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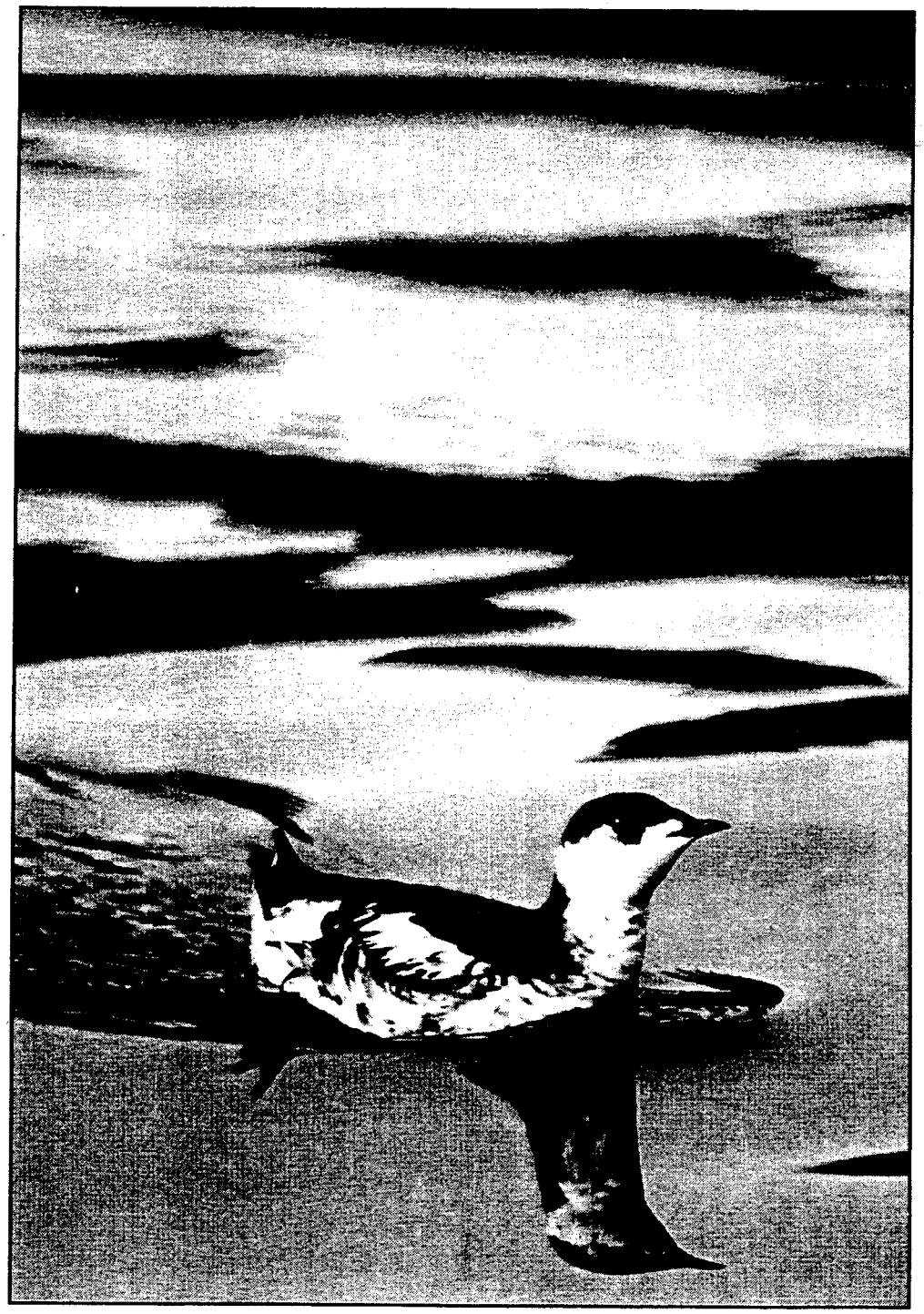
Ecology and Conservation of the Marbled Murrelet



Abstract:

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This report on the Marbled Murrelet (*Brachyramphus marmoratus*) was compiled and editied by the interagency Marbled Murrelet Conservation Assessment Core Team. The 37 chapters cover both original studies and literature reviews of many aspects of the species' biology, ecology, and conservation needs. It includes new information on the forest habitat used for nesting, marine distribution, and demographic analyses; and describes past and potential effects of humans on the species' habitats. Future research needs and possible management strategies for both marine and forest habitats are suggested.

Retrieval Terms: Brachyramphus marmoratus, Marbled Murrelet, old-growth forests, habitat use, marine distribution, seabird.

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Cover: Late-winter-plumaged Marbled Murrelet, Auke Bay, Alaska —Photograph by Gus van Vliet

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Chapter 37

Population Trends of the Marbled Murrelet Projected From Demographic Analyses

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Abstract: A demographic model of the Marbled Murrelet is developed to explore likely population trends and factors influencing them. The model was structured to use field data on juvenile ratios, collected near the end of the breeding season and corrected for date of census, to estimate fecundity. Survivorship was estimated for the murrelet based on comparative analyses of allometric relationships from 10 species of alcids. Juvenile ratios were generally low, and were higher for counts made from shore or in kelp beds (typically 10 percent) than conducted offshore (<5 percent). Annual survivorship was strongly related to body size in alcids. Survival for the Marbled Murrelet was predicted to be 0.845 and range to 0.90. Lambda, the expected annual growth rate of the population, was estimated for likely combinations of fecundity and survival, and indicated that under all combinations murrelet populations are expected to be declining. Based on the best data, rates of decline are predicted to be 4-6 percent per year, but the rate of decline could conceivably be twice as large. Studies in Alaska and British Columbia suggest population declines at 3-5 percent per year, supporting model predictions. Results are discussed in relation to the factors affecting murrelet population growth, and the use of juvenile ratios for monitoring murrelet populations.

