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AGE RATIOS AS ESTIMATORS OF PRODUCTIVITY: TESTING ASSUMPTIONS ON A THREATENED SEABIRD, THE MARBLED MURRELET (*BRACHYRAMPHUS MARMORATUS*)

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Abstract.—The ratio of hatch-year (HY) to after-hatch-year (AHY) individuals (HY:AHY ratio) can be a valuable metric for estimating avian productivity because it does not require monitoring individual breeding sites and can often be estimated across large geographic and temporal scales. However, rigorous estimation of age ratios requires that both young and adult age classes are sampled in an unbiased manner, an assumption that is rarely tested. We estimated HY:AHY ratios for Marbled Murrelets (*Brachyramphus marmoratus*), a threatened seabird, using at-sea surveys and captures to assess whether age-specific differences in behavior and distribution result in biased productivity estimates in central California. AHY and HY Marbled Murrelets were distributed similarly at sea, and HY individuals did not congregate in nursery areas. Moreover, dispersal by radiomarked AHY Marbled Murrelets out of our survey area occurred at a low rate, and AHY densities were constant over the survey period, which suggests that AHY immigration and emigration did not significantly bias productivity estimates. HY density increased linearly over the survey period as expected if little dispersal occurred, which suggests that productivity estimates were not significantly biased by HY dispersal. Finally, simulation analyses indicated that annual variation in the timing of breeding resulted in only small biases in HY:AHY ratios. HY:AHY ratios were corrected for the proportion of AHY Marbled Murrelets that were incubating and the proportion of HY individuals that had not fledged at the time of sampling. Mean corrected HY:AHY ratios were low on the basis of both at-sea surveys conducted from 1996 to 2003 (0.032; SE = 0.011) and captures conducted from 1999 to 2003 (0.037; SE = 0.028), implying that productivity was poor in central California. Estimating age ratios may be an effective way of monitoring changes in reproductive success and identifying environmental factors that affect Marbled Murrelet populations, though tests of assumptions are needed in other regions. *Received 22 June 2005, accepted 7 April 2006.*

Key words: age ratios, *Brachyramphus marmoratus*, dispersal, Marbled Murrelet, monitoring, productivity.

Le Rapport des Âges comme Estimateur de la Productivité: Tester les Hypothèses avec un Oiseau de Mer Menacé, *Brachyramphus marmoratus*

Résumé.—Le rapport entre les jeunes de l'année (HY) et les jeunes de plus d'un an (AHY) (HY:AHY) peut être une mesure très utile pour estimer la productivité aviaire car il ne nécessite pas le suivi de sites de reproduction individuels et

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peut souvent être estimé sur de grandes échelles géographiques et temporelles. Toutefois, l'estimation rigoureuse du rapport des âges nécessite que les classes d'âge des jeunes et des adultes soient échantillonnées d'une manière non biaisée, une hypothèse qui est rarement testée. Nous avons estimé le rapport HY:AHY pour l'Alque marbrée (*Brachyramphus marmoratus*), un oiseau de mer menacé, dans le centre de la Californie en utilisant des inventaires et des captures en mer afin d'évaluer si les différences de comportement et de répartition spécifiques à l'âge résultent en des estimés de productivité biaisés. Les Alques marbrées AHY et HY étaient similairement répartis en mer et les individus HY ne se rassemblaient pas sur des aires de crèches. De plus, la dispersion des Alques marbrées AHY marquées d'un émetteur à l'extérieur de notre aire d'inventaire s'est produite à un faible taux et les densités des AHY étaient constantes pendant la période d'inventaire, ce qui suggère que l'immigration et l'émigration des AHY n'a pas biaisé significativement les estimés de productivité. La densité des HY a augmenté linéairement durant la période d'inventaire tel qu'attendu si peu de dispersion se produisait, ce qui suggère que les estimés de productivité n'étaient pas significativement biaisés par la dispersion des HY. Finalement, des modèles de simulation ont indiqué que la variation annuelle associée à la synchronisation de la reproduction n'a entraîné que de faibles biais des rapports HY:AHY. Les rapports HY:AHY ont été corrigés en tenant compte de la proportion d'Alques marbrées AHY en train d'incuber et de la proportion d'individus HY n'ayant pas atteint l'envol au moment de l'échantillonnage. Les rapports HY:AHY corrigés moyens étaient faibles pour les inventaires réalisés entre 1996 et 2003 (0.032; SE = 0.011) et les captures effectuées de 1999 à 2003 (0.037; SE = 0.028), ce qui suggère que la productivité était faible dans le centre de la Californie. L'estimation des rapports d'âge peut être un moyen efficace pour suivre les changements du succès de reproduction et identifier les facteurs environnementaux qui affectent les populations d'Alque marbrée, même si des tests d'hypothèses sont nécessaires dans d'autres régions.

Quantifying the production of young is of fundamental importance in avian population ecology and conservation. Productivity is often estimated by monitoring a sample of breeding sites and recording the number of young produced at each site. However, this approach is difficult to implement for species with secretive breeding behavior or inaccessible breeding sites. An alternative approach is to estimate the ratio of juvenile to adult individuals in areas where both age classes congregate (e.g., Newton 1999, Rodway et al. 2003, Iverson et al. 2004). If measured near the end of the breeding season, ratios of juveniles to adults provide a "snapshot" census of productivity, because they implicitly incorporate all components of productivity, such as the proportion of the population that breeds, number of breeding attempts, clutch size, hatching success, and fledging success (Ricklefs and Bloom 1977). Ratios of juveniles to adults have been used to estimate productivity for a range of animal taxa for both theoretical and applied purposes (Scribner and Warren 1990, Ricklefs 1997, Miller 2000, Rodway et al. 2003, Flanders-Wanner et al. 2004, Iverson et al. 2004, Norrdahl et al. 2004, Peery et al. 2004b, Rohwer 2004).

Robust estimation of productivity with age ratios requires that both age classes are sampled in an unbiased manner, but several forms of sampling bias can occur. First, juvenile and adult individuals must be equally observable or trappable. Differences in detectability could arise for several reasons, including nest attendance by adults and the timing of fledging in relation to the timing of surveys used to estimate ratios. Second, juveniles and adults must have equal per-capita immigration rates into, and emigration rates out of, the sampling area. Finally, sampling designs must adequately account for differences in distribution between age classes within the sampling area. If, for example, juveniles are more likely to be sampled than adults because of age-specific differences in behavior or distribution, age ratios will yield productivity estimates that are biased high. Despite the importance of age-specific differences in behavior and distribution for the estimation of age ratios, most studies make little attempt to assess the magnitude of potential biases beyond selecting periods of peak juvenile abundance for sampling.

