$\phi(.)P(.)$], and (2) comparing the fit of the model with time dependent recapture [$\phi(.)\ P(t)$] with that of the model with constant recapture [$\phi(.)P(.)$]. We used $1 - \phi$ as an estimate of the daily rate of permanent emigration (which included mortality and radio loss, as well as true emigration). Residence time (R) was estimated as $1/-\ln(\phi)$ (White 1999). We estimated the weekly local survival rate of HY birds (ϕ^7) to allow comparison with that of AHY birds.

CORRECTED JUVENILE COUNTS

Each at-sea HY count was adjusted for juvenile turnover rate using the correction $J_n = J_o - (J_p \times \phi^d)$, where J_n = the number of ''new'' juveniles in the observed sample from the present at-sea survey, J_o = the number of juveniles observed on the present at-sea survey, J_p = the number of juveniles observed on the previous survey, ϕ^d = the daily probability of a juvenile staying in the survey area (local survival), and d = the number of days between the present survey and the previous survey. This correction estimates the number of ''new'' HY birds counted during a survey by calculating the number of HY birds seen on the present survey that are likely to have been seen on a previous survey, and subtracting that number from the total count. We estimated the cumulative number of HY birds for the season by summing J_n from all the surveys each year.

Assuming that the distribution of laying dates and fledging dates were equal, the proportion of fledging dates covered by the surveys (0.76) was calculated by extrapolating the range and distribution of fledging dates from the range and distribution of laying dates determined by birds with high vitellogenic-zinc blood titers (Lougheed et al. 2002). The total number of HY birds for the season was calculated by dividing the observed number of fledglings by 0.76, the proportion of fledglings covered by the surveys.

ESTIMATION OF MOVEMENT BY AHY MURRELETS

We estimated the weekly rate of adult local survival in the survey area. Radio-transmitters were used on 40 adult Marbled Murrelets in 1998; 31 were captured in the survey area and are used in the present analysis. Murrelets were captured by nightlighting from 4–18 May. Transmitters used for adults were similar to those used for HY birds, but were attached by a subdermal anchor following the technique of Newman et al. (1999); epoxy glue (Bird Adhesive, Titan Corporation, Washington) was used instead of a suture to secure the device. Birds were radio-tracked by boat telemetry from the first week of May to the second week of August using the same methodology as described for HY movements (above). Telemetry stations were monitored three times per day (morning, afternoon, and night) during four consecutive days every 7-day period. Additional data were gathered with a Robinson 22 helicopter during aerial telemetry from 12 May to 4 July. Two H-antennae were mounted on the helicopter struts, one on each side to determine directionality, connected to a switch box and the receiver. Radios lasted an estimated 60 days, based on ad hoc observations of radios with aberrant pulse rates or tones. Three birds were removed from the analysis due to early radio malfunction.

Cormack-Jolly-Seber open population models were used, as described for HY birds, to estimate the weekly rate of local survival of AHY birds in the survey area. Presence and absence of radio-tagged AHY birds in the survey area were aggregated into nine 1-week periods, beginning on 8 May and ending on 10 July 1998. After this period, emigration, death, and radio malfunction would be confounded. Residence time of AHY birds was estimated as $1/-\ln(\phi)$ (White 1999). We arbitrarily defined ''low'' weekly adult emigration as less than 10% (greater than 90% local survival).

JUVENILE RATIOS

We calculated ''corrected'' juvenile ratios using the estimated total number of HY birds from at-sea surveys (corrected for turnover and proportion of the fledging period covered by surveys) divided by the mean of the AHY bird counts during the peak fledging period. The mean of the AHY counts peak was calculated from all surveys done from 10 days before to 10 days after the peak AHY count each year. The rationale for using this mean for the corrected juvenile ratios was that high local survival of AHY birds (see Results) indicates the presence of a resident population in the survey area during the breeding season. In a resident population, the fluctuation in numbers of AHY birds on the water should reflect seasonal changes in breeding chronology; therefore, the mean of the peak period would better reflect the size of the local adult population. This is a minimum estimate of