Recovering a threatened or endangered species depends on determining its rate of population change and correcting the factors that limit population growth. Despite the important information on the biology and life history of the Marbled Murrelet (*Brachyramphus marmoratus*) that has been brought together in this volume, population trends for the murrelet remain elusive because little long term data are available. Christmas bird counts from five sites in Alaska found a 50 percent decline in the population over a 20 year period (Piatt and Naslund, this volume). Murrelet censuses conducted in Clayoquot Sound, British Columbia 10 years apart found a 40 percent decline in the population (Kelson and others, in press). Comparison of historic and current data suggests that the murrelet has disappeared or become very rare in large portions of its nesting range in California, Oregon, and Washington (Carter and Morrison 1992). But current population trends in the Pacific Northwest remain unknown.

Demographic modeling can give indications of likely population trends and play an important role in the conservation of the Marbled Murrelet. Simple demographic models based on estimates of annual survival and fecundity can be used to determine the rate of decline or increase of a species. They can also help focus attention on critical demographic information that needs to be gathered for future studies. Sensitivity analyses, where demographic values are altered to see the effect on population growth, can indicate which components of the life history are most likely to affect population growth and where the potential for management may be greatest.

Unfortunately, only a little is known about the demography of the murrelet. There are no estimates of survivorship for birds of any age. Reproduction is slightly better understood. Clutch size is known to be one egg, and a substantial proportion of nests are known to fail (Nelson and Hamer, this volume b). However, neither the age of first breeding nor the proportion of adults that breed is known. The ratio of young-of-the-year (hereafter juveniles) to after-hatch-year birds (subadults and adults) has been monitored at-sea and is often very low (e.g., Ralph and Long, this volume).

This paper represents an initial attempt to model the demography of the Marbled Murrelet to explore likely population trends. Although few data are available, there is enough reproductive information from murrelets to use, in conjunction with predictions of survivorship derived from analyses of past studies of alcids, to yield crude estimates of the rate and direction of change of the murrelet population.

Model Structure

The model was structured to take advantage of the one population parameter that could be best estimated from field data - fecundity. In the absence of detailed data, the simplest way to model the murrelet population is based on three life stages: adults (birds that are breeding age or older), subadults (birds that are greater than one year old but younger than the age of first breeding) and juveniles (fledged young that have reached the ocean but have not yet survived their first year of life). The latter stage takes particular advantage of one of two estimates of productivity available from field data - namely the ratio of young to after-hatch-year birds surveyed at sea. The virtue of this scheme - simplicity - is also its weakness. Undoubtedly there may be age variation among the demographic rates of murrelets, as there is with other seabirds (Hudson 1985, Nur 1993, Wooller and others 1992). But without any specific information on the age structure of vital rates, assigning age structure to them would be arbitrary. For the moment, simplicity has its virtue.

The simplified population life cycle given in *figure 1* is based on post-breeding season censuses with a projection interval of one year (Caswell 1989, Noon and Sauer 1992) and is typical for long-lived monogamous birds (McDonald and Caswell 1993). The flow of events is (1) censuses are conducted at the end of the breeding season, (2) birds must then survive to the next breeding season, (3) all individuals are aged one year, (4) surviving adults then breed, and (5) post-breeding censuses are conducted again. Circles or nodes

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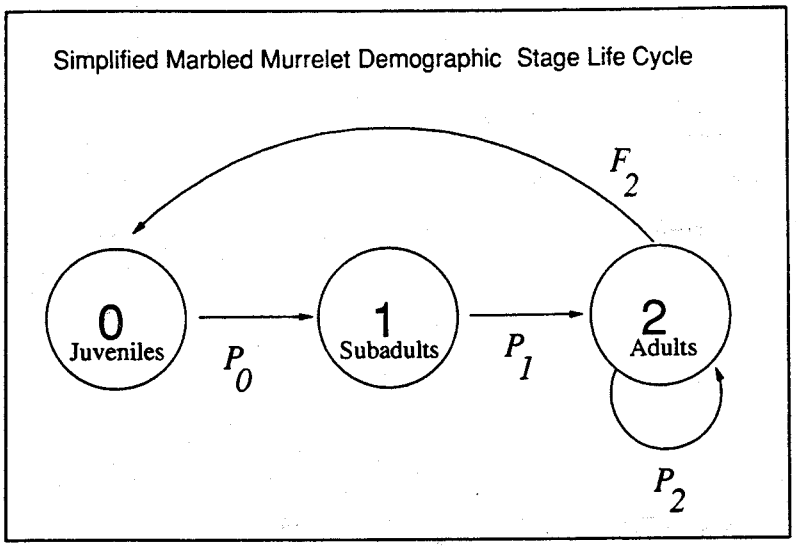

Figure 1—A simplified life cycle diagram for the Marbled Murrelet used in developing predictions of demographic trends: P_0 = Probablity of annual survival for fledglings that have reached the oceans; P_1 = Probablity of annual survival for subadults; P_2 = Probablity of annual survival for adults; and F_2 = annual fecundity, i.e., the number of young reaching the ocean per pair.

