Research Article

Local Survival of Marbled Murrelets in Central California: Roles of Oceanographic Processes, Sex, and Radiotagging

M. ZACHARIAH PEERY,[1] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720-3110, USA
STEVEN R. BEISSINGER, Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720-3110, USA
ESTHER BURKETT, Habitat Conservation Planning Branch, California Department of Fish and Game, Sacramento, CA 95814, USA
SCOTT H. NEWMAN,[2] Wildlife Health Center, School of Veterinary Medicine, University of California, Davis, CA 95616, USA

Abstract

*We estimated annual local survival rates for after-hatch-year ($\geq$1-yr old) marbled murrelets (*Brachyramphus marmoratus*) in central California using Cormack-Jolly-Seber mark–recapture models and radiotelemetry, and we modeled the effect of oceanographic conditions, sex, and radiotagging. We captured 331 after-hatch-year murrelets from 1997 to 2003, of which 117 were radiotagged. Recapture rates were best modeled using a term that reflected differences in capture effort among sampling occasions (p_{effort}) and ranged from 0.068 to 0.166. The most highly ranked model ($\Phi_{PDO+radio}$, p_{effort}) indicated that survival rates were positively related to the strength of the Pacific Decadal Oscillation (PDO) and were negatively affected by radiotransmitters in the year following tagging. Mortality was relatively low in warm-water years, perhaps because murrelets flew inland to breed less frequently and were less exposed to avian predators. Two competing models indicated that survival in the year following tagging was affected by (1) only radiotagging (model Φ_{radio}, p_{effort}), and (2) radiotagging and sex (model $\Phi_{sex+radio}$, p_{effort}). Model-averaged survival estimates were 0.868 (SE = 0.074) and 0.896 (SE = 0.067) for males and females, respectively, that were not radiotagged and 0.531 (SE = 0.175) and 0.572 (SE = 0.181) for males and females, respectively, that were radiotagged. Mortality of radiomarked individuals was greatest during a domoic acid (a neurotoxin in the marine environment) bloom in 1998 (Φ = 0.160–0.400) and radiomarking impacts were much less pronounced during typical years (Φ = 0.724–0.810). Additional causes of mortality included predation by peregrine falcons (*Falco peregrinus*) and oil spills. Survival for nonmarked individuals was similar or higher than what was estimated for murrelets in British Columbia and what was predicted for murrelets based on comparative analyses of other Alcid species, suggesting that mortality of after-hatch-year murrelets is not an immediate threat to population viability in the region.* (JOURNAL OF WILDLIFE MANAGEMENT 70(1):78–88; 2006)

Key words

Brachyramphus marmoratus, *marbled murrelet, mark–recapture, model selection, oceanographic processes, radiotelemetry, survival rates.*

Estimating demographic rates is essential for estimating population trends (Caswell 2000), identifying causes of declines (Green 1995, Peery et al. 2004*a*), and evaluating competing management options (Beissinger and Westphal 1998) for threatened wildlife populations. Equally important for management is an understanding of the magnitude and causes of variation in demographic rates. Spatial, temporal, and individual variation in survival and reproductive rates determine how populations fluctuate over time and have a major influence on extinction probabilities and persistence times (Goodman 1987, Lande 2002). Without reliable demographic estimates and an understanding of the intrinsic and extrinsic factors that affect those rates, population modeling efforts may be misleading or unfeasible and the outcome of management decisions uncertain (Beissinger and Westphal 1998, Ralls et al. 2002).

Conducting demographic analyses has been particularly challenging for the marbled murrelet (*Brachyramphus marmoratus* [hereafter murrelet]), a high-profile, threatened seabird in western North America. Murrelets are unusual among seabirds in that they forage in coastal waters and nest in commercially valuable coastal old-growth forests throughout most of their range (Nelson 1997). Murrelet populations are believed to have declined due to logging of nesting habitat, oil spills, gill-netting, declines in prey availability, and nest predation (Carter and Erickson 1992, USFWS 1997, Becker 2001, Peery et al. 2004*a*), but the demography of this species is poorly understood because locating nests and capturing individuals are difficult. Beissinger (1995) and Beissinger and Nur (1997) estimated an adult ($\geq$3-yrs old) survival rate of 0.845 (95% CI = 0.811–0.880) for murrelets based on an allometric relationship of survival rate against body mass and clutch size for 10 other Alcid species. Cam et al. (2003) recently used mark–recapture analyses of banded individuals in Desolation Sound, British Columbia, to produce the first direct estimate of survival rates for after-hatch-year murrelets ($\geq$1-yr old [0.829, 95% CI = 0.716 to 0.903]). Murrelet survival has not been estimated for other regions and is uncertain because of differences in marine and terrestrial habitats.

