Evaluating uncertainty in estimating population trends of Marbled Murrelets

John Boulanger, Kathy Martin, Gary Kaiser, Andrew E. Derocher

Abstract

We used a mathematical matrix model to explore life history strategies and evaluate conservation measures for the Marbled Murrelet (*Brachyramphus marmoratus*), a threatened seabird species. Demographic parameter estimates for Marbled Murrelets are crude, but existing data and allometric comparisons with other seabirds suggest that both productivity and adult survival are low. This combination of low parameter values is not possible if populations are to maintain stability. As a result, we examine two possible alternative life history scenarios (high survival and high productivity) which represent the extremes of plausible murrelet parameter values. For both life history scenarios we used a matrix model to conduct sensitivity analyses of life history parameters. We found that regardless of life history scenario, murrelet populations are very sensitive to changes in adult survival, and less sensitive to juvenile survival and productivity. This leads us to conclude that reduction in adult survival may constitute the most immediate threat to murrelet populations even if habitat loss is the most significant long-term factor affecting conservation. Our power analyses show that only large reductions (20% reduction in adult survival, > 50% reduction in productivity) in individual parameters would be detected in 10 years by current monitoring techniques. Results of recent field studies document lower power of most census monitoring methods. We suggest that more emphasis be placed on obtaining estimates of adult survival and easily obtained measures of productivity such as juvenile/adult ratios using recently refined field techniques. Given low power to detect population changes using current methods, managers and policy-makers must implement active conservation strategies before researchers can detect population declines statistically and fully document the causes.

Résumé

Nous avons utilisé un modèle mathématique matriciel pour explorer les stratégies d'histoire naturelle et évaluer les mesures de conservation de l'Alque marbré (Brachyramphus marmoratus), une espèce d'oiseau de mer menacée. Les estimés des paramètres démographiques de l'Alque marbré sont grossiers. Cependant, les données disponibles et les comparaisons allométriques avec les autres espèces d'oiseaux de mer suggèrent que la productivité et la survie des adultes sont faibles. Cette combinaison de faible productivité et survie n'est pas possible si une population doit demeurer stable. C'est pourquoi nous examinons deux scénarios alternatifs (survie élevée et productivité élevée) qui représentent les extrêmes plausibles des paramètres démographiques de l'Alque marbré. Pour ces deux scénarios, nous utilisons un modèle matriciel pour conduire des analyses de robusteste des paramètres démographiques. Nous avons démontré que, indépendamment du scénario d'histoire naturelle, les populations d'Alques sont très sensibles aux variations dans le taux de survie des adultes, et moins sensibles au taux de survie des juvéniles et au taux de productivité. Ceci nous amène à conclure que la réduction dans le taux de survie des adultes pourrait constituer la menace la plus immédiate aux populations d'Alques, même si la perte d'habitats est le facteur le plus significatif affectant la conservation à long terme. Notre analyse de puissance démontre que seules des réductions importantes (20% dans le taux de survie, >50% dans la productivité) dans les paramètres démographiques pourraient être détectées en 10 ans avec nos techniques actuelles de suivi. Les résultats d'études de terrain récentes documentent une puissance même plus réduite pour la plupart des méthodes de suivi. Nous suggérons que plus d'emphase devrait être mise à obtenir des estimés de taux de survie des adultes de même que des mesures simples de productivité telles que les ratios juvéniles/adultes en utilisant quelques techniques de terrain récemment développées. Vu la faible puissance des méthodes actuelles à détecter des changements

de population, les gestionnaires doivent implanter des stratégies proactives de conservation bien avant que les chercheurs ne puissent détecter statistiquement des déclins et en documenter les causes.