(Caswell 1989, McDonald and Caswell 1993) represent the stage classes: juveniles (0), subadults (1), and adults (2). P_0 is the probability of annual survival for fledglings that have reached the ocean. P_1 is the annual survivorship of subadults. Note that this stage may take several years for birds to mature and additional nodes would need to be added for each year that the age of first breeding exceeded 2 years old. The annual rate of adult survival is given by P_2. By definition, only adults breed and their average annual fecundity (i.e., the number of young reaching the ocean per pair) is given by F_2.

I explored only the simplest deterministic version of the model because no data yet exist on the magnitude of fluctuations of demographic characteristics from year to year. The model assumed: (1) survivorship and fecundity would change little from year to year; (2) populations were near a stable age structure; (3) a 1:1 sex ratio, supported by Sealy (1975a); (4) no density dependence; and (5) no senescence occurs and adult birds have no maximum life span. Such assumptions, although sometimes violated to varying extents in real populations, are typical for models of this nature (Lande 1988, Noon and Biles 1990). Usually such models are constructed only for females, since it is often difficult to know much about male fecundity. Thus, all rates needed for *figure 1* were expressed on a per female basis. Since there are little data available for murrelets, the model was evaluated for a range of feasible demographic values.

Methods

Survivorship estimates were derived from the literature, because there have been no studies of individually-marked murrelets. A comparative analysis of survivorship of auks was conducted by Nadav Nur (1993). Allometric relationships and multiple regression models between body size (32-8000 g), reproductive rate (which is clutch size [1–2 eggs] times brood number [1–2 broods per year]), and annual survival were developed for 10 species of Alcidae. Estimates of annual survival for adult murrelets were then made assuming an adult body size of 222 g (Sealy 1975a) and a clutch size of 1 egg. Estimates of annual survival for juveniles and subadults were assumed to be proportional to adult survival as revealed from the literature survey of other seabird species.

Fecundity values indicate the average number of female young produced annually by a female that has reached or exceeded the age of first breeding. The only murrelet demographic data that I have found pertains to the reproductive potential of the species: ratios of juveniles to after-hatch-year birds (adults and subadults) in the ocean (hereafter called the "juvenile ratio"), and an estimate of nesting success (the number of young produced per nesting pair). Information on nesting success was derived from Nelson and Hamer (this volume b).

Arguably the best data on reproductive potential are ratios of juveniles from at-sea surveys. If measured at the end of the breeding season, these ratios act like a "snapshot" census of recruitment rates because they implicitly incorporate all of the parameters needed to estimate fecundity: clutch size, the proportion of nests fledging young, the proportion of birds nesting, the number of nesting attempts per year, and the survivorship of fledglings to the sea until the time of census. Because this "snapshot" is taken immediately near the end of the breeding season, a

post-breeding population model was used. Similar ratios have been used to examine population trends in a variety of other wildlife studies (Hanson 1963, Lambeck 1990, Paulik and Robson 1969, Roseberry 1974).

At-sea surveys should be conducted before subadults and adults begin to molt into winter plumage and become difficult to distinguish from young-of-the-year (Carter and Stein, this volume). In most years, molting adults and subadults are first detected in mid- to late August (Carter and Stein, this volume; Ralph and Long, this volume). Therefore, I used survey data collected on or before 16 August, and pooled results for two week periods to yield reliable sample sizes. However, fledging of young can occasionally occur until late September (Hamer and Nelson, this volume a). When the at-sea surveys were conducted, it is likely that some young had not yet fledged (and thus would not be detected), but most adults were censused since they were in the ocean gathering food to feed young. Therefore, this ratio will tend to underestimate recruitment. To correct for this problem, I used the cumulative frequency distribution for estimates of "known" fledging dates for all nests or young found throughout the range (Hamer and Nelson, this volume a). From this distribution, I determined what proportion of young would have fledged by the end-point of the census date and then adjusted the juvenile ratio upwards by this factor.

There is one problem with using juvenile ratios to estimate fecundity. Fecundity is the number of female young per *adult female* produced annually. But during the censuses, *subadults* can not be distinguished from adults that are capable of breeding. Therefore, just using the ratio of juveniles to after-hatch-year birds from the censuses will tend to underestimate fecundity because the proportion of adults will be overestimated. This can be seen by conducting a deterministic projection of a population for 25 years and looking at the proportion of the population that fledglings comprise. Just using the value from the ratio usually results in a lower ratio of young-of-the-year birds to older birds than expected. Fortunately, the ratio can be corrected by increasing it incrementally until the population projection yields the proper starting ratio of juveniles to older birds.

Alcids typically exhibit delayed ages of first breeding (Croxall and Gaston 1988, Hudson 1985). One of the earliest recorded ages of first breeding is for Cassin's Auklet (*Ptychoramphus aleuticus*) where some birds begin at 2 years but most start at 3 years of age (Croxall and Gaston 1988). Hudson (1985) estimated 5 years in general for Atlantic alcids. The age of first breeding of individuals, however, ranged between 3 and 15 years (Harris and others 1994). Given its small body size, it is unlikely that the murrelet would require 5 years to reach sexual maturity, although it could require longer to obtain a nest site if sites were limiting. On the other hand, nest sites were probably much more abundant historically than they are today as a result of deforestation. Thus, in comparison to most other seabirds, which nest colonially on islands where obtaining a breeding site can sometimes be difficult (Hudson 1985), it seems likely that the Marbled Murrelet would have a young, rather than old, age of first breeding. I suspect that an age of first breeding would be 3 years, but explored ages from 2 to 5 in the model.