Seabird populations in the California Current System (CCS) are strongly influenced by annual variation in primary production that is largely driven by the upwelling of cold nutrient-rich waters (Ainley and Boekelheide 1990, Mann and Lazier 1994, Bakun 1996). Natural variation in sea-surface temperatures occurs on multiple temporal scales due to El Niño-Southern Oscillations (2–7 years) and Pacific Decadal Oscillations (PDO [20–30 years]) in the region (Zhang et al. 1997). In general, the upwelling of cold nutrient-rich waters is inhibited during warm-water periods and primary productivity, fisheries landings (Mantua et al. 1997,

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[1] *E-mail: zpeery@nature.berkeley.edu*
[2] *Present Address: Wildlife Trust, Palisades, NY 10964, USA*

Francis et al. 1998), and seabird reproductive success and survival rates (Hoddard and Graybill 1985, Ainley and Boekelheide 1990, Massey et al. 1992, Nur and Sydeman 1999, Jehl et al. 2002) are all reduced. Reproductive success for murrelets in central California is low in warm-water years (Becker 2001), but the effect of oceanographic condition on survival is unknown.

We used mark–recapture and radiomarking techniques in this study to 1) estimate annual local survival rates for after-hatch-year (i.e., ≥1-yr old) murrelets in central California; and 2) model the effect of variation in oceanographic processes, radiotagging, and sex on survival rates.

Study Area

We studied the central California population of murrelets in San Mateo and Santa Cruz Counties, California (Carter and Erickson 1992, Becker et al. 1997, Becker and Beissinger 2003). This population numbers between 496 and 637 individuals (Peery et al. 2004*b*; M. Z. Peery, University of California, Berkeley, unpublished data) and nests in old-growth redwood–Douglas-fir forests in the Santa Cruz Mountains (Fig. 1). During the breeding season, most birds congregate in near-shore waters between Half Moon Bay and Santa Cruz, but individuals disperse several hundred kilometers to the north and south during the nonbreeding season (M. Z. Peery, University of California, Berkeley, unpublished data).

Methods

Capturing and Marking Murrelets

Murrelets were captured at night using the nightlighting-dipnetting technique from 1997–2003 from an inflatable vessel (Whitworth et al. 1997). Birds were captured during either the breeding (Apr through Jun) or the postbreeding periods (Aug through Oct). Trapping was conducted at 5 locations that had relatively high densities of murrelets based on radiotelemetry information (Peery et al. 2004*a*,*b*) and that were accessible by boat (Fig. 1). Upon capture, murrelets were marked with uniquely numbered stainless steel U.S. Fish and Wildlife Service bands and previously banded murrelets were identified by their band numbers. A blood sample ranging from 0.25 to 1.5 mL was taken from the medial metatarsal vein for molecular-genetic analyses to determine sex (Zoogen$^{\mathrm{TM}}$ sex analysis, Celera AgGen, Davis, California). A subsample of individuals was radiomarked in all years except 2003 by affixing a 2.3-gram radiotransmitter (~1% of mean murrelet body mass [model BD-2G made by Holohil