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Introduction

Uncertainty about population size and life history attributes of rare or cryptic species is a common problem in conservation biology. Failure to confront uncertainty regarding population dynamics, and the low power of monitoring strategies to detect changes in population trends, have been used to forestall management decisions, sometimes leading to disastrous population declines of cryptic species (Ludwig et al. 1993). Evaluation of conservation strategies using theoretical methods such as matrix models and power analysis have been restricted mainly to species for which solid data exist as a result of large investments in field research (Crouse et al. 1987; Lande 1988; Caswell 1989; Taylor and Gerrodette 1993). However, for many cryptic species there are insufficient data to allow precise parameter estimates, and as a result little effort has been directed at understanding population dynamics using the rigorous framework of a population model. Furthermore, little attempt has been made to determine the ability of monitoring methods to detect declines (but see Thomas and Martin 1996).

This study focuses on the Marbled Murrelet (*Brachyramphus marmoratus*), a Pacific seabird (Alcidae) that nests in coastal old-growth temperate forests from California to Alaska. Populations of Marbled Murrelets face negative impacts from the extensive loss and fragmentation of old-growth forests as well as oil spills, fishing mortality, and other anthropogenic disturbances. Because of these and related concerns, the Marbled Murrelet was designated as a threatened species in Canada (Rodway 1990; Rodway et al. 1992) and in California, Oregon, and Washington in the United States (Carter and Morrison 1992; Nelson and Hamer 1995; Ralph et al. 1995). The world population size of Marbled Murrelets has been estimated at about 287,000 - 300,000 individuals, with most (approximately 220,900) in Alaska (Ralph et al. 1995). A significant number of the remaining Marbled Murrelets breed in British Columbia.

Despite the Marbled Murrelet being a high priority species for conservation, many basic life history details required for effective management are poorly known. Because Marbled Murrelets nest high in the inner branches (next to the tree trunk) of coastal conifers (except in some northern Alaska populations), their nests are very difficult to locate. Summaries of breeding information and suspected nesting activities for British Columbia were given by Sealy (1974). The first active nest for British Columbia was located in 1993 (Jones 1993). Thus, estimation of productivity parameters has been very difficult. High spatial variability in at-sea distributions has also hampered estimation of survival rates and related population parameters (Ralph et al. 1995). Improved statistical techniques for estimating productivity from juvenile/adult ratios, and advances in techniques in mist-netting and radio telemetry (Kaiser et al. 1995; Becker et al. 1997; Kuletz and Kendall 1998; Cooke 1999) offer new insights into murrelet life history. However, it appears unlikely that sufficient information will be collected to estimate precisely murrelet population status before substantial declines have occurred in most of the southern part of its distribution (Rodway et al. 1992; Ralph et al. 1995).

Adult and juvenile survival of Marbled Murrelets are unknown. Features of their breeding biology such as crepuscular nest attendance, cryptic plumage, and open nests high in trees suggests that murrelets have low survival and attempt to avoid high predation risks (Nelson and Hamer 1995). Marbled Murrelets have low potential productivity (1 egg per clutch, no evidence of renesting) and apparently high loss of

young during incubation and after fledging (DeSanto and Nelson 1995; Nelson and Hamer 1995). Low observed juvenile/adult ratios of Marbled Murrelets at sea also suggest low productivity (Beissinger 1995). In contrast, other seabird species of similar body mass (guillemot *Cepphus*) and other murrelet species (*Synthliboramphus* sp.) produce two eggs per clutch and nest on islands or in colonies that are less vulnerable to predators. Larger alcid species such as murres (*Uria*) and Razorbill (*Alca torda*) produce one egg, but appear to compensate for low fecundity with effective breeding strategies and unusually high annual adult survival (Hudson 1985). Overall, allometric comparisons of Marbled Murrelets with other piscivorous seabirds suggest that Marbled Murrelets show lower productivity and possibly lower survival rates when compared to similar sized alcids (DeSanto and Nelson 1995).

The apparently unlikely combination of low fecundity and low adult survival has caused some authors to argue that murrelets must have higher survival than similar-sized alcids to maintain stable populations (Rodway et al. 1992; Ralph et al. 1995). Alternatively, murrelets may have higher productivity than estimated by juvenile/adult ratios or direct estimates of nesting success (DeSanto and Nelson 1995; Ralph et al. 1995). In a demographic analysis of Marbled Murrelet populations, Beissinger (1995) compiled data from a research compendium (Ralph et al. 1995) to provide likely population parameter estimates. Using a matrix model, he concluded that murrelets were declining annually by 2-12 percent. However, he did not discuss the limitations on detecting population trends given the uncertainty about the input values available and the difficulty of making inferences without power analyses when using data from available monitoring methods.