Once demographic traits were selected, values were used to calculate lambda (the expected annual growth rate of the population) and the stable stage distribution. Populations decline when lambda is less than 1 and increase when lambda exceeds 1. The stable stage distribution is the proportion of the total population that is comprised of each stage class and can be used to yield an expected juvenile ratio. Lambda and the proportion of juveniles in the stable age distribution were calculated: (1) analytically by constructing Leslie matrices and solving for the dominant eigenvalue and right eigenvector (Caswell 1989) using MATLAB (1992); and (2) numerically using spreadsheets to project population changes over 25 years (Burgman and others 1993). I used these same methods to explore what levels of adult survival and fecundity are required to yield estimates of lambda equal to 1 for different ages of first breeding and the juvenile ratios that these combinations would produce. A sensitivity analysis was conducted by determining the partial derivative of lambda with respect to each element in the Leslie matrix (Caswell 1989, McDonald and Caswell 1993).

Results

Estimating Fecundity

Reproduction in the marbled murrelet appears to be highly asynchronous. The cumulative frequency distribution for estimated dates of fledging throughout the range of the murrelet shows a regular increase during the breeding season (*fig. 2*). Fledging has occurred as early as the first week in June and very rarely as late as September, although 94 percent of the nests had fledged by the end of August. Fledging finished by the end of August in Alaska, British Columbia, and Washington, but in Oregon and California, it extended into September (see fig. 3 in Hamer and Nelson, this volume a). A linear model fit the data well, especially through the middle portions of the range of fledging dates (*fig. 2*). This model was used to estimate the cumulative proportion of nests that had fledged to adjust juvenile ratios for differences in the date of surveys.

Table 1 summarizes the ratio of juveniles for different localities, survey periods, and years for surveys made from shore or from a boat cruising only through kelp beds, which juveniles appear to frequent preferentially (Sealy 1975a). Similar data are shown for the juvenile ratio from boat surveys at sea (*table 2*). Several trends are evident. First, the proportion of juveniles encountered was much greater near shore (<800 m from shore) and on kelp bed surveys (*table 1*), than on boat surveys (*table 2*) of near shore (500-800 m) and distant waters (from 1400 m up to 5 km off shore in some cases). All at-sea surveys had adjusted ratios of juveniles of less than 5 percent, while onshore surveys typically had adjusted ratios of 9–16 percent juveniles. Juveniles were

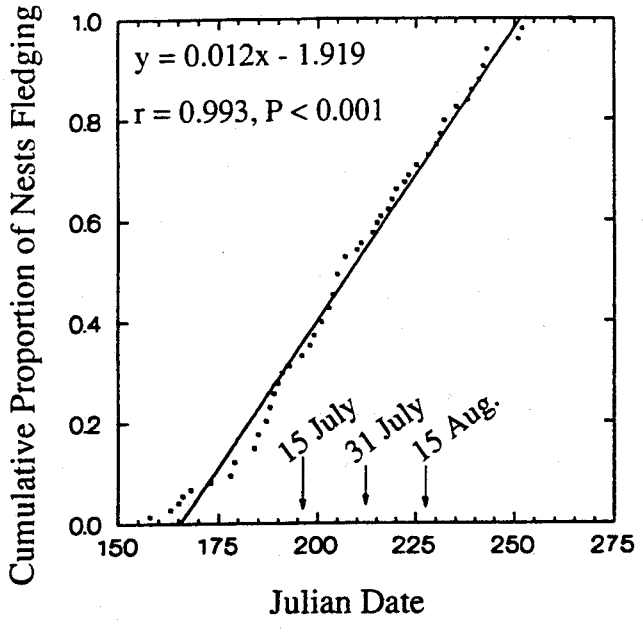

Figure 2—The cumulative probability distribution function for fledging dates of 74 Marbled Murrelet nests. Results of a linear regression of Julian date (x) on the cumulative proportion of nests that fledged (y) was fit to data and are given. No probability value can be calculated for the regression because cumulative fledging values are not independent. Data are from Hamer and Nelson (this volume a). Dates shown refer to the end point of censuses used to adjust the juvenile ratio.

rarely seen beyond 1 km offshore, whereas adults have frequently been seen up 3 km off shore and were still encountered up to 5 km (Ralph and Miller, this volume; Strong, pers. comm.). A good example of this effect is from studies in Clayoquot Sound, British Columbia (*tables 1* and *2*). Surveys through kelp beds where juveniles were known to forage found juvenile ratios 3–4 times greater than total area counts (surveys of all individuals in the sound). Thus, it seems likely that onshore surveys will overestimate the juvenile ratio, and at-sea surveys will underestimate them unless the at-sea surveys include some transects close to shore or through kelp beds.