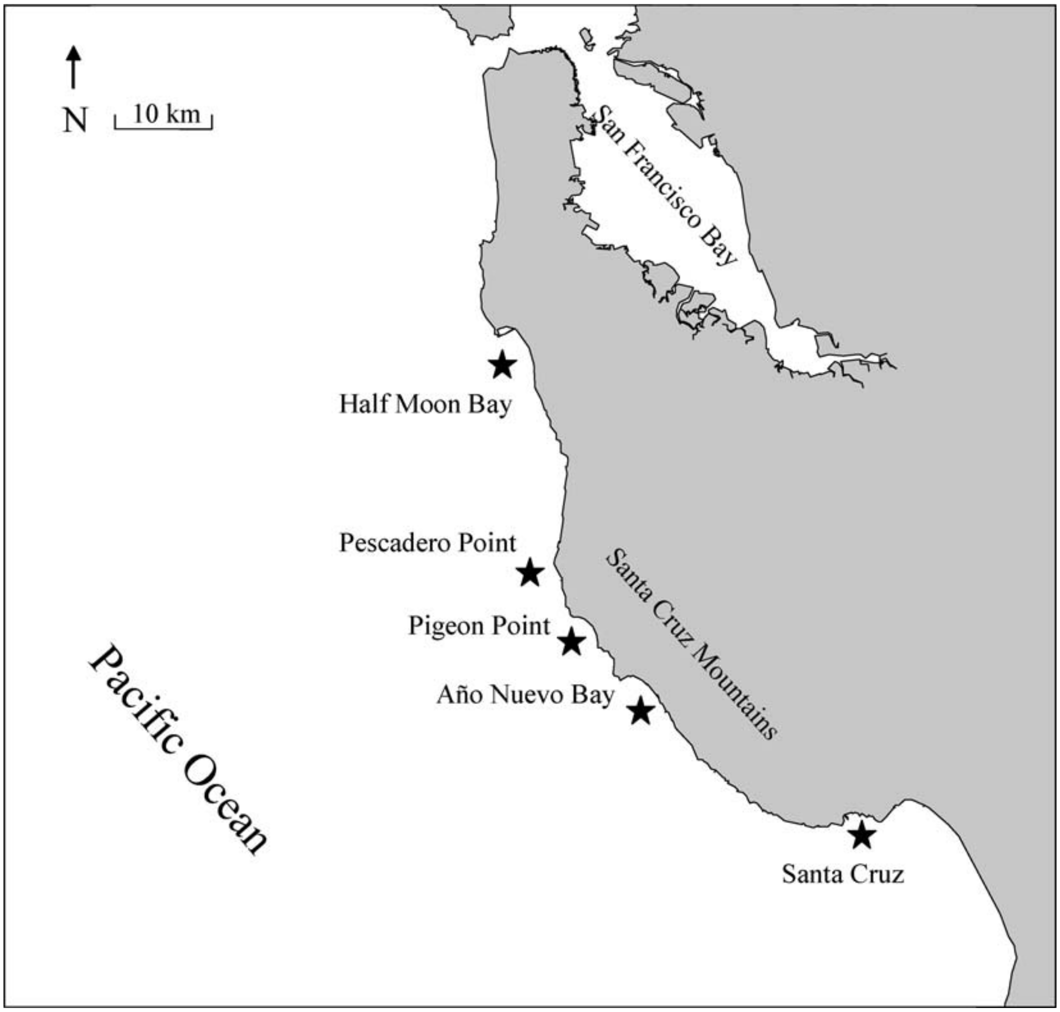

Figure 1. Map of capture locations (stars) for marbled murrelets (*Brachyramphus marmoratus*) in central California.

Systems Ltd., Carp, Ontario, Canada]) with a 20-cm external antenna to the back of each bird (Newman et al. 1999). The cranial end of the transmitter was attached with a small anchor inserted subcutaneously at the level of the scapula, the caudal end was attached with a subcutaneous suture, and a thin coat of marine epoxy (Marine epoxy #332©, Titan Cooperation, Lynnwood, Washington) applied to the bottom of the transmitter. Most birds were lightly sedated with an inhalation anesthetic (isoflurane) prior to attaching transmitters. Radio signals were not used to help identify or recapture radiomarked individuals.

Estimating and Modeling Survival Rates with Mark–Recapture Models

We estimated survival rates for after-hatch-year murrelets as a group using mark–recapture techniques because it was not possible to distinguish prebreeders (1–2 years of age) from adults ($\geq$3 years of age) using plumage characteristics or other criteria. Too few juveniles were captured to estimate juvenile survival rigorously. Analyses of the banding data were conducted using Cormack-Jolly-Seber (CJS) mark–recapture models for open populations (Cormack 1964, Jolly 1965, Seber 1965) implemented in program MARK (White and Burnham 1999). This class of models uses maximum likelihood techniques to estimate annual local survival (Φ_t) and recapture probabilities (p_t), where Φ_t is the probability that an individual survives from year $t - 1$ to year t and does not permanently emigrate out of the study area, and p_t is the probability that an individual is recaptured in year t given that it is alive in year t (Lebreton et al. 1992). We defined our survival interval to be from 1 July in year t to 30 June in year $t + 1$, which reflects the approximate mid-point of our trapping period. Although sampling periods were long relative to the interval for which we estimated survival, sample size did not permit treating the breeding and postbreeding capture sessions as separate sampling periods. Survival and recapture parameters were estimated using a logit link function.