The Marbled Murrelet (*Brachyramphus marmoratus*; herafter "murrelet") is a threatened seabird in western North America that forages in nearshore coastal waters and nests in commercially valuable coastal old-growth forests (Nelson 1997, Baker et al. 2006). Here, we test assumptions associated with using age ratios as estimators of productivity for murrelets in central California by characterizing the movements and breeding behavior of radiomarked adults, the distribution of adults and juveniles at sea, and seasonal trends in the at-sea densities of both age classes. Murrelet populations are believed to have declined dramatically from logging of nesting habitat, oil spills, gillnetting, declines in prey availability, and nest predation (Carter and Erickson 1992, USFWS 1997, Becker 2001, Peery et al. 2004b). The demography of this species is poorly understood because murrelets exhibit solitary and secretive nesting behavior and nest high in the canopy of large trees (Nelson 1997). Following individual murrelets and determining their nesting fates is not a feasible approach for estimating and monitoring reproductive success over large temporal and geographic scales, because of logistical and financial difficulties associated with capturing and radiomarking murrelets at sea. However, ≥1-year old murrelets (hereafter "after-hatch-year" [AHY] individuals) have plumage characteristics different from those of juvenile murrelets (hereafter "hatch-year" [HY] individuals) that can be identified readily from a boat before late August, but can be identified only in hand after late August, when AHYs initiate their prebasic molt and begin resembling HYs (Carter and Stein 1995, M. Z. Peery pers. obs.).

The extent to which HY:AHY ratios of murrelets represent unbiased estimators of productivity is uncertain, despite frequent ship-based surveys used to estimate HY: AHY ratios (Ralph and Long 1995, Kuletz and Kendall 1998, Kuletz and Piatt 1999, Lougheed et al. 2002a, Peery et al. 2004b, Kuletz 2005). Sampling of HY:AHY ratios must be conducted before all fledging has occurred, because AHY murrelets molting into their prebasic plumage become indistinguishable (unless captured) from HY murrelets before all HYs have fledged, potentially biasing ratios low. Ratios are typically "corrected" for the proportion of HYs that have not fledged at the time surveys are conducted (Beissinger 1995, Peery et al. 2004b), but uncertainty in corrected estimates has not been assessed. A potentially competing bias results from the fact that some AHYs may still be incubating and unavailable for sampling by at-sea surveys. Moreover, HY individuals sometimes segregate spatially into "nursery" areas in Alaska (Andersen and Beissinger 1995, Kuletz and Piatt 1999), and sampling designs that under- or over-sample such areas will result in biased productivity estimates. Seasonal declines in local AHY densities in Alaska and British Columbia can occur because of post-breeding dispersal and may result in positive biases in productivity estimated from age ratios (Kuletz and Kendall 1998, Lougheed et al. 2002a). Similarly, some radiomarked HY murrelets in British Columbia emigrate out of survey areas at the end of the breeding season, potentially biasing productivity estimates low (Lougheed et al. 2002a). Whether age-specific differences in behavior and distribution bias age ratios in other parts of the murrelet's range, particularly the threatened populations in the Pacific Northwest of the United States, has not been evaluated.

Methods

Field Work

We estimated HY:AHY ratios for murrelets with at-sea, ship-based surveys and captures. We conducted at-sea surveys from Half Moon Bay to Santa Cruz, California, from 1996 to 2003, as described in previous studies (Becker et al. 1997; Becker and Beissinger 2003; Peery et al. 2004a, b). We conducted two types of at-sea surveys to estimate ratios: (1) transects parallel to and 400 m from shore (400-m surveys), which is the distance from shore typically containing the greatest numbers of murrelets in central California (Becker et al. 1997); and (2) transects delineated in a zig-zag pattern (zig-zag surveys) 200–2,500 m from shore. Zig-zag surveys were divided into nearshore (200–1,350 m from shore) and offshore (1,350–2,500 m from shore) strata, with ~4× more effort placed in the nearshore stratum. In addition to recording plumage-based ages and group sizes, we estimated the distance of the group from the transect line for subsequent analysis with distance-sampling techniques (Becker et al. 1997, Buckland et al. 2001). We conducted 38 400-m surveys from June through August, 1996–2000, and 55 zig-zag surveys from June through August, 1999–2003. We also estimated HY:AHY ratios by capturing 227 murrelets at sea from 2 August to 19 October, 1999–2003, between Santa Cruz and Half Moon Bay with a salmon dipnet from a small boat at night (Whitworth et al. 1997; Peery et al. 2006a, b).

To assess the effect of dispersal on HY:AHY ratios, we captured and radiotagged an additional 46 AHY murrelets in Año Nuevo Bay from 25 April to 16 May in 2000 and 2001 (Newman et al. 1999; Peery et al. 2004a, b). Not enough HY individuals were captured to conduct radiotelemetry work for this age class. We tracked radiomarked AHY murrelets with aerial and ground-based telemetry from Half Moon Bay to Santa Cruz (i.e., the same area covered by at-sea surveys). When birds were not detected, we conducted aerial-telemetry surveys with a fixed-wing aircraft as far north as the California–Oregon border and ~50 km south of Cambria, California. We conducted aerial surveys parallel to and ~1 km from shore. Radio signals were generally audible up to a distance of 5 km, so radiomarked murrelets were detectable when they were within ~6 km of shore, considerably farther offshore than the area sampled by at-sea surveys (2,500 m).

TESTING ASSUMPTIONS FOR USING HATCH-YEAR: AFTER-HATCH-YEAR RATIOS AS ESTIMATORS OF PRODUCTIVITY

Testing for age-specific differences in at-sea distribution.—To evaluate the effect of age-specific differences in spatial distribution on HY:AHY ratios, we compared the distributions of HY and AHY murrelets characterized with at-sea surveys in three different ways. First, using a chi-square test, we tested the null hypothesis that the proportion of HY and AHY individuals was equal in seven bands that differed in relation to their distance from shore. Second, using a chi-square test, we compared the proportion of HYs and AHYs in eight 10-km segments of coastline between Half Moon Bay and Santa Cruz to test the null hypothesis that HY and AHY individuals were distributed similarly along the coast. Finally, we tested the null hypothesis that HYs were not aggregated near other HYs by comparing the number of HY individuals detected within 2.5 km of 92 HY and 92 AHY individuals using a two-factor analysis of variance (ANOVA) with age class and year as factors.

Detecting and estimating immigration and emigration.—To evaluate the effect of movements by murrelets on HY:AHY ratios estimated with at-sea surveys, we estimated the proportion of radiomarked AHY murrelets that emigrated outside of the survey area used to estimate HY:AHY ratios (i.e., >2,500 m from shore or either north of Half Moon Bay or south of Santa Cruz) by dividing the number of radiomarked murrelets that were detected outside the survey area by the total number of radiomarked murrelets with active transmitters detected over several 10-day intervals. An individual was considered to have dispersed if it was located outside the survey area used to estimate ratios with at-sea surveys at any time during a 10-day interval, even if it was also located inside the survey area during that period. If an individual recorded as having dispersed in one interval returned to the survey area in a subsequent interval, it was no longer considered to have dispersed.