Second, the juvenile ratio increased during the breeding season in every case at locations with repeated surveys (*tables 1 and 2*). This would be expected if nests in a population were asynchronously fledging young (*fig. 2*), and juveniles, subadults and adults remained in the general vicinity so that populations were being surveyed. The universal increase in juvenile ratios during the breeding season indicates that juvenile ratios may be useful tools for tracking productivity of a population. Third, sequential surveys often yielded similar juvenile ratios after the percentage of juveniles observed was adjusted for different survey dates using the linear model in *figure 2*. The closest values generally occurred for surveys conducted in late July and early August (*tables 1 and 2*). These adjusted ratios differed by about 3 percent or less, in 6 out of 7 instances. Thus, juvenile ratios appear to be sensitive to seasonal change, yet provide repeatable measures for fecundity estimates.

Table 1—Surveys of the ratios of juveniles to after-hatch-year birds (adults and subadults) for Marbled Murrelets conducted during the breeding season along shorelines or from boats cruising only along kelp beds. The percentage of juveniles (Pct. juv.) was adjusted for the timing of the survey (survey period) by using the cumulative frequency of fledging dates (fig. 2) to estimate an adjusted percentage of juveniles (Adj. pct. juv.) for the end of the nesting season

Region	Year	Survey period	*n*	Survey results		Source
				Pct. juv.	Adj. pct. juv.	
British Columbia	1993	1–15 July	206	7.3	16.9	Manley and Kelson
		16–31 July	157	8.9	14.2	(pers. comm.)
Central Oregon	1988	16–31 July	107	2.8	4.5	Nelson
		1–15 Aug.	90	7.8	9.7	(pers. comm.)
	1989	16–31 July	112	5.4	8.6	
		1–15 Aug.	101	7.9	9.8	
	1990	1–15 July	555	0.4	0.9	
		16–31 July	200	7.0	11.2	
		1–15 Aug.	58	8.6	10.6	
	1991	1–15 July	391	1.3	3.0	
		16–31 July	486	9.9	15.8	
		1–15 Aug.	319	11.6	14.4	

Table 2—Surveys of the ratios of juveniles to after-hatch-year birds (adults and subadults) for Marbled Murrelets during the breeding season conducted from boats cruising at a variety of distances from shore. The percentage of juveniles (Pct. juv.) was adjusted for the timing of the survey (survey period) by using the cumulative frequency of fledging dates (fig. 2) to estimate an adjusted percentage of juveniles (Adj. pct. juv.) for the end of the nesting season

Region	Year	Survey period	*n*	Survey results		Source
				Pct. juv.	Adj. pct. juv.	
British Columbia	1993	16 Aug.	2732	4.0	4.9	Manley and Kelson (pers. comm.)
Central Oregon	1992	1–15 July	1609	0.1	0.2	Strong (pers. comm.)
		16–31 July	902	0.6	1.0	
		1–15 Aug.	1032	3.3	4.1	
Northern California	1993	15–31 July	355	1.4	2.2	Ralph (pers. comm.)
		15–30 Aug.	192	2.1	2.1	

The adjusted ratios of young-of-the-year murrelets to after-hatch-year birds were generally low, although there was considerable variation among juvenile ratios (*tables 1 and 2*). The most reliable ratios for estimating murrelet fecundity would come from at-sea surveys which covered long distances (>20 km) or large areas and surveyed close to shore (≤ 500 m) as well as farther away in order to have a better chance of encountering clumps or groups of juveniles. To the best of my knowledge, only two data sets fulfill both requirements - total area counts in Clayoquot Sound, British Columbia and surveys off the coast of central Oregon (*table 2*). Both studies had seasonally adjusted juvenile ratios around 4–5 percent, so I chose to use 5 percent as a realistic estimate of fecundity. Although Ralph and Long's (this volume) surveys indicate that juvenile ratios may be as low as 2 percent, their transects did not consistently extend closer than 800 m from shore and may have underestimated the true ratio. Likewise, the 15 percent ratios from onshore counts appear to greatly overestimate the proportion of juveniles because the vast majority of adults would have been too far from shore to be detected (Ralph and Miller, this volume). However, onshore counts do suggest that the 5 percent estimate of fecundity could be too low if at-sea surveys had missed many juveniles. Thus, I also evaluated optimistic estimates of adjusted juvenile ratios of 10 percent, twice the realistic value and similar to corrected nesting success derived below.

Fecundity might also be estimated from studies of nesting success, but this is more difficult to do for the murrelet. A total of 22 nests have been found in the Pacific Northwest—see table 2 of the study by Nelson and Hamer (this volume b). Only 36 percent of the murrelets successfully fledged young. This would yield an estimate of 0.36 young produced per nesting pair (since murrelets can fledge only 1 young), or 0.18 female young per nesting female, assuming half of the young fledging would be males based on the sex ratio found by Sealy (1975a).

This value overestimates fecundity for two reasons. First, many nests were found after the young had hatched. This would greatly overestimate overall nesting success because murrelet nests often fail (>50 percent) in the egg or early stages of chick-rearing before they are likely to be detected—see table 3 of the study by Nelson and Hamer (this volume b). The true number of female chicks fledging per female may be closer to 0.15. Second, it is unlikely that all females would attempt to nest every year and a significant proportion of the population (5–16 percent) may be nonbreeders (Hudson 1985). Third, the estimate of fecundity for the post-breeding model assumes that the young have safely reached the ocean. The long flight from the nest to the ocean can be expected to be hazardous for nestlings as exemplified by grounded young birds that have been found (Carter and Erickson 1992, Rodway and others 1992). Thus, to arrive at a fecundity value, the true number of female young per nesting female (0.15) would have to be corrected by multiplying it by: (1) the estimated proportion of adult birds nesting (averaged from the estimates of Hudson cited above to yield 0.9); (2) the proportion of young that survive from fledging to until the time of census (anybody's guess, but 0.9 might be a reasonable estimate); and (3) the number of nesting attempts per pair per year which is assumed to be 1 (Hamer and Nelson, this volume a). This would result in a fecundity value around 0.12, similar to average estimates from onshore juvenile ratios (*table 1*).