We developed a suite of competing a priori models with different structures for survival and recapture rates and ranked them in terms of how well they were supported by the capture data (Lebreton et al. 1992). We first modeled all possible effects on recapture probability using a survival term that varied by year (Φ_t). Typically, recapture rates are initially modeled using the most general survival term that includes all time and group effects (i.e., Φ_{sex*t}), but sample sizes were insufficient to estimate survival (and recapture) rates for each sex in each year. Once we selected the best structure for recapture rates, we used this term to model and rank all possible survival effects. The notation Φ_t, $p.$, for example, denoted a model parameterized with survival rates that varied among years and a recapture probability that was constant over time. We also considered models in which survival and recapture probabilities differed by sex (Φ_{sex} and p_{sex}) and where recapture probabilities differed between 1998 and 1999–2003 (p_{effort}) because capture effort was greater in the latter years.

We also constructed models in which survival varied among El Niño, La Niña, and normal years. A severe El Niño event occurred from 1997–1998 (Hayward et al. 1999), resulting in low reproductive success for a variety of seabirds that forage in the CCS during the 1998 breeding season, including murrelets (Becker 2001). It was followed by a strong La Niña event beginning in the fall of 1998 and several subsequent cold-water years until a moderate El Niño event peaked in early 2003 (Hayward et al. 1999, Bograd et al 2000, Durazo et al. 2001, Schwing et al. 2002, Vernick et al. 2003). Therefore, we constructed models in which 1) El Niño years (1997–1998 and 2002–2003) differed from all other years (Φ_{EN}); and 2) El Niño years differed from the La Niña year (1998–1999), which differed from all other years ($\Phi_{EN\text{-}LN}$). The series of cold-water years bracketed by El Niño events may have been a consequence of a shift in the northeastern Pacific to a cold phase of the PDO (Bograd et al. 2000). Therefore, we also used an index of the PDO as a proxy for prey availability and as a continuous, annual covariate for murrelet survival (Φ_{PDO}). Positive values for the PDO index represented warm-water conditions and negative values represented cold-water conditions (Mantua et al. 1997). We calculated a single value for the PDO index for each survival interval using the mean of monthly estimates from 1 July in year t to 30 June of year $t + 1$. We also modeled the potential effect of a domoic acid bloom that occurred in the late spring and early summer of 1998 and likely reduced murrelet survival. Domoic acid is a neurotoxin secreted by chain-forming diatoms in the *Pseudo-nitzschia* genus that is known to kill a variety of fishes, marine mammals, and seabirds in the region (Beltrán et al. 1997; Lefebre et al. 2000, 2002). To estimate the effect of domoic acid, we constructed models in which the 1998–1999 survival interval differed from all other intervals (Φ_{DA}).

Finally, we considered models in which survival (and recapture) rates were affected by radiotransmitters (Φ_{radio}). Radiotransmitters and remote recording devices can impact the behavior, energy budgets, reproductive success, and survival of seabirds, but effects vary by device type, attachment method, and species (Wanless et al. 1988, Wilson et al. 1989, Culik and Wilson 1991, Croll et al. 1992, Wanatuki et al. 1992, Meyers et al. 1998). In the only study that estimated the effect of the subcutaneous anchor technique on a pursuit diving seabird, Ackerman et al. (in press) demonstrated that radiotransmitters reduced the reproductive performance of Cassin's auklets (*Ptychoramphus aleuticus*). We hypothesized that survival rates would be lower for radiomarked murrelets in the year following tagging compared to previous or subsequent years, and lower than rates for birds that were never radiomarked. Radio-tagging effects should only be important the year following tagging because 8 of 9 (89%) radiotagged murrelets that were recaptured in the subsequent year had lost their transmitter and the remaining individual was in the process of shedding its transmitter. Moreover, 9 other radiotagged murrelets that were recaptured more than 1 year after tagging had lost their transmitters. Although almost all transmitters were lost within a year, retention times were variable, as 1 murrelet that was recaptured several times shed its transmitter in 75–122 days and another lost its radio in <23 days. The analytical approach for modeling the effect of radiotransmitters on survival follows that of Reynolds et al. (2004) and is presented in Appendix A.

We assessed the goodness-of-fit of model Φ_t, p_t using a bootstrapping procedure in program MARK. This involved simulating 500 data sets with the same number of individuals as the original data set using parameter estimates from model Φ_t, p_t