We also tested hypotheses about emigration and immigration with seasonal trends in the density of HY and AHY individuals estimated from at-sea surveys. Specifically, we predicted that the density of HY individuals would increase linearly as the breeding season progressed if emigration was low because, based on known fledging events, the cumulative proportion of young fledged increases linearly over the breeding season (Hamer and Nelson 1995, T. Hamer unpubl. data, M. Z. Peery unpubl. data; see below). If significant HY dispersal occurred, seasonal increases in HY density should slow. The density of AHY murrelets should show no seasonal trend if immigration or emigration is negligible, but should decline if dispersal occurs from the survey area and should increase if dispersal into the survey area from other populations occurs. We estimated density (individuals per square kilometer) for AHY murrelets with distance-sampling techniques implemented in DISTANCE (Buckland et al. 2001; see Peery et al. [2004a] for a detailed description of methodology). Too few juveniles were detected, however, to estimate densities for HY individuals with distance-sampling methods; instead, we treated surveys as 100-m-wide strip transects and assumed that a low proportion of HY murrelets went undetected within 50 m of the transect line, which was a reasonable assumption based on detection functions developed for AHY murrelets (Becker et al. 1997, Peery et al. 2004a).

To ensure that annual variation in density and differences in density between 400-m and zig-zag surveys did not mask seasonal trends in density, we used *Z*-scores to standardize survey-specific density estimates. *Z*-scores represent the number of standard deviations from the mean a particular density estimate was located (Zar 1984). Specifically, the Z-score ($\hat{Z}_{ijk}$) for density estimated during survey *i* of type *j* (400-m or zig-zag) in year *k* ($\hat{D}_{ijk}$) was estimated as

$$\hat{Z}_{ijk} = \frac{\hat{D}_{ijk} - \hat{\bar{D}}_{jk}}{\hat{\sigma}_{jk}}$$

where $\hat{\bar{D}}_{jk}$ is the mean density estimate for survey type *j* in year *k* and $\hat{\sigma}_{jk}$ is the standard deviation associated with the mean density estimate (Zar 1984).

We evaluated the level of support for a linear trend, quadratic change, (density + density^2), and no change (intercept only) in density *Z*-scores for each age class using regression models and the model-selection criteria of Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) (Burnham and Anderson 2002). Although it was theoretically possible to observe HY murrelets during at-sea surveys as early as Julian date 140 (based on known fledging events; see below), no HYs were observed before Julian date 178. Therefore, for HY murrelets, we also evaluated support for segmented regression models implemented in PROC NLIN of SAS (SAS Institute, Cary, North Carolina), where density changed linearly until Julian date 178 and afterwards could increase either linearly with a different slope or nonlinearly according to a quadratic model.

CORRECTING HATCH-YEAR:AFTER-HATCH-YEAR RATIOS FOR INCUBATING AFTER-HATCH-YEAR AND UNFLEDGED HATCH-YEAR INDIVIDUALS

To correct for potential bias in HY:AHY ratios associated with not sampling incubating AHYs, we estimated the proportion of 32 radiomarked AHY murrelets that incubated during the period used to estimate HY:AHY ratios (Julian dates 192–234) as described by Peery et al. (2004b); we were unable to determine whether 14 of the 46 radiomarked murrelets incubated. Incubating murrelets were identified by locating nest sites in inland areas with a fixed-wing aircraft equipped with VHF telemetry receivers and ground-based searches. We regressed the proportion of incubating AHYs on any given day against Julian date using a quadratic (date + date^2) regression analysis to develop a correction factor for the number of AHYs observed during at-sea surveys.

We also date-corrected the number of HYs observed on a given at-sea survey for young that had not fledged at the time the survey was conducted. To this end, we estimated the proportion of young expected to have fledged as a function of date on the basis of 47 known fledging events in California (Hamer and Nelson 1995, T. Hamer unpubl. data, M. Z. Peery unpubl. data) using linear regression analysis, with the cumulative proportion of young fledged as the dependent variable and Julian date as the independent variable.

Assessing bias in hatch-year:after-hatch-year ratios due to interannual variation in timing of fledging.—The regression model that we used to date-correct HY:AHY ratios for young that had not fledged did not take into account annual variation in the timing of fledging. It was estimated from fledging events pooled across multiple years, even though mean fledging dates and fledging durations can vary considerably among years for murrelets (Lougheed et al. 2002b, McFarlane-Tranquilla et al. 2003). If, for example, mean fledging occurred earlier than average in a particular year, using a pooled correction model would result in an annual HY:AHY ratio estimate that was biased high. We assessed the magnitude of such biases with Monte Carlo simulations, where we simulated the effect of changes in the timing and duration of fledging on the number of HY birds available for sampling by at-sea surveys at any given time in the sampling period (Julian dates 192–234). For each of 1,000 simulations, the duration of the fledging period was varied according to a uniform distribution of 50–100 days (high-variability scenario) and 75–100 days (low-variability scenario). On the basis of studies at higher latitudes in British Columbia (Lougheed et al. 2002b, McFarlane-Tranquilla et al. 2003), we consider it unlikely that fledging occurred within a shorter window than 50 days. The mean fledging date was varied according to a uniform distribution from Julian dates 179 to 239 (i.e., 30 days earlier or later than the observed mean fledging date) but was constrained so that the first and last fledging dates never exceeded the first and last expected fledging dates estimated from the 47 known fledging events (Julian dates 158 and 260). Thus, the mean fledging date varied the most when fledging occurred over a short period (i.e., high-variability scenario).

We developed a linear-regression model from the randomly determined mean fledging date and fledging duration that predicted how many of 24 HY individuals were available for sampling at any given date (600 AHY individuals were assumed to be available for sampling; i.e., an expected HY:AHY ratio of 0.04). We then randomly selected eight dates on which to sample the HY:AHY ratio data and corrected the number of simulated HYs with the pooled correction model used to date-correct actual HY:AHY ratio estimates. Mean percentage error was estimated as the absolute value of the difference between the expected HY:AHY ratio and the simulated date-corrected HY:AHY ratio divided by the expected HY:AHY ratio. We simulated HY:AHY ratios over study periods of 1–15 years to assess the effect of study-period duration on errors in HY:AHY ratios arising from annual variation in breeding chronology.