Estimating Survivorship

Nur (1993) found that the annual probability of survival for adults (P_2) was positively related to body size for 10 species of alcids. Similar data are presented in *figure 1* of De Santo and Nelson (this volume). Adult survivorship ranged from about 0.75–0.77 for small-bodied Least Auklets (*Aethia pusilla*) and Ancient Murrelets (*Synthliboramphus antiquus*) to 0.91–0.94 for large-bodied Atlantic Puffins (*Fratercula arctica*), and Common and Thick-billed murres (*Uria aalge* and *U. lomuia*). Nur also found that adult survivorship was negatively related to annual reproductive effort (clutch size times broods per year) after controlling for the effects of body size. Together these two variables accounted for 72 percent of the variation in annual survivorship among the 10 species. Nur then derived a multiple regression model to

estimate an annual survival rate of alcids on the basis of body mass and clutch size. This resulted in an estimate of 0.845 for the Marbled Murrelet. Two standard errors of the estimate for the prediction, encompassing 95% of the likely values for typical murrelet survivorship (Steel and Torrie 1960), fell between 0.811 and 0.880. I used 0.85 for adult survival and also explored the possibility that the annual probability of survival might be as high as 0.90, a value typical for larger Atlantic alcids (Hudson 1985). Values of survivorship as low as 0.81 were not considered because they would have required extremely high fecundity values for populations to persist.

Annual survival for juveniles and subadults of most bird species is usually less than adult survival. Survival for juvenile and subadult alcids is not as well known as adult survival. These values are hard to estimate and can often be underestimated due to emigration. Frequently these values are simply given as the probability of surviving to the age of first breeding. Hudson (1985) gives a range for the probability of surviving to first breeding of 13-53 percent, with a mean close to 30 percent, but this is for large-bodied birds with late ages of first breeding. Nur (1993) suggested that survival of juveniles and subadults could be considered to be proportional to adult survival. Using data from Hudson (1985) for five populations of murres, Nur calculated that juveniles survive their first year of life at about 70 percent the rate of adult survival, first year subadults survived slightly less well than adults (0.888), and that after 2 years of age survivorship was approximately equal to adult survivorship. I used these proportions for juvenile and subadult survival estimates in the model.

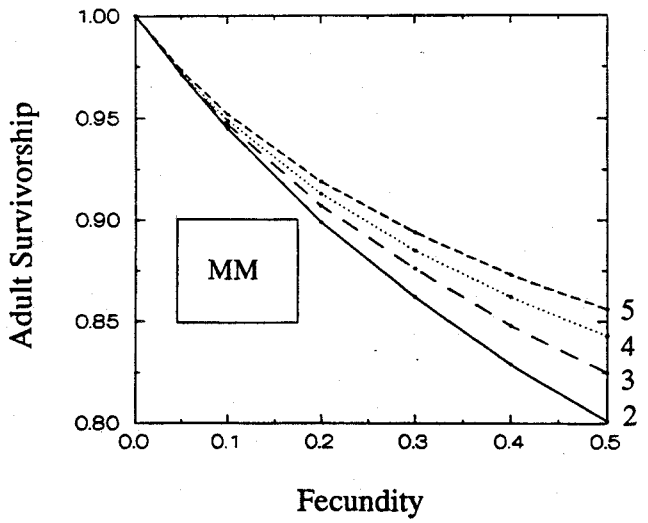

Figure 3—Sets of isobars where lambda equals 1 (i.e. populations are neither increasing or decreasing) for different combinations of fecundity and annual survivorship. Above the isobars populations should increase and below the isobars populations should decline. Isobars are shown for ages of first breeding from 2 to 5 years. Survivorship of juveniles and subadults was set at 0.700 and 0.888 times adult survivorship, respectively. Likely Marbled Murrelet values for survivorship and fecundity are delimited within the box. See text for details.

Predicted Murrelet Population Trends

Figure 3 shows the possible combinations of adult survival and fecundity for populations experiencing no growth (lambda equal to 1) for different possible ages of first breeding. Combinations above the lambda isobar result in increasing populations and combinations below the lambda isobar result in declining populations. For the Marbled Murrelet, fecundity may not exceed 0.5 because females are thought to lay only 1 egg per year and, on average, only half of the young that fledge would be females. Note that the lambda isobars for different ages of first breeding converge as survivorship increases and fecundity declines. As fecundity values drop below 0.20 and survivorship rises above 0.90, our assumption of the age of first breeding will have little effect on the predicted population trends.