In this paper we use a mathematical matrix model coupled with statistical power analysis to evaluate current monitoring strategies used for Marbled Murrelets. We conduct sensitivity analysis of several life history parameters to compare the relative effects of individual parameter change on population trajectories. We simulate hypothetical population declines, and test the power of current methods to detect these declines. Each analysis is conducted for two opposing life history scenarios which represent the extremes of plausible life history parameter values. Using this approach we determine the robustness of sensitivity and power analyses across a full range of plausible parameter values. Unlike the demographic study of Marbled Murrelets by Beissinger (1995), we

do not attempt to predict actual population trends. Instead, we focus on determining optimal strategies for future research and monitoring programs.

Methods
Population model and sensitivity analyses

To aid in the conceptual process of exploring murrelet population dynamics we constructed a stage-based matrix model (Caswell 1989). The parameters of the matrix model and the life cycle model of Marbled Murrelets are shown in Figure 1 and a mathematical description of the model is given in Appendix 1. By calculating the dominant eigenvalue (λ) from the matrix we can determine the future population trajectory for a set of population parameters. If the population is stable, λ equals one over time (if decreasing, $\lambda < 1$ and if increasing, $\lambda > 1$; Caswell 1989). We used sensitivity analysis to investigate the relative importance of each life history parameter in maintaining murrelet populations. In each analysis we started with parameter combinations that maintained a stable population ($\lambda = 1$), then decreased a given parameter by percentage increments while holding the others constant, and recorded the response of λ. To evaluate the sensitivity of juvenile/adult ratios to changes in population and life history parameters, we simulated population declines and calculated corresponding juvenile/adult ratios from the model (Appendix 1).

Figure 1. A life cycle diagram for the Marbled Murrelet for age of first breeding at 2 yrs. Note that this life history diagram pertains to a population in which a post-breeding census is conducted. S_j=survival from first fall census to 2 years of age. S_a=adult survival, P=productivity.
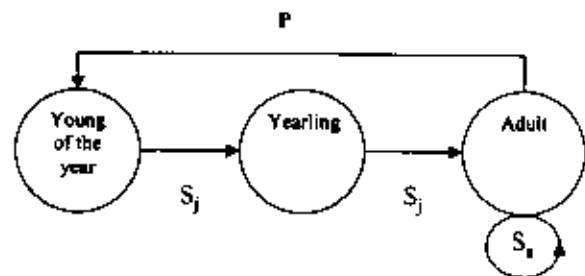
Some assumptions apply to this matrix model. First, the model considers only females, and assumes an even sex ratio and that breeding age females always find mates (Sealy 1975). Second, the population is

censused in the fall after breeding. Third, the population is at equilibrium, i.e. always has a stable age structure. Fourth, the model is linear with no density-dependent effects. Finally, we assume there is no senescence.

Marbled Murrelet life history parameters

We define adult survival as the annual probability that an individual murrelet (aged ≥ 2 years) will survive to the next age class. Most inference about murrelet survival has been through allometric comparison with other alcid species. Adult survival was estimated at 0.845 (95% CI: 0.81-0.88) by Beissinger (1995) and at 0.83 by DeSanto and Nelson (1995). Recently, a mark-recapture study in Desolation Sound, British Columbia, produced an adult survival rate estimate of 0.85 (95% confidence interval: 0.47 to 0.97; Lougheed et al. 1998).

We define juvenile survival as the annual probability that a fledgling will survive its first two years of life. Beissinger (1995) estimated that Marbled Murrelets survive at 70% of adult survival in their first year of life and at 88% in their second. To keep our model simple, we compressed pre-breeding survival into one parameter by taking the geometric mean of 0.88 and 0.70. Juvenile survival was then calculated by multiplying this value (0.78) by the adult survival for each simulation.