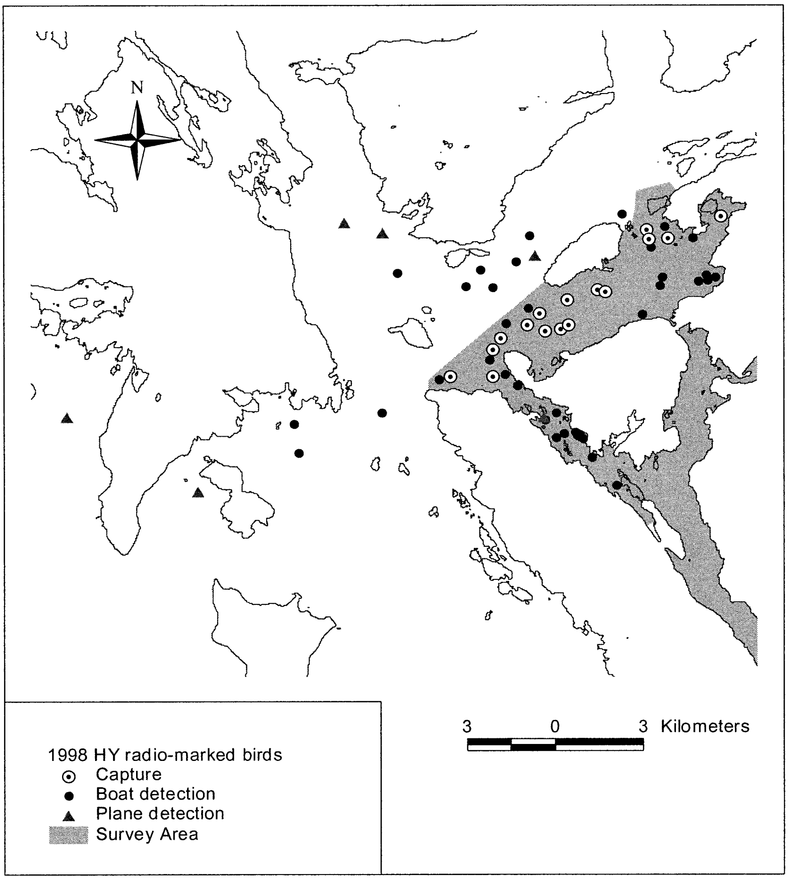


FIGURE 2. Capture and detection locations for 16 hatch-year (HY) Marbled Murrelets marked with radio-transmitters in Desolation Sound, British Columbia. Capture was within the survey area, but many radio-tagged HY birds were subsequently detected outside it, where these birds would not have been sighted during at-sea surveys.

the local adult population because of the weekly emigration rate of adults.

We also calculated ''concurrent'' juvenile ratios using the common technique of dividing the number of HY birds by the number of AHY birds counted concurrently during surveys at sea conducted throughout the fledging period. We calculated the mean juvenile concurrent ratio for all surveys done from the first observation of a HY bird at sea to the end of the survey period each year.

RESULTS

LOCAL SURVIVAL

Twelve of the 16 juveniles were detected by telemetry in the survey area on at least one occasion after capture; nine of these were not detected in the vicinity of Desolation Sound once they left the survey area. Two other juveniles were never detected in the survey area, but were detected on one occasion each outside the survey area, one by boat telemetry and the other by aerial telemetry. Two juveniles were never detected after tagging and release. Aerial telemetry detected three birds on 10 August, one in the survey area and two outside it, and three on 19 August all in the vicinity of Desolation Sound, but outside the survey area. Capture and sighting locations are shown in Figure 2. No juveniles with radios were detected in any other area of the Strait of Georgia.

The daily local survival rate of juveniles in the survey area (ϕ) was 0.829 $\pm$ 0.046 (95% CI = 0.720–0.902), and the recapture rate (P) was

TABLE 1. Fit of survival models to detection data for hatch-year and after-hatch-year Marbled Murrelets in Desolation Sound, British Columbia. For both age groups, the most parsimonious model (with the lowest AIC) is the reduced model with constant survival (ϕ) and recapture (P) rates, $\phi(\cdot)P(\cdot)$.