Likely combinations of adult survivorship and fecundity are shown for the murrelet in the box on *figure 3*. These estimates are well below the lambda isobars, and indicate that murrelet populations are likely to be declining. Given an annual survivorship of 0.85–0.90, murrelet fecundity would have to range from 0.20 to 0.46 to result in stable populations for different ages of first breeding. Such values would result in adjusted juvenile ratios of 15 percent to 22 percent, well below the values currently observed. Fecundity at these levels is typical for other auks, which generally experience nesting success in excess of 70–80 percent (Hudson 1985, Nur 1993). For example, if murrelets experienced nesting success similar to other seabirds (75 percent), nests were attempted by 90 percent of the potential breeding population each year, and 90 percent of the young survived to reach the ocean (i.e., fecundity = 0.30), then murrelet populations would grow when adult survivorship exceeded 0.862–0.894. These values fall well within the expected range of survivorship values. Unfortunately, even the most favorable estimate of fecundity, conceivable from current field data for the Marbled Murrelet (i.e., uncorrected nesting success = 36 percent), would require survivorship values to exceed 0.908–0.924 for populations to grow. Such survivorship values may occur during some years, but seem likely to be higher than the long term average expected for this species (Nur 1993).

The above analyses suggest a predicted rate of decline for the murrelet population that is substantial. Using the estimates of survival and fecundity obtained above, likely combinations of demographic rates and their resulting annual change in population size are compiled (*table 3*). It appears that murrelet populations are likely to be declining 2-4 percent per year and it is conceivable that the decline may even be 2-3 times larger.

A sensitivity analysis (*table 4*) indicated that estimates of lambda were most strongly affected by adult survivorship. Changes in fecundity had about half the effect on lambda that changes in adult survivorship had. Neither juvenile survivorship nor adult survivorship had strong effects on lambda.

Table 3—Predicted rates of annual change for Marbled Murrelet populations based on likely combinations of demographic rates based on three different scenarios of juvenile recruitment and nesting success measured in the field, and two levels of adult survival from comparative analysis. Lambda, the expected growth rate of the population, was virtually unaffected by changes in age of first breeding

Fecundity scenario	Resulting fecundity	Adult survival	Lambda	Annual pct change
At-sea juvenile ratio (5 pct)	0.06	0.85	0.88	−12
	0.06	0.90	0.93	−7
On-shore juvenile ratio (10 pct) or corrected nesting success (24 pct)	0.12	0.85	0.91	−9
	0.12	0.90	0.96	−4
Uncorrected nesting success (36 pct)	0.18	0.85	0.94	−6
	0.18	0.90	0.98	−2

Table 4—Sensitivity of lambda to changes in the Leslie matrix elements for the Marbled Murrelet based on the three different fecundity scenarios for an age of first breeding of 3 years. See Table 3 *for values used in each of the fecundity scenarios*

Parameter	At-sea juvenile ratio	On-shore juvenile ratio	Uncorrected nesting success
Fecundity	0.487	0.544	0.444
Juvenile survival	0.084	0.047	0.114
Subadult survival	0.066	0.037	0.090
Adult survival	0.890	0.937	0.854

Discussion

Model Parameter Estimates

There are a number of sources of uncertainty in the parameter estimates that may have affected model outcomes. Lambda was most sensitive to changes in adult survivorship (*table 4*), which is typical for potentially long-lived birds like the murrelet. Estimates of survival have the greatest uncertainty, since they were not derived from field data but instead were based on comparative analyses of allometric models. Nevertheless, there are reasons for confidence in the estimates evaluated. Survivorship is often strongly related to both body size and reproductive effort in birds (e.g., Gaillard and others 1989, Saether 1988), and this trend was also strong in the Alcidae (Nur 1993). The range of annual survivorship values for adults evaluated in the model (0.85-0.90) included more than two standard errors for the upper bound of the prediction from the regression, which should encompass > 95 percent of the variation in potential mean estimates. Higher annual survival rates (0.90-0.94) are typical only for three species of auks with body masses exceeding 600 g (Nur 1993; De Santo and Nelson, this volume), three times the size of the murrelet. Survivorship ranges from 0.75-0.88 for seven alcid species with medium and small body sizes (< 600 g); only the Atlantic Puffin had annual survival rates routinely above 0.90.

It is likely that annual survivorship for Marbled Murrelets will be among the upper range of values evaluated in this model (e.g., 0.87-0.90), because the murrelet's inherently low reproductive rate (1 egg per nesting attempt) requires high survivorship for populations to grow. On the other hand, because the murrelet's unusual life history strategy of nesting in old growth forests often far from the sea, it probably faces higher mortality risks than other seabirds. Field studies to determine survival rates are needed, and are becoming more feasible as marking and telemetry techniques are perfected for this bird (Quinlan and Hughes 1992; Priest and Burns, pers. comm.).

All measures of fecundity from field data for the Marbled Murrelet appear to be low. Arguably the most complete measures of fecundity were derived from juvenile ratios based on extensive at-sea censuses corrected for the date of census in relation to the timing of fledging (*table 2, fig. 2*). Extensive at-sea censuses conducted recently have universally produced low percentages of juvenile birds (*table 2*). Such low ratios indicate poor reproductive success that could be due to high nest failure rates from predation (Nelson and Hamer, this volume b), or a low proportion of adults attempting to breed, perhaps because they are unable to find suitable nest sites. Some portion of the low reproductive success could have been due to El Niño effects on food supplies. Although there is ample evidence that El Niño affects nesting success of

seabirds that nest and forage offshore (Ainley and Boekelheide 1990), there is no evidence that fish populations within 2 km of shore, which murrelets mostly utilize, are affected.