We define productivity as the proportion of breeding age females that produce one female offspring that survives to the census period. Estimates of murrelet productivity have been derived from two sources: observed nesting success and juvenile/adult ratios of murrelets observed at sea.

Murrelet productivity can be estimated by the percent of murrelet nests that fledge young. Nelson and Hamer (1995) calculate that 28% of 32 murrelet nests produced young. Since their analysis, 83 nests have been found in British Columbia, which will allow a better productivity estimate. For the matrix model, this yields an estimated productivity of 0.17 if half of the fledglings are female, but this value does not account for mortality during the actual fledging event or in the subsequent winter.

Beissinger (1995) used cumulative sightings of juvenile/adult ratios at sea to obtain a post-breeding season estimate of productivity. By averaging juvenile/adult ratios from different studies in the United States, productivity was estimated at 5%, with some estimates as high as 10%. Assuming an equal sex ratio, this estimate of productivity describes the percentage of breeding females that produced one female offspring at the end of a breeding season.

Productivity is also influenced by age of first breeding. In alcids this ranges from 2-15 years (Hudson 1985; Gaston 1992; Harris et al. 1994). Given the low productivity, and possible low annual survival of Marbled Murrelets (as estimated from body mass), it seems plausible they have an early age of first breeding. Therefore, we set age of first breeding at 2 years. Later ages of first breeding (e.g., 4 years) require higher survival and/or productivity parameter values to maintain population stability (Figure 2).

Figure 2. Combinations of adult survival and productivity resulting in a stable population conducted for ages of first breeding of 2 (solid line) and 4 years (dashed line). Labeled points are the parameter values in which we conducted our analysis. The survival and productivity values proposed by Beissinger (1995) are displayed in the labeled box.
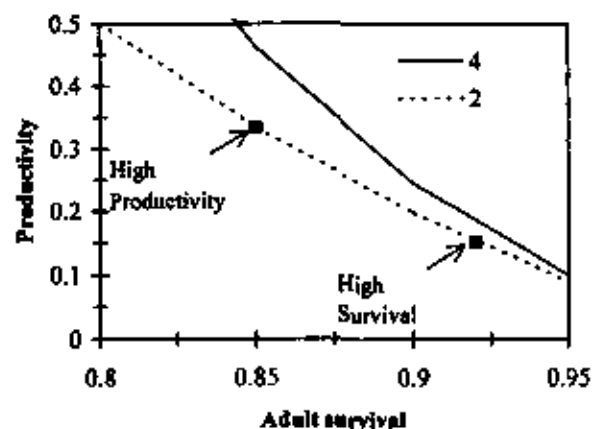
Marbled Murrelet life history scenarios

We focus our analysis on two alternative life history scenarios with parameter values that maintain a stable population (Figure 2). In the first "high productivity" scenario we consider that productivity could be higher than estimated by juvenile/adult ratios or nest success (DeSanto and Nelson 1995; Ralph et al. 1995). With this scenario, adult survival falls within the range suggested for other alcid species. In the second "high survival" scenario, adults have higher survival than suggested by their body size (Beissinger 1995; Ralph et al. 1995). This scenario is most plausible if current juvenile/adult ratios and estimated nesting success reflect true productivity. With this scenario adult

survival is similar to other longer-lived alcid species such as the razorbill which also have low fecundity (DeSanto and Nelson 1995).

Evaluation of at-sea surveys using power analysis

The main method for evaluating overall population status of murrelets is at-sea surveys or line transect counts (Strong et al. 1995). The power analysis we used is for regression analysis of population trends. The parameters for this model are: the number of annual surveys conducted, coefficient of variation (CV) of yearly surveys, the level, and true rate of change of population each year (Gerrodette 1987; Taylor and Gerrodette 1993). We considered a power level of 0.8 to be adequate to detect a population decline (Cohen 1988) and used an level (probability of Type 1 error) of 0.05 for our analysis.