Estimating Hatch-year:After-hatch-year Ratios

We estimated HY:AHY ratios for murrelets on the basis of at-sea surveys conducted from Julian dates 192 to 234, when 34% to 75% of young were expected to have fledged. We estimated the (observed or date-corrected, see below) HY:AHY ratio R in year t with the following equation:

$$\hat{R}_t = \frac{\sum_1^n H_i}{\sum_1^n A_i}$$

where H_i and A_i are the number of HY and AHY individuals for survey i, respectively, and n is the number of surveys conducted in year t (Levy and Lemeshow 1991). We estimated $\operatorname{var}(\hat{R}_t)$ as

$$\hat{\operatorname{var}}(\hat{R}_t) = \frac{1}{n}\left(\begin{array}{l}\dfrac{\hat{\operatorname{var}}(\hat{H}_t)}{\hat{\bar{A}}_t^2} + \dfrac{\hat{\bar{H}}^2\,\hat{\operatorname{var}}(\hat{A}_t)}{\hat{\bar{A}}_t^4} \\ -\dfrac{2\hat{\bar{H}}_t\,\hat{\operatorname{cov}}(H_t, \hat{A}_t)}{\hat{\bar{A}}_t^3}\end{array}\right)$$

where $\hat{\operatorname{var}}(\hat{H}_t)$ is the variance in the number of HYs observed in year t, $\hat{\operatorname{var}}(\hat{A}_t)$ is the variance in the number of AHYs observed in year t, $\hat{\operatorname{cov}}(\hat{A}_t, \hat{H}_t)$ is the covariance between the number of HYs and AHYs observed in year t, and $\hat{\bar{H}}_t$ and $\hat{\bar{A}}_t$ are the mean numbers of HYs and AHYs observed in year t, respectively (van Kempen and van Vliet 2000). We estimated the mean HY:AHY ratio for the entire study period ($\hat{\bar{R}}$) by averaging unweighted annual estimates, and $\hat{\operatorname{var}}(\hat{\bar{R}})$ was estimated as

$$\hat{\operatorname{var}}(\hat{\bar{R}}) = \frac{\sum_1^n \hat{\operatorname{var}}(\hat{R}_t)}{n}$$

where n was the number of years in which surveys were conducted (Thompson et al. 1998).

Results

We detected 94 HY murrelets during 93 ship-based, at-sea surveys from 1996 to 2003 ($\bar{x}$ = 1.0, SD = 1.2, range = 0–6) compared with 6,951 AHY murrelets ($\bar{x}$ = 74.7, SD = 50.2, range = 13–225). The date of first detection for HY murrelets averaged 13 July but was as early as 26 June in 2001 and as late as 11 August in 1998.

At-Sea Distributions of Hatch-year and After-hatch-year Murrelets

On the basis of at-sea surveys, mean distance from shore for HY ($\bar{x}$ = 607 m, SE = 32, *n* = 54) and AHY individuals ($\bar{x}$ = 640 m, SE = 7, *n* = 1458) did not differ significantly (*t* = 0.89, df = 1,510, *P* = 0.371), and there was no difference in the frequency distributions of HY and AHY murrelets with respect to distance from shore (χ^2 = 5.17, df = 6, *P* = 0.522; Fig. 1A). There was also no significant difference in the proportion of HY and AHY murrelets detected in eight 10-km segments of coastline between Half Moon Bay and Santa Cruz (χ^2 = 6.57, df = 7, *P* = 0.475; Fig. 1B).

There was no evidence from ship-based surveys that HY murrelets occurred in highly clumped nurseries. For surveys that detected at least two HYs, the mean distance between consecutive HY locations was 14.3 km (SD = 13.6, *n* = 41). Hatch-year individuals (*n* = 92) occurred in significantly smaller groups than AHY individuals (χ^2 = 73.1, df = 3, *P* < 0.001, *n* = 3,984), because HY murrelets most often occurred by themselves, whereas AHY murrelets most often occurred in pairs (Fig. 2). Only 2 of 92 (2.2%) groups with an HY murrelet present contained more than one HY murrelet. Over all years, the number of HY murrelets detected within 2.5 km of an HY murrelet did not differ from the number of HY individuals detected near AHY murrelets (*F* = 0.05, df = 1 and 168, *P* = 0.827), though a significant interaction occurred between age and year (*F* = 2.22, df = 7 and 168, *P* = 0.035). Student's *t*-tests of least-squares means indicated that more HY individuals were detected near HY than AHY individuals in 2000 and 2001 (*t* = 2.80, df = 1 and 40, *P* = 0.006; and *t* = 2.56, df = 1 and 36, *P* = 0.025, respectively), but not in any other year (all *P* > 0.05).

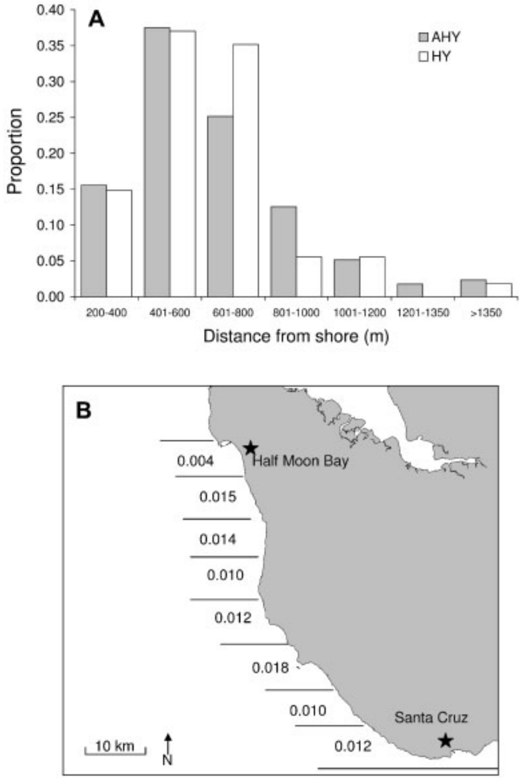

Fig. 1. At-sea distribution of after-hatch-year (AHY) and hatch-year (HY) Marbled Murrelets in central California in the breeding season, 1996–2003. (A) Distribution of distances from shore based on zig-zag line transects that ranged from 200 to 2,500 m from shore (*n* = 54 HY and 1,458 AHY groups). Approximately three times more effort was allocated between 200 and 1,350 m than between 1,350 and 2,500 m. (B) Uncorrected HY:AHY ratios in eight 10-km long segments of coast based on zig-zag line transects and transects parallel to and 400 m from shore (*n* = 94 HY and 6,951 AHY individuals).