Some uncertainty in the measure of fecundity derived from juvenile ratios is associated with the timing of censuses. To convert juvenile ratios to a fecundity estimate, ratios had to be increased to account for young fledging after the date of census by using the cumulative frequency distribution for fledged nests with known dates (*fig. 2*). This distribution was comprised of nests from Alaska to California, because sample size was not large enough to partition nests among portions of the murrelet's range. Variation in the fledging dates exists between Alaska, British Columbia, and the Pacific Northwest (Hamer and Nelson, this volume a), although there is much overlap. Future research might employ bootstrapping techniques (Crowley 1992) to calculate an error estimate for the cumulative frequency by date, as one way to determine the inherent variability of the correction factor.

Other approaches to estimating fecundity also yielded low values, but are likely to have too many biases to be useful yet. Juvenile ratios measured only using on-shore counts tended to be higher than off-shore counts (*table 2*). But fecundity will be overestimated by using only on-shore counts because they undersample adults. Estimates of fecundity from nesting success are likely to be less useful than juvenile ratios because they must be corrected for many factors that are difficult to measure (such as the proportion of adults nesting, fledgling survival to the ocean, and renesting frequencies). Furthermore, for the foreseeable future, fecundity estimates based on nesting success are likely to depend on small sample sizes because of the difficulty in finding nests.

Predicted Rates of Decline of Murrelet Populations

All scenarios of the demographic model predicted that murrelet populations are likely to be declining (*table 3*). The estimated rate of decline varied from 2-12 percent per year, depending on the parameter estimates used. Based on the discussion of the parameters above, the most likely rate of decline would be based on fecundity values from juvenile ratios intermediate between offshore juvenile ratios (which may underestimate reproductive success) and nesting success (which certainly overestimates fecundity), used with an estimate of survival close to 0.90. These intermediate fecundity values would suggest a rate of decline around 4 percent per year.

A predicted decline of 4 percent per year is in close agreement with population declines documented in two field studies of murrelets. A 50 percent decline in murrelets detected over 20 years of Christmas Bird Counts in Alaska (Piatt and Naslund, this volume), despite an increase in observer effort during this period, would represent a 3.4 percent average annual decline. Similarly, the 40 percent decline in the Clayoquot Sound murrelet population in British Columbia over 10 years (Kelson and others, in press) would average to a 5 percent annual decline. These studies are based on either periodic but intensive sampling during few annual periods (British Columbia), or low intensity but extensive sampling every year (Alaska). Despite, the sampling shortcomings inherent in these two studies, the population trends that they have documented are in good agreement with trends predicted by the model in this paper.

Model results suggest that murrelet populations may even be declining at greater rates (*table 3*). A 7 percent annual decline would be predicted from juvenile ratios based on offshore counts in conjunction with high survival estimates. This value is certainly a possibility for Pacific Northwest populations of murrelets, which exhibit low offshore juvenile ratios. It is even conceivable that murrelet populations could be declining at 9-12 percent per year (*table 3*). However, this rate of decline is so high that it seems unlikely to go unnoticed by field researchers. Furthermore, it is based on the most pessimistic combinations of fecundity and survivorship. I interpret the model predictions, in conjunction with the field evidence, to suggest that murrelet populations are likely to be declining at least 4 percent per year and perhaps as much as 7 percent per year.

Use of Juvenile Ratios for Murrelet Conservation

Conservation efforts for Marbled Murrelets have been hampered in part because of a lack of reliable biological information. Demographic characteristics have been especially difficult to measure because nests are very hard to find and monitor, murrelets fly long distances both over the ocean and across land, and the birds are difficult to capture, mark, and telemeter (Quinlan and Hughes 1992). Juvenile ratios provide one estimator of murrelet population health that may be reasonably measured in the field.

Juvenile ratios have great potential as estimators of productivity. It is easy to obtain large sample sizes of juvenile ratios compared to the difficulty of finding and monitoring nests. It will be many years before enough nests are found to yield sample sizes sufficient for accurate estimates of nesting success. Additional information needed to convert nesting success into annual fecundity (the proportion of birds that nest and the number of attempts per year) will perhaps be even more difficult to obtain. Juvenile ratios implicitly incorporate these factors. Research will need to determine optimal protocols for sampling juvenile ratios at-sea that take into account apparent differences in habitat use by juveniles and adults (*tables 1* and *2*) as well as other factors that could bias these ratios.

Changes in juvenile ratios could be a useful tool to understand factors limiting murrelet population growth. Juvenile ratios could be monitored in a regional areas (e.g., over 30-50 kms of shoreline) and compared to landscape characteristics to determine the effects of forest management and other land use practices. Juvenile ratios may also be useful for monitoring murrelet population trends. However, changes in juvenile ratios can be caused either by changes in recruitment (increased nesting success results in greater proportions of juveniles) or changes in adult survivorship (decreased survivorship results in greater proportions of juveniles). Whether juvenile ratios change due to improved

recruitment or decreased adult survivorship should be apparent by examining year-to-year changes in population size. Increases in juvenile ratios coupled with increased population size should indicate increased productivity. However, if coupled with decreased population size, increased juvenile ratios would indicate decreased adult survivorship.

For making sound conservation decisions based on population trends and demography, there is no substitute for good field data based on direct estimates of population change, survival and fecundity. For the Marbled Murrelet, such information is likely to remain scarce. Future research should explore the strengths and weakness of using the ratio of juveniles to after-hatch-year birds as a proxy for direct demographic measurements.

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