Gerrodette's power calculation makes some restrictive assumptions. First, the population being monitored follows an exponential model of population decrease. Second, line transect or similar sighting per unit effort technique is used for population monitoring. Third, the CV input parameter takes into account variation due to demographic stochasticity as well as sampling variance. The model used for the power analysis accounts for change in coefficient of variation with decreasing abundance of animals being surveyed so that only an initial coefficient of variation is needed for the analysis. Coefficient of variations were calculated from 7 replicated strip transects at sea along the coast of Oregon during 1992 and 1993 (Strong et al. 1995). Data were used from transects that were replicated at least 4 times and as many as 13 times for coefficient of variation calculation. The mean coefficient of variation from these transects was 0.57 (range: 0.31-0.84).

We feel this simplistic power model is the most parsimonious approach given the requirements for data of more complicated simulation methods. Gerrodette's power estimate ignores the statistical problems created by non-independence of points when linear regression is used to analyze time series data and as a result power will always be overestimated using this routine (Gerrodette 1987; Gerrodette 1991; Link and Hatfield 1990; Taylor and Gerrodette 1993). Therefore, the results of this analysis are an estimate of relative rather than absolute statistical power.

Results and Discussion
Sensitivity analysis

Sensitivity analysis suggests that regardless of life history scenario, murrelet populations are most influenced by changes in adult survival, followed by juvenile survival and productivity (Figure 3).

Figure 3. Results of sensitivity analysis of high survival(a) and high productivity (b) scenarios. ▲ Productivity (P), ■ Juvenile survival (S_j), ◆ Adult Survival (S_a).

a) High survival

b)High productivity
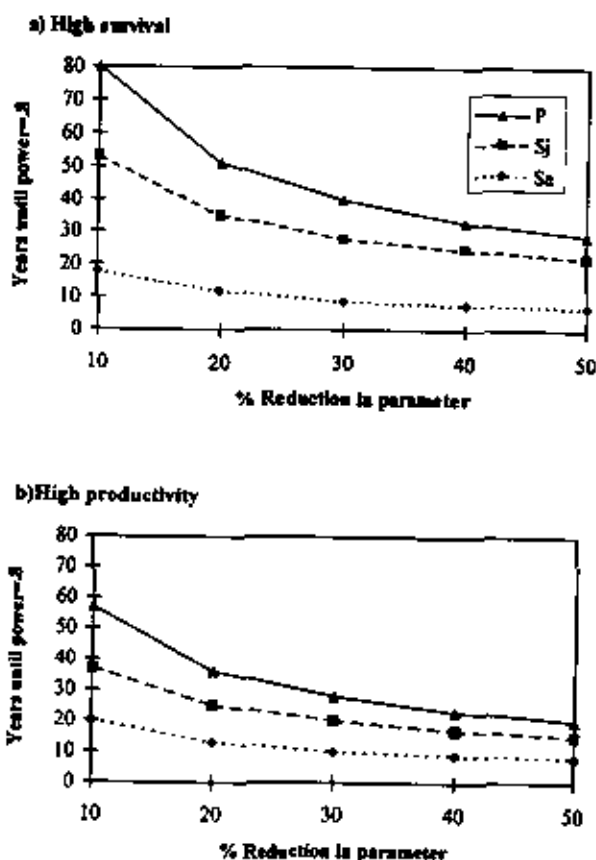
Adult Survival

High model sensitivity to adult survival is of great conservation concern given the potential impacts of gill-net fishing by-catch and oil spills on murrelets (Carter and Kuletz 1995; Carter et al. 1995). Marbled Murrelets have the highest oil vulnerability index of birds in the Alaska region (King and Sanger 1979). Carter and Sealy (1984) estimated that 7.8% of the fall population of murrelets were killed in 1980 in Barkley Sound in fishing nets. If this type of mortality reduces

adult survival even slightly, it will result in a rapid population decline. A mark-recapture study in Desolation Sound which uses newly-developed mist-net and dip-net capture techniques recently produced an adult survival rate estimate of 0.845 (95% confidence intervals 0.47 to 0.94; Kaiser et al. 1995, Lougheed et al. 1998, F. Cooke submitted). This estimate is based on four sampling sessions (conducted yearly from 1994-1997) and therefore precision is low due to low numbers of recaptures. Future estimates from this project should provide critical information regarding survival rates as the sample size of marked birds and corresponding precision of estimates increases (Lougheed et al. 1998).