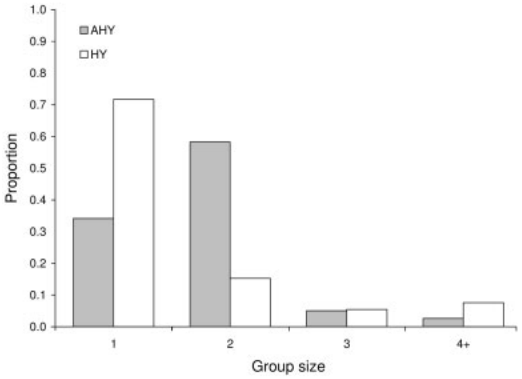

Fig. 2. Frequency distribution of group sizes, by age class, for Marbled Murrelets detected at sea during the breeding season in central California, 1996–2003. Distributions are presented separately for groups containing at least one after-hatch-year (AHY; *n* = 3,984 groups) and one hatch-year (HY; *n* = 92 groups) individual.

Emigration and Immigration by Murrelets

Five (10.9%) of 46 radiomarked AHY murrelets were detected north or south of the area sampled by at-sea surveys. Three individuals made long-distance movements (>200 km) in a southerly direction; two were not detected again in the survey area, but the remaining one returned on two separate occasions. Two other individuals made short movements out of the survey area (<15 km); both returned within a week of emigrating. A sixth murrelet was detected 2 km outside of the survey area on a single occasion and was not considered to have emigrated. Only 11 (1.2%) of 913 of aerial-telemetry locations were >2,500 m from shore, which indicates that offshore movements by AHY individuals had little effect on HY:AHY ratios estimated with at-sea surveys. The proportion of AHY individuals emigrating out of the survey area was similar in 2000 and 2001, tended to increase as the breeding season progressed, and averaged 0.11 until radiotransmitters failed in early August (Fig. 3). The two synchronous jumps in dispersal (on Julian dates 160–169 and 190–199) were probably coincidental, given that each of these increases represents the dispersal of a single bird.

There also was no evidence that large numbers of AHY murrelets immigrated into or emigrated from the survey area during the survey period, because no seasonal trend in AHY density was detected (Fig. 4A). The highest-ranked regression model describing seasonal change in AHY density contained only an intercept term, indicating little support for a positive or negative trend (Table 1). Models containing date terms had ΔAIC_c values ranging from 1.90 to 2.69 and were 2.6–3.8× less likely than the intercept-only model based on AIC_c weights (Burnham and Anderson 2002).

Hatch-year density began increasing around Julian date 180, though variability was high among surveys (Fig. 4B). The regression model containing a linear date term was ranked 1.07 and 2.73 AIC_c values higher and was 1.7× and 3.9× more likely than the quadratic and intercept only models, respectively (Table 1). This model was also 2.1× and 2.9× more likely than segmented linear and quadratic models, respectively. Thus, at-sea survey data supported the hypothesis that HY density increased at a constant rate as the breeding season progressed, as predicted if dispersal by HY individuals was low (see below).

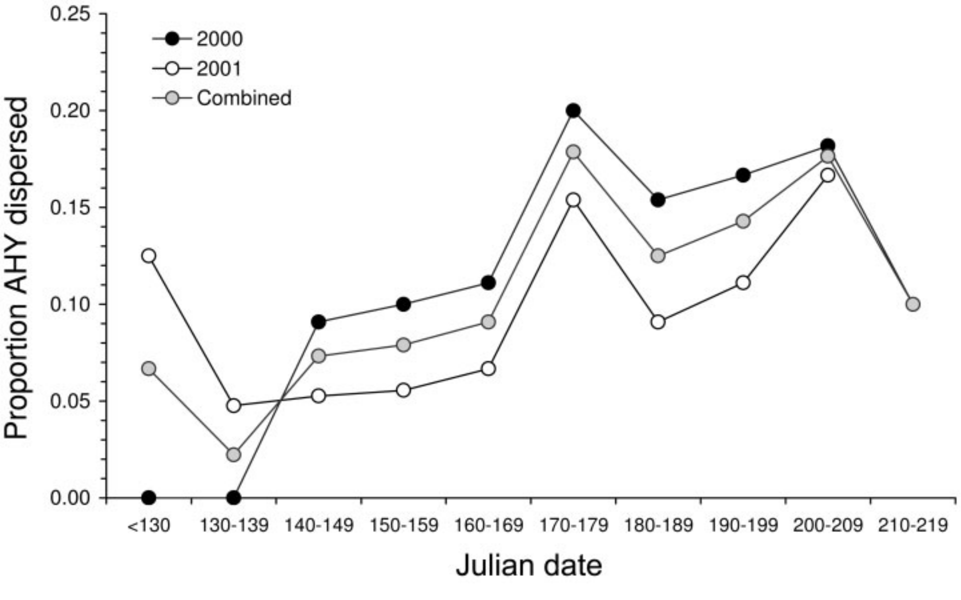

Fig. 3. Proportion of 46 after-hatch-year Marbled Murrelets radiomarked in Año Nuevo Bay, California, in the 2000 and 2001 breeding seasons that dispersed outside of waters sampled by at-sea surveys conducted adjacent to nesting habitat.

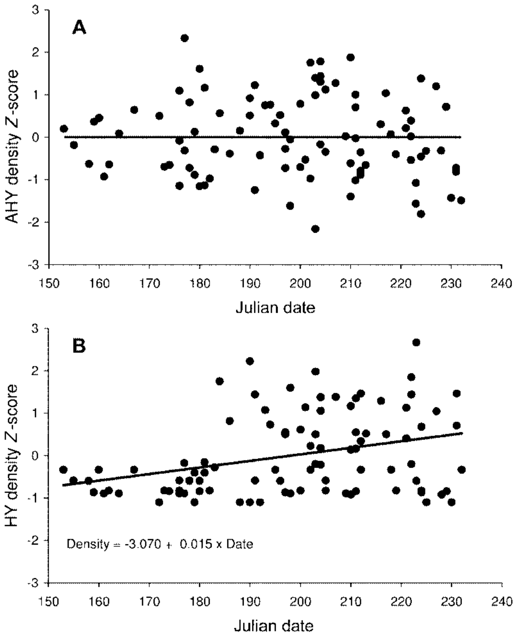

Fig. 4. Seasonal change in at-sea density of (A) after-hatch-year (AHY) and (B) hatch-year (HY) Marbled Murrelets in central California based on 93 at-sea surveys from Julian date 153 to 232. Densities are presented as standardized *Z*-scores to account for differences in density among years and differences between survey methods (zig-zag vs. 400-m transects).