Age group	Model	AIC	ΔAIC	No. of parameters	Model deviance
Hatch year	$\phi(\cdot)P(\cdot)$	92.71	0.00	2	77.33
	$\phi(t)P(\cdot)$	147.55	54.85	21	54.29
	$\phi(\cdot)P(t)$	162.75	70.04	23	53.09
	$\phi(t)P(t)$	616.14	523.44	38	35.05
After hatch year	$\phi(\cdot)P(\cdot)$	241.94	0.00	2	105.41
	$\phi(\cdot)P(t)$	246.70	4.77	9	94.95
	$\phi(t)P(\cdot)$	252.62	10.68	9	100.87
	$\phi(t)P(t)$	257.66	15.73	15	91.58

0.718 ± 0.084 (95% CI = 0.528–0.853). The daily rate of emigration was 0.171. The model with the best fit to the data (the one with the lowest AIC) was the model of constant survival and constant recapture rates $\phi(.)P(.)$ (Table 1). There was no significant variation in survival rate [model $\phi(t)P(.)$ vs. $\phi(.)P(.)$, $\chi^2_{19} = 23.0$, $P = 0.24$], or recapture rate [model $\phi(.)P(t)$ vs. $\phi(.)P(.)$, $\chi^2_{21} = 24.2$, $P = 0.28$] over time. The weekly local survival rate (ϕ^7) was 0.269 (weekly emigration rate = 0.731), and the average residence time of HY birds in the survey area was 5.3 days.

The weekly rate of AHY local survival (ϕ) in the survey area, during the early part of the breeding season, was 0.946 ± 0.019 (95% CI = 0.893–0.974), and the recapture rate was 0.771 ± 0.036 (95% CI = 0.694–0.833). The weekly rate of emigration was 0.054. The most parsimonious model (the one with the lowest AIC) was the model with constant survival and constant recapture rates, $\phi(.)P(.)$ (Table 1). There was no significant variation in survival rate (model $\phi(t)$ $P(.)$ vs. $\phi(.)$ $P(.)$, $\chi^2_7 = 4.5$, $P = 0.72$), or recapture rate (model $\phi(.)P(t)$ vs. $\phi(.)P(.)$, $\chi^2_7 = 10.5$, $P = 0.16$) over the 9-week study period. The average residency time of AHY birds in the survey area was 18 weeks (126 days).

CORRECTED JUVENILE COUNTS

After correcting for HY dispersal, more than twice as many ''new'' juveniles were estimated per survey in 1996 (3.9 ± 1.5, range 0–21, n = 17) than in either 1997 (1.6 ± 0.4, range 0–4, n = 13), or 1998 (1.7 ± 0.4, range 0–5, n = 12). The cumulative number of juveniles, after correcting for turnover and proportion of fledging surveyed, was 88 in 1996, 28 in 1997, and 26 in 1998 (Table 2). AHY counts during at-sea surveys decreased with increasing cumulative numbers of HY counts (Fig. 3).

JUVENILE RATIOS

Five surveys were done during the 20-day peak period (from 10 days before to 10 days after the peak) in 1996 (22 June–12 July), 5 in 1997 (2–22 June), and 3 in 1998 (25 June–15 July). The mean corrected juvenile ratio for 1996 to 1998 was 0.13 ± 0.05 (range 0.06–0.24; CV = 0.70). Uncorrected totals of HY birds were 17 in 1996 (25 June–14 August), 14 in 1997 (27 June–5 August), and 12 in 1998 (11 June–12 August).

TABLE 2. Juvenile ratios calculated using the mean AHY bird counts from 10 days before to 10 days after the peak count of the season, and HY bird counts adjusted for turnover and proportion of fledging missed by ending surveys early.