Juvenile survival

In both life history scenarios, the model showed relatively low sensitivity to juvenile survival (Figure 3). However, this might be an artifact of the assumption that juvenile survival is directly proportional to adult survival. This assumption may be valid if adults and juveniles congregate in similar areas and are vulnerable to the same mortality sources and experience mortality factors similar to other alcids. Hudson (1985) commented that juvenile survival could represent a "bottleneck" in population dynamics and affect population trends more than shown by sensitivity analysis.

Productivity

Productivity is of great interest in Marbled Murrelet population dynamics given the wide scale removal of old-growth forests. Low model sensitivity to productivity may suggest that murrelet populations are adapted to a breeding strategy dependent on yearly food resources where high variation in productivity might have minimal population effects. Murrelet populations therefore may not show immediate detectable effects of reduction in productivity given that the natural variation in this parameter will minimize power to determine any type of downward trend. Possibly murrelets, like other seabirds, exhibit high temporal variation in productivity. For instance, in a 12-year period Common Murre pairs produced an average of 0.86 young per season, but this value varied from 0.10 to 0.96 (Boekelheide et al. 1990). Current estimates of murrelet productivity could be negatively biased because the data were collected in El Nino years (Ralph et al. 1995) in which other alcids had low reproductive success (Boekelheide et al. 1990).

Figure 4. Results of power analysis, based on line transect surveys documented by Strong et al. (1995), for high survival (a) and high productivity (b) scenarios. The y-axis represents the number of years it would take to statistically detect a population decrease resulting from a percentage reduction in a given parameter. ▲ Productivity (P), ■ Juvenile survival (S_j), ◆ Adult Survival (S_a).

a) High survival
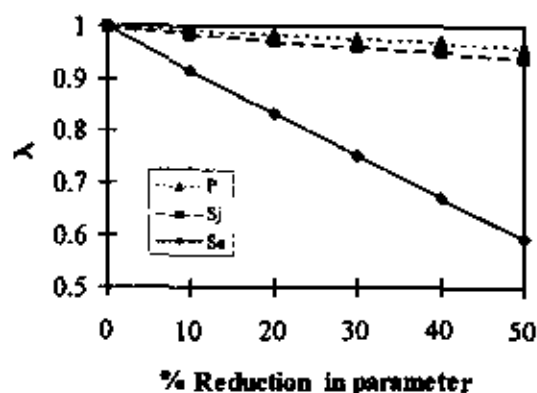
b) High productivity
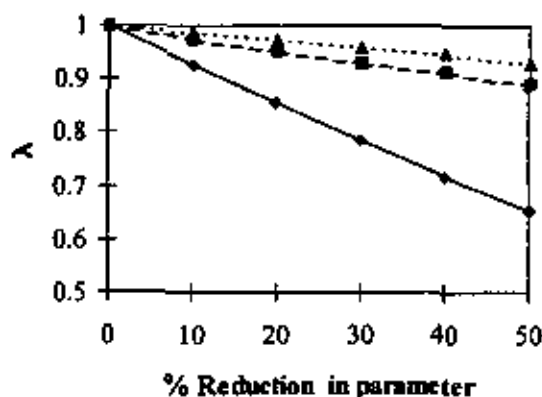
Evaluation of monitoring methods

Power analysis of population surveys

Power analysis of at-sea survey data reflects the difficulty in detecting statistically significant declines in populations based upon current monitoring methods (Figure 4). With high productivity, it took less time to detect decreases in population due to productivity as opposed to the high survival scenario. However, even with the high productivity scenario it still took six times as long to detect the decline in population based

on a productivity decline of 10%. This finding suggests that only comparatively large changes in productivity might be detectable with present survey methods. With high productivity and high survival scenarios, the population decreased by an average of 68% and 72%, respectively, before the power to detect the decline reached 0.8 when parameters were individually reduced by 10%. Results from power analysis suggest that only the most rigorous, replicated surveys will be able to detect population declines. To increase power of detection researchers can increase the number of yearly surveys (increase precision) or increase the level in the analysis. We found that with surveys that had a CV of 0.2, it would take ten years to detect a population decline caused by a 10% decrease in adult survival.