Correcting Hatch-year:After-hatch-year Ratios for Incubation and Asynchronous Fledging

Potential bias caused by incubating birds not being on the water during at-sea surveys was likely to be small. The proportion of individuals that initiated breeding was low (0.31), and >90% of incubation was completed by Julian date 192, when at-sea surveys for HY:AHY ratios began (Peery et al. 2004b; Fig. 5A). On the basis of the behavior of 32 radiomarked AHYs of known reproductive status, the proportion of AHYs incubating on any given day between Julian dates 192 and 199 ranged from 0 to 6%. No incubation was observed after Julian date 199. The mean proportion of individuals incubating on any given day during the period used to estimate HY:AHY ratios (Julian dates 192–234) was <0.01. For surveys conducted from Julian dates 192 to 199, we used the following equation to correct the number of AHYs observed during at-sea surveys for the proportion of AHYs incubating at the time the survey was conducted

$$A_{corrected} = A_{observed} / (1 - [18.7145545 - 0.18445455 \times DATE_i + 0.00045455 \times DATE_i^2])$$

where the right side of the denominator represents the regression model for the proportion incubation AHY regressed against date, $A_{corrected}$

Table 1. Competing regression models ranked by AIC$_c$ for estimating seasonal trends in the density of hatch-year (HY) and after-hatch-year (AHY) Marbled Murrelets in central California, 1996–2003. Julian date was treated as a continuous variable; segmented models were models where the density of murrelets increased linearly until Julian date 178 and then could increase linearly either with a different slope [segmented (date)] or in a quadratic manner [segmented (date + date^2)]. ΔAIC$_c$ is the difference in AIC$_c$ between the best model and the model in question; ω is AIC$_c$ weights that indicate the relative likelihood of the model and sum to 1.0 across models; *K* is the number of parameters in the model and includes the intercept term and the error sums of squares (Burnham and Anderson 2002).

Model	AIC$_c$	ΔAIC$_c$	ω	*K*
		HY		
Date	–3.196	0.000	0.377	3
Date + date^2	–2.119	1.077	0.220	4
Segmented (date + date^2)	–1.678	1.518	0.177	5
Segmented (date)	–1.072	2.125	0.130	4
Intercept	–0.461	2.735	0.096	2
		AHY		
Intercept	–0.461	0.000	0.607	2
Date	1.441	1.902	0.235	3
Date + date^2	2.231	2.693	0.158	4

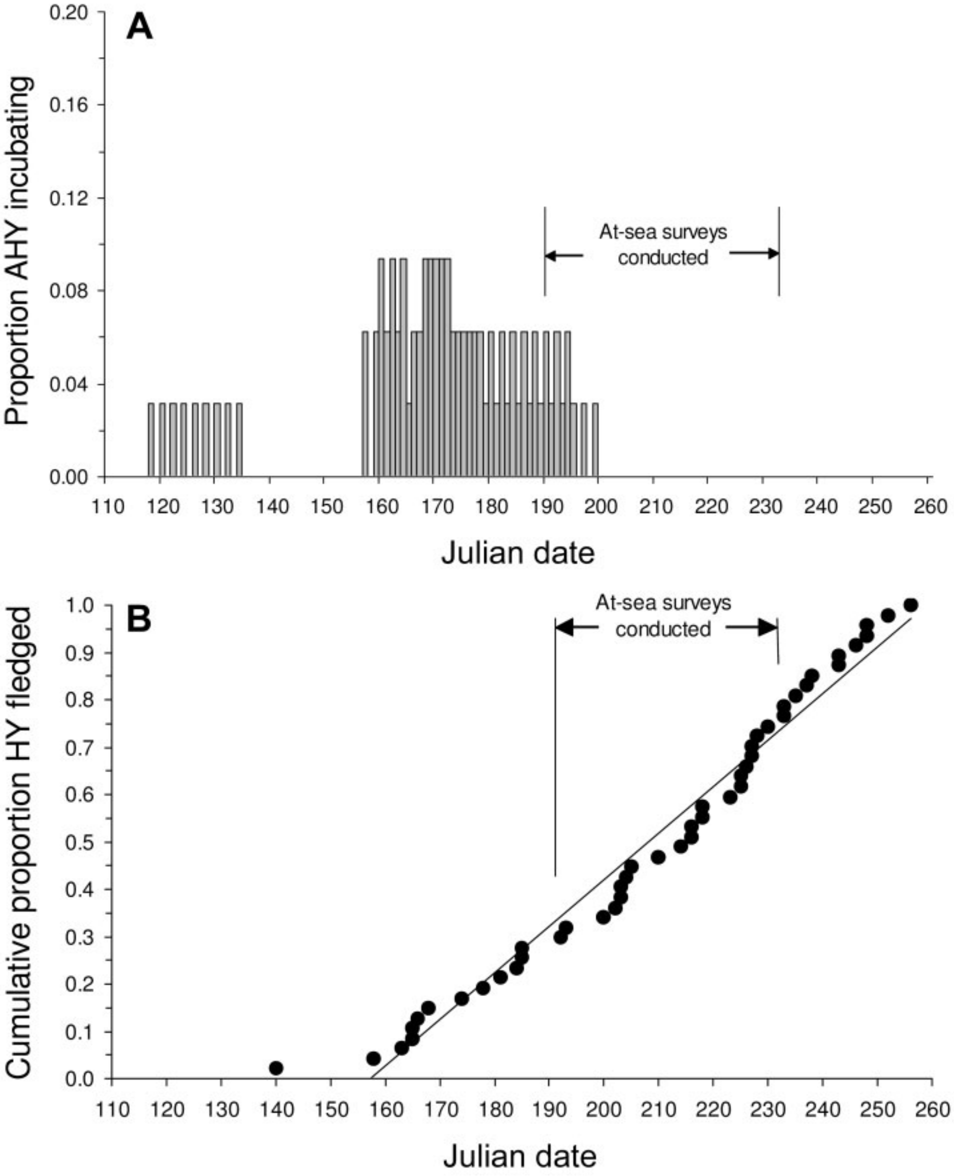

Fig. 5. (A) Proportion of 32 after-hatch-year (AHY) radiomarked Marbled Murrelets incubating as a function of date. (B) Cumulative proportion of hatch-year (HY) Marbled Murrelets fledged as a function of date based on 47 known fledging events in California (Hamer and Nelson 1995, T. Hamer unpubl. data, M. Z. Peery unpubl. data). On the basis of a linear regression analysis, proportion fledged = 0.0098 × Julian Date – 1.5433.

is the date-corrected number of AHY individuals, and $DATE_i$ is the Julian date for survey or capture session i. For surveys after Julian date 199, we assumed that no birds were incubating and did not correct the observed number of AHYs. The HY:AHY ratios estimated using captures were not corrected for incubating AHY murrelets, because no incubation was detected using radiotelemetry during the period when we captured murrelets.

The cumulative proportion of HY fledged increased linearly with date (Fig. 5B). A linear regression model predicted a median fledging date of 209, with the expected fledging period ranging from Julian dates 158 to 260, a period of 102 days. This model explained 97% of the variation in the cumulative proportion of young fledged and encompassed all 47 observed fledging events except one, which occurred on Julian date 140. This event was 18 days before the second known fledging event and was considered an outlier. The number of HY observed or captured ($H_{observed}$) during a given at-sea survey or capture session was corrected for the proportion of HYs that had not yet fledged with the following equation

$$H_{corrected} = H_{observed} / (-1.5433 + 0.0098 \times DATE_i)$$

where the denominator represents the regression model for the cumulative proportion of HY fledged regressed against date, $H_{corrected}$ is the date-corrected number of HY individuals, and $DATE_i$ is the Julian date for survey or capture session i.