Year	Mean peak AHY counts (n surveys)	Corrected number of HY birds	Corrected juvenile ratios	Concurrent juvenile ratios (means)
1996	374 (5)	88	0.23	0.08
1997	283 (5)	28	0.10	0.03
1998	435 (3)	26	0.06	0.01
Mean ± SE	364.0 ± 44.2	43.3 ± 20.3	0.13 ± 0.05	0.04 ± 0.02

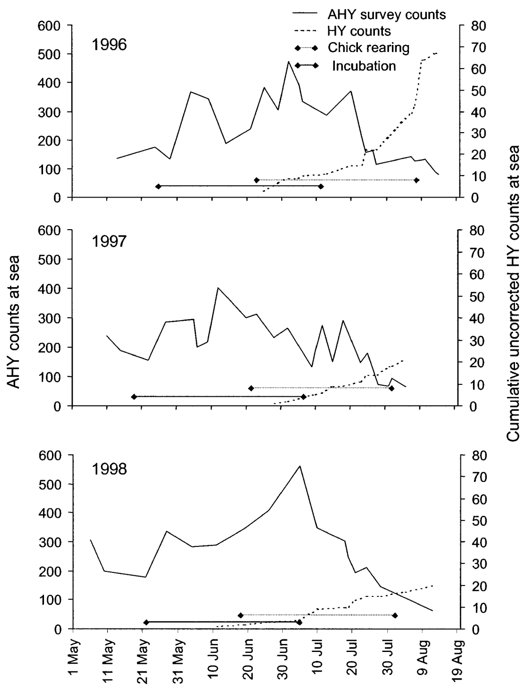


FIGURE 3. After-hatch-year (AHY) and cumulative uncorrected hatch-year (HY) Marbled Murrelet counts during at-sea surveys. Incubation and chick-rearing periods are shown for each year.

The mean concurrent juvenile ratio was 0.04 ± 0.02, ranging from 0.02–0.08 (Table 2).

DISCUSSION

This study provides the first estimates of the emigration rates of HY and AHY Marbled Murrelets during the breeding season. HY birds had a high emigration rate compared to AHY birds. Juveniles do not accumulate in the same areas adults do, and because it is logistically difficult to cover large areas of water, emigration of HY birds must be accounted for prior to the calculation of the juvenile ratio in our study area. It appears, however, that there are other factors affecting juvenile ratios. Although AHY birds were residents, unpredictable variation in breeding success could lead to variation in at-sea counts. This may make year-to-year variation in juvenile ratios difficult to interpret. Although our estimates are unique to Desolation Sound, this study highlights the importance of understanding local movements of Marbled Murrelets at sea.

Emigration of AHY birds from the survey area was low during incubation and early chick rearing (high weekly local survival, about 95%), confirming that birds using the area of Desolation Sound during the breeding season are residents, rather than transients. The weekly 5% adult emigration rate is possibly related to nesting failure. We could not estimate local survival of AHY birds after chick rearing because most of the radio-transmitters had either fallen off or failed by that time. It is unlikely that AHY local survival remains constant toward the end of the breeding season, given the decreases of at-sea counts which are possibly due to emigration of adults after breeding. This is one of the reasons that juvenile ratios calculated using peak breeding season AHY numbers more accurately reflect fecundity than those calculated from concurrent at-sea surveys.

Although the weekly emigration rates of AHY birds were low, counts of birds on the water increased from incubation to chick rearing (during 1996 and 1998; see Fig. 3). We interpret this as nesting birds returning to the water after either the egg had hatched or the nest had failed. In 1997, however, counts of birds on the water increased during incubation and decreased during chick rearing, which might have been related to extensive breeding failure early in the season. Little is known about long-term variation in reproductive success of Marbled Murrelets. If the birds that failed early emigrated before the birds that hatched chicks appeared on the water, then the peak numbers during those years may not accurately estimate the number of breeders.

In contrast to AHY birds, HY dispersal was rapid (a weekly emigration rate of 73%). HY birds did not accumulate in the survey area. The estimated residency time for juveniles in the survey area (5.3 days) is a minimum estimate because of the unknown age of the juveniles at the time of capture. In general, most juveniles moved beyond boat or plane detection range shortly after leaving the survey area, and in some cases (7 of 16 birds), they were not detected after leaving the survey area. The flight covered only a portion of the Strait of Georgia, and birds might have moved out of detection range. An adult Marbled Murrelet is known to have migrated to the San Juan Islands area in Washington (Beauchamp et al. 1999), and it is possible that some of the juveniles followed the same route. An influx of Marbled Murrelets occurs in the San Juan Islands starting in late July (M. G. Raphael, pers. comm.). There was no evidence of juveniles moving to nursery areas in the vicinity of Desolation Sound as reported for Alaska (Kuletz and Piatt 1999). Although there is no evidence of mortality of marked juveniles or radio loss during the study, either are possible and cannot be ruled out. Both mortality and radio loss would lead to an overestimate of the emigration rate, and consequently, an overestimate of the number of juveniles.