The observed CV from strip transect surveys of Strong et al. (1995) used in this exercise was 0.57 (range: 0.31-0.84) which reflects the current range of survey values. A recent study by Becker et al. (1997) tested the power of line transect methods (Buckland et al. 1993) used in at-sea surveys to detect population declines. Using data from line transect surveys Becker et al. (1997) found they could detect annual population declines of 9% over 10 years with an estimated power of 0.8 (=0.1) if areas were sampled at least 5 times per year using line transects. Note that a 9% annual decline would compound to a 57% total population decline over a 10-year period. Becker et al. (1997) did not publish CV estimates for line transect results; they used a Monte Carlo simulation based power analysis method (Gibbs 1995) which is more conservative than the power analysis method of Gerrodette (1987) used in this study (Link et al. 1990). The study of Becker et al. (1997) was conducted on a relatively straight section of coastline in California and it is questionable whether similar levels of precision could be attained in the more complex fjords and inlets in British Columbia and further north. We conclude that given present monitoring techniques, populations will be reduced significantly before a statistically significant decline is detected.

Monitoring of productivity

The sensitivity of detecting a population decline using juvenile/adult ratios was responsive only to changes in productivity (Figure 5). Juvenile/adult ratio was stable or increased slightly during simulations of population decline caused by reduced adult or juvenile survival. When less substantial decreases in population size were simulated (lower sensitivity of the model to

Figure 5. Changes in juvenile/adult ratios resulting from reductions in individual parameter values for the high survival (a) and high productivity (b) scenarios. ▲ Productivity (P), ■ Juvenile survival (S_j), ◆ Adult Survival (S_a).

a) High survival

b) High productivity
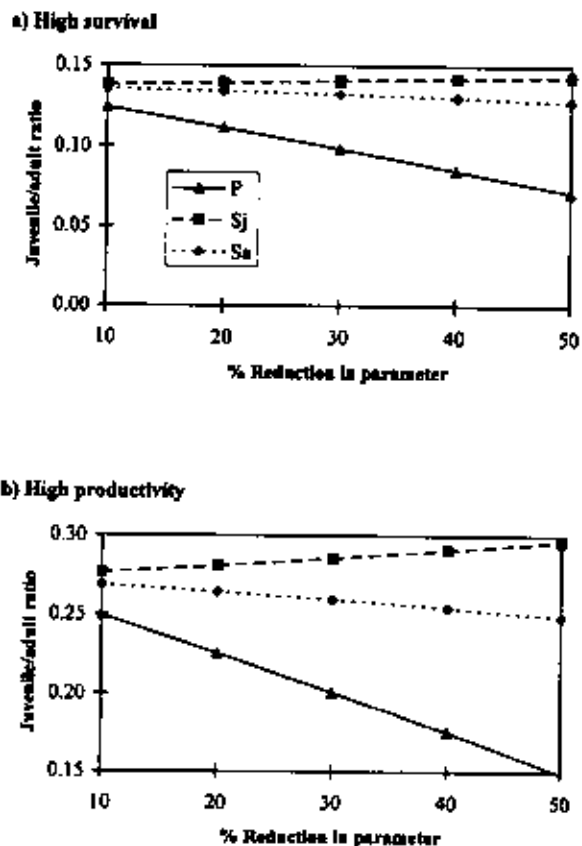
productivity), juvenile/adult ratio declined by 0.08.