Assessing bias in hatch-year:after-hatch-year ratio because of annual variation in fledging.—Monte Carlo simulations indicated that error in estimated HY:AHY ratios was greatest when annual variation in the timing and duration of fledging was high (Fig. 6). For example, when ratios were estimated in a single year, mean error was 10% and 23% for the low- and high-variability scenarios, respectively. However, this error declined substantially as HY:AHY ratios were estimated over more years (Fig. 6). When ratios were estimated over eight years, as in the present study, mean error was only 3% and 9% for the high- and low-variability scenarios, respectively.

Hatch-year:After-hatch-year Ratio Estimates

Because densities of HY and AHY murrelets did not differ with respect to distance from shore (Fig. 2A), we present combined HY:AHY ratios for both at-sea survey types (zig-zag and 400 m). Mean estimates of uncorrected HY:AHY ratios were 0.016 (SE = 0.005, n = 59 surveys) for surveys and 0.035 (SE = 0.020, n = 227 individuals) for captures (Table 2). Date-correcting HY:AHY ratios for incubating AHYs and unfledged HYs nearly doubled estimates from at-sea surveys (0.032, SE = 0.011, n = 59), whereas HY:AHY ratios from captures increased only slightly because birds were caught mostly when fledging was complete or nearly complete (0.037, SE = 0.028) (Table 2). Corrected HY:AHY

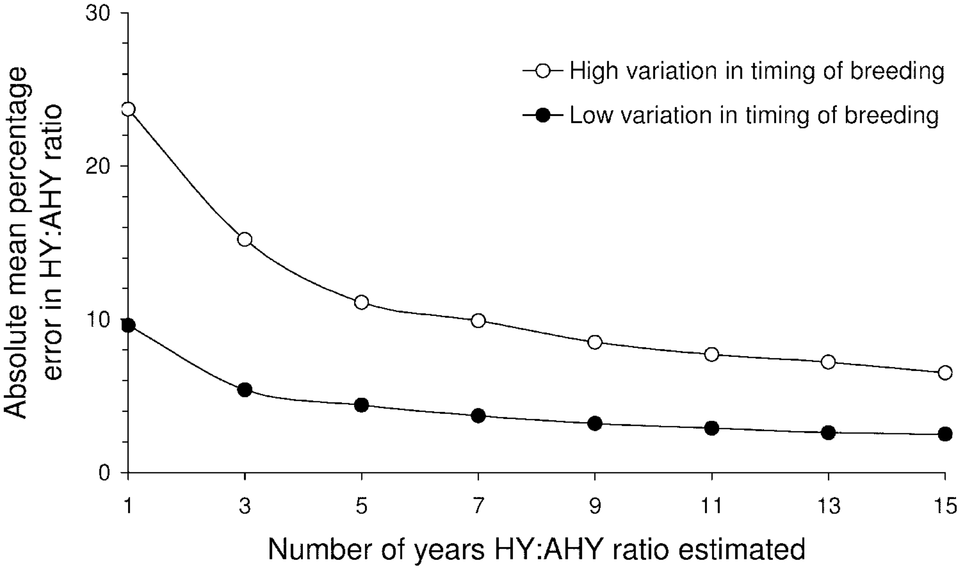

Fig. 6. Mean percentage error in HY:AHY ratios from uncertainty in the timing and duration of fledging as a function of the number of years ratios were estimated, as estimated with Monte Carlo simulations.

Table 2. Annual estimates of hatch-year to after-hatch-year ratios (*R*) and standard errors (SE) for Marbled Murrelets from at-sea surveys and captures conducted in the breeding season in central California, 1996–2003. Surveys and captures used to estimate ratios were conducted from 10 July to 23 August, 1996–2003, and from 4 August to 16 October, 1999–2003, respectively. Corrected estimates were corrected for the proportion of hatch-year murrelets that had not fledged and proportion of after-hatch-year murrelets still incubating at the time the survey was conducted (all captures were conducted after the end of incubation).

	Uncorrected		Corrected		Individuals observed or captured	Surveys conducted
Year	*R*	(SE)	*R*	(SE)	(*n*)	(*n*)
			Surveys			
1996	0.004	(0.003)	0.006	(0.004)	517	3
1997	0.010	(0.003)	0.022	(0.007)	701	5
1998	0.002	(0.003)	0.004	(0.004)	437	6
1999	0.015	(0.005)	0.030	(0.010)	693	10
2000	0.021	(0.010)	0.034	(0.016)	495	8
2001	0.031	(0.006)	0.063	(0.016)	400	8
2002	0.022	(0.005)	0.045	(0.011)	601	11
2003	0.024	(0.005)	0.049	(0.011)	424	8
Total	**0.016**	**0.005**	**0.032**	**0.011**	**4,268**	**59**
			Captures			
1996	–	–	–	–	–	–
1997	–	–	–	–	–	–
1998	–	–	–	–	–	–
1999	0.000	(0.000)	0.000	(0.000)	46	8
2000	0.107	(0.047)	0.111	(0.049)	47	17
2001	0.000	(0.000)	0.000	(0.000)	44	11
2002	0.044	(0.035)	0.050	(0.041)	47	9
2003	0.023	(0.035)	0.025	(0.024)	43	10
Total	**0.035**	**0.030**	**0.037**	**0.028**	**227**	**55**

ratios varied annually but were generally ≤0.06 for both at-sea surveys and captures (Table 2).

Discussion

Most assumptions associated with using at-sea HY:AHY ratios to estimate productivity for murrelets in central California were well supported. Both age classes were distributed similarly offshore and alongshore, and no difference existed in the number of HY individuals detected near AHY versus other HY individuals, which suggests little chance of sampling bias because of transect layout. Unlike studies conducted by Andersen and Beissinger (1995) and Kuletz and Piatt (1999) in Alaska, we found little evidence for the existence of HY nursery areas. Dense concentrations of juveniles were likely not located because of the small population size of breeding adults and low HY densities, but the few juveniles that were observed with at-sea surveys were not aggregated together and did not appear to be distributed differently than AHYs. Why the level of segregation among age classes differed between regions is uncertain, but there are fewer protected waters for HY murrelets to seek refuge along the California coast (as well as in other regions such as Oregon and the outer Washington coast). Regardless of the mechanism, the existence of dense, isolated patches of young birds does not appear to present a potential source of bias in the estimation of HY:AHY ratios in central California.