The 1996–1998 average juvenile ratio (corrected for movement) was 0.13, about 3 times the ratio obtained from concurrent counts (0.04). Reported juvenile ratios from British Columbia, Washington, Oregon, and California range between 0.004 and 0.04 (Beissinger 1995), and are similar to the ratios estimated from concurrent counts in this study. In Alaska, where the ratios were calculated using breeding-season AHY counts, the reported ratios ranged between 0.02 and 0.11 (Kuletz and Kendall 1998), similar to our corrected juvenile ratios. Because the ratios were calculated with different methods, location and calculation method are confounded. These ratios cannot be compared directly.

Year-to-year variation in fecundity is common in alcids (Ainley and Boekelheide 1990) and this is another confounding factor. We found a substantial amount of annual variation in juvenile ratio (CV = 70%) for the three years of the study. Since we extrapolated information on relative movements from 1998 only, it is possible that relative movements were different in 1997, and this could explain some of the observed variation in the estimated counts of juveniles.

Despite that the average corrected juvenile ratio from Desolation Sound was higher than those reported for other areas, it is low compared to independent estimates of fecundity obtained by radio-telemetry from the same population, which suggest that fecundity should be in the range of 0.18–0.22 female fledglings per breeding female (LWL, unpubl. data). Corrected juvenile ratios were also lower than nest success in the area, estimated by tree climbing (0.33, Manley 1999); however, these two measures are not directly comparable because nest success will always be higher than fecundity. There are two possible explanations for low juvenile ratios from at-sea surveys. The first one is an unexpectedly high proportion of nonbreeding birds in the survey counts: because both adult and subadult AHY birds have the same plumage characteristics (Carter and Stein 1995, Strong et al. 1995), subadult AHY birds cannot be identified during at-sea surveys. Therefore, a high proportion of subadult AHY birds in the survey area would cause juvenile ratios to be underestimated. The second explanation for low juvenile ratios is that there are differences in behavior and distribution between AHY birds and recently fledged young. AHY birds are concentrated in and philopatric to the survey area, but juveniles are not. There is no evidence that juveniles follow their parents to the ocean (Nelson 1997); it is possible that they disperse randomly from water locations close to their nest site. Evidence from radio-telemetry shows that the nests of Marbled Murrelets using the survey area are widely distributed throughout an area much greater than the local hills and drainages (Hull et al. 2001). Surveys in the Desolation Sound area, which count birds that nest over this wider area, will not count juveniles produced from the farther nest sites; these surveys will only detect fledglings which have flown in from the local hills and drainages. Therefore, the HY birds counted in the survey area would have been produced by a locally nesting (unknown) proportion of the total number of birds using Desolation Sound, resulting in low ratios.

Although the age structure of the murrelet population in Desolation Sound is unknown, almost all AHY birds captured in the area had a brood patch (LWL, unpubl. data), suggesting that only a relatively small proportion of the population are subadults. The reason that juvenile ratios are lower than other independent measures of fecundity in Desolation Sound is more likely due to differences in the distribution and behavior of AHY birds and juveniles. However, because of the assumptions and possible problems in obtaining consistent estimates of AHY numbers across years, it may be that juvenile ratios from at-sea surveys will not yield reliable estimates of fecundity. Accurately estimating the number of breeding-age birds is essential for the calculation of representative juvenile ratios. Although these estimates are an improvement over concurrent ratios in that they correct for juvenile emigration, they may still be biased, and long term trends could be masked. Because of these unknown biases, caution is needed when interpreting juvenile ratios from at-sea surveys, and they might not be appropriate for long-term monitoring, even if magnitude of the index were disregarded.

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