Monitoring of annual variation in productivity could provide valuable insight into whether murrelets show a typical alcid pattern of high variation in productivity (Boekelheide et al. 1990). Results from a recent study in Alaska by Kuletz and Kendall (1998) suggest that juvenile density estimates with lowered coefficients of variation (mean CV=0.42, range 0.17-0.86) can be obtained by identification of icore survey periodsi in which juvenile densities are highest. Kuletz and Kendall conducted power analysis using the same methods of Gerrodette (1987) that were used in this study. Using the lower estimated CV range of 0.17 to 0.42, they could detect total declines of 24% and 50%, respectively, in juvenile abundance in 10 years with an estimated power of 0.8 (at ⁼0.1) when 5 surveys were conducted each year. This level of power is higher then that documented by Becker et al. (1997);

however, this may be due partly to potential positive biases with the Gerrodette (1987) method of power calculation as discussed previously in this paper (Link et al. 1990). Using these data Kuletz and Kendall (1998) developed an index of regional productivity based on the slope of paired juvenile and adult abundance estimates. The study of Kuletz and Kendall (1998) was conducted in fjords and inlets and therefore this technique may be more easily applied then the methods of Becker et al. (1997) to Marbled Murrelet populations in British Columbia and farther north. We conclude that monitoring juvenile/adult ratios or monitoring of juvenile density using methods similar to Kuletz and Kendall (1998) may be the best way to monitor and evaluate temporal and spatial variation in productivity.

Effect of uncertainty regarding life history strategies

It is important that researchers conducting demographic analyses account for the effects of uncertainty in parameters on calculation of population trajectories. In his demographic analysis of Marbled Murrelets, Beissinger (1995) used an adult survival value (estimated from other alcids) of 0.85 (confidence limits 0.81-0.88) for his demographic analysis to conclude that murrelet populations were declining from between 2 and 12 percent. Given high sensitivity of the model to adult survival values, even a small change in adult survival, well within the confidence limits estimated for this parameter, would drastically affect the calculated population change. It is our opinion that estimation of population decline rates based on models will be valid for murrelets only when more information is known about adult survival values.

Optimal Management and Research Strategies

We suggest that matrix modeling and power analysis can be used as design tools even in situations where data are sparse for the species in question. Power analysis computer software packages are now available to facilitate this process (Thomas and Krebs 1997). From our study we conclude that regardless of life history parameter assumptions, adult survival will most significantly affect the overall population trajectory and may influence detection of changes in other parameters. Low model sensitivity, and evidence from seabird species that are suspected to have similar life histories, suggest that Marbled Murrelets may show high temporal variability in productivity. Given

this constraint, and the low power of monitoring methods, it will be difficult to document statistically immediate declines in population size based on small decreases in this parameter.

We suggest that future work be focused on estimation of survival parameters such as is currently being conducted in British Columbia (Lougheed et al. 1998, Cooke 1999). More effort should also be directed at documenting the variability in productivity by developing better statistical methods to detect changes in populations using available and improved monitoring programs (Thomas 1996; Becker et al. 1997; Kuletz and Kendall 1998). Most importantly, the wider effort ito confront uncertaintyî should include caution in management integrated with a diverse conservation program that considers a number of promising research directions and efforts to improve existing monitoring programs.

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APPENDIX 1

The matrix model we used is described mathematically by the population vector:

N_0 - number of fledged young during a breeding season

N_1 - number of murrelets from the N_0 cohort that survive to the N_1 cohort

N_2 - number of murrelets in the N_2 and above cohort

The form of the model for a population in which a post-breeding census is conducted (with an age of first breeding of 2 years) in matrix form is:

$$
\begin{bmatrix} N_0 \\ N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & P \\ S_J & 0 & 0 \\ 0 & S_J & S_a \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \end{bmatrix}_t
$$

This type of population matrix model is defined as a stage matrix. It differs from the fundamental Leslie matrix (Leslie 1945) in that each "stage" may represent an age class, or a general class (such as N_2 which represents adult birds). Because this matrix is primitive, λ can be found by raising the matrix to successive powers and calculating the ratio of N_{t+1}/N_t (to the point of convergence) to determine λ. Also at the point of convergence the ratios of stage classes in the population vector that form a stable age distribution can be determined. The juvenile/adult ratio was calculated as:

$$
J/A \ ratio = \frac{N_0}{N_1 + N_2}
$$

The stage-based matrix model method is documented in Caswell (1989) and Crouse et al. (1987).