Radiotelemetry indicated that most AHY murrelets remained within the 209-km^2 study area during the breeding season, and the proportion of individuals recorded outside of the sampling area was low (mean = 11%). Moreover, the density of AHY murrelets did not change significantly as the breeding season progressed, unlike AHY murrelets in British Columbia and Alaska that decline in density because of postbreeding dispersal (Kuletz and Kendall 1998, Lougheed et al. 2002a). Thus, substantial immigration or emigration by AHY individuals did not occur in central California in July and August and should not be an important source of bias in productivity estimated from HY:AHY ratios. Peery et al. (2006b) suggested that immigration (~16% annually) by murrelets into central California may sustain this population on the basis of the fact that the population was stable despite low reproductive success. Here, however, we tested for immigration in July and August only, whereas Peery et al. (2006b) tested for the occurrence of immigration at any time during the year. If the 16% immigration rate estimated by Peery et al. (2006b) occurs uniformly throughout the year, immigration would be only ~2% during our July and August at-sea survey period. Such a low level of immigration would be difficult to detect with at-sea surveys, given the high level of variability in AHY density among surveys (Fig. 4A) and would only result in a very small bias in HY:AHY ratios.

Dispersal by HY murrelets out of at-sea sampling areas probably did not result in a significant underestimation of productivity with HY:AHY ratios, because HY density increased linearly over the breeding season, as expected based on the linear increase in the cumulative proportion of young fledged. If HY dispersal was important during our at-sea surveys, HY densities should have increased initially and then either leveled out or declined (i.e., providing more support for a quadratic density model). Immigration by HY murrelets into our survey area was clearly not important, because so few HY murrelets were detected with at-sea surveys or captures. Radiotelemetry would have provided a more definitive means for estimating HY dispersal than estimating seasonal trends in density, but very few HY murrelets were available in central California for capture and radiomarking.

Lougheed et al. (2002a) found that radiomarked HY murrelets in British Columbia dispersed from at-sea survey areas adjacent to nesting habitat during the breeding season, potentially biasing HY:AHY ratios. However, Lougheed et al.'s work was conducted in a small area of Desolation Sound, and many "dispersal events" were <6 km from the capture location. Juvenile dispersal in this context seems an unlikely explanation for our low HY:AHY ratios, because our at-sea surveys covered an 86-km stretch of coastline and 209 km^2. At least three other lines of evidence suggest that HY murrelets did not disperse out of sampling areas in significant numbers during our surveys. First, in British Columbia, radiomarked HY murrelets dispersed >50 km from capture locations, an average of 19 days after dispersal by AHY individuals (N. Parker unpubl. data). In central California, the mean departure date for 20 AHY murrelets radiomarked at the end of the breeding season was 20 October (M. Z. Peery unpubl. data). Hence, if the difference in the timing of dispersal between age classes is similar between regions, most HY murrelets should remain within the area sampled by our at-sea surveys and captures. Second, HY:AHY ratios are low from central California to Washington, despite the fact that at-surveys encompass nearly the entire coastline in this region (Beissinger 1995, Huff et al. 2006). If HY murrelets disperse from at-sea areas adjacent to nesting habitat from which they fledged, they should be detected by surveys conducted in other areas. Finally, judging from museum specimens, HY:AHY ratios at the end of the 19th century and the beginning of the 20th century in the Monterey Bay region were an order of magnitude higher than they are currently, which suggests that low contemporary HY:AHY ratios are a result of a decline in productivity rather than dispersal by HY murrelets out of sampling areas (Beissinger and Peery 2007). In summary, there is no compelling evidence that HY movements resulted in biased estimates of HY:AHY ratios in the present study, but characterizing the movements of HY murrelets with radiotelemetry is needed to estimate HY dispersal directly.

Monte Carlo simulations indicated that date-correcting the number of HY murrelets observed at sea only resulted in small errors in HY:AHY ratios, especially when ratios were estimated over multiple years. Errors for longer studies were small, because years when the ratio was biased high because of early fledging tended to be balanced by years with late fledging and a negative bias. Simulated errors were larger (10–23%) when HY:AHY ratios were estimated in a single year but were still relatively small when compared with annual variation in date-corrected ratios estimated here (ranging by 16-fold from 0.004 in 1996 to 0.063 in 2001). Therefore, annual variation in the timing of breeding should not obscure annual variation in productivity as reflected in HY:AHY ratios, unless annual differences in reproductive success are small.

Here, we did not test the assumption that HY and AHY murrelets were equally detectable during at-sea surveys. Not all murrelets on the transect line are detected by at-sea surveys (Mack et al. 2002), presumably because a proportion of individuals are diving below the surface when encountered by boat. If such behavior differs between HY and AHY murrelets, HY:AHY ratios would be biased. Differential detectability could not be tested using radiotelemetry because no HYs were radiomarked, and could not be tested by comparing detection functions from distance analyses because distance sampling assumes that all animals are detected on the transect line regardless of age. Nevertheless, in our opinion, it is unlikely that the very low HY:AHY ratio was from AHY murrelets being much more detectable than HY murrelets.

The fact that mean HY:AHY ratios estimated with at-sea surveys and captures yielded similar results was encouraging because differences in methodology can affect estimates of age ratios (Domènech and Senar 1997). Annual HY:AHY ratio estimates from at-sea surveys and captures were not correlated, which is likely attributable to high sampling variation around capture estimates that were based on small samples (Table 2). However, at-sea surveys and captures yielded similar mean date-corrected estimates of fecundity over the eight-year study period (0.032 and 0.037, respectively). Moreover, these estimates were similar to mean fecundity estimates derived from the reproductive histories of radiomarked individuals and nest monitoring (0.044; Peery et al. 2004b). Thus, there appears to be strong support for the conclusion of low levels of productivity by murrelets in central California.

HY:AHY ratios could be used to monitor trends in reproductive success and determine how murrelet populations respond to the management of forested and marine (foraging) habitats, particularly in the threatened portion of the murrelet's range. The HY:AHY ratios and HY densities could be estimated in a series of sampling units and correlated with landscape and marine characteristics to determine the influence of factors such as the amount, distribution, and fragmentation of old-growth forest, water temperatures, and prey availability on murrelet productivity. Indeed, the fact that HY:AHY ratios were particularly low in 1998 (Table 2), when a strong El Niño–Southern Oscillation event negatively affected seabird populations in the northeast Pacific Ocean (Gaston and Smith 2001, Jehl et al. 2002), indicates that HY:AHY ratios are sensitive to and provide a measure of changes in murrelet reproductive success mediated by food resources. Moreover, Kuletz (2005) showed that detecting temporal trends and spatial differences in HY/AHY ratios and HY densities in Alaska was feasible within reasonable time frames and with reasonable levels of survey effort. However, more research is needed in other regions to test assumptions associated with using age ratios as estimators of productivity before a regional sampling design for monitoring productivity is developed and implemented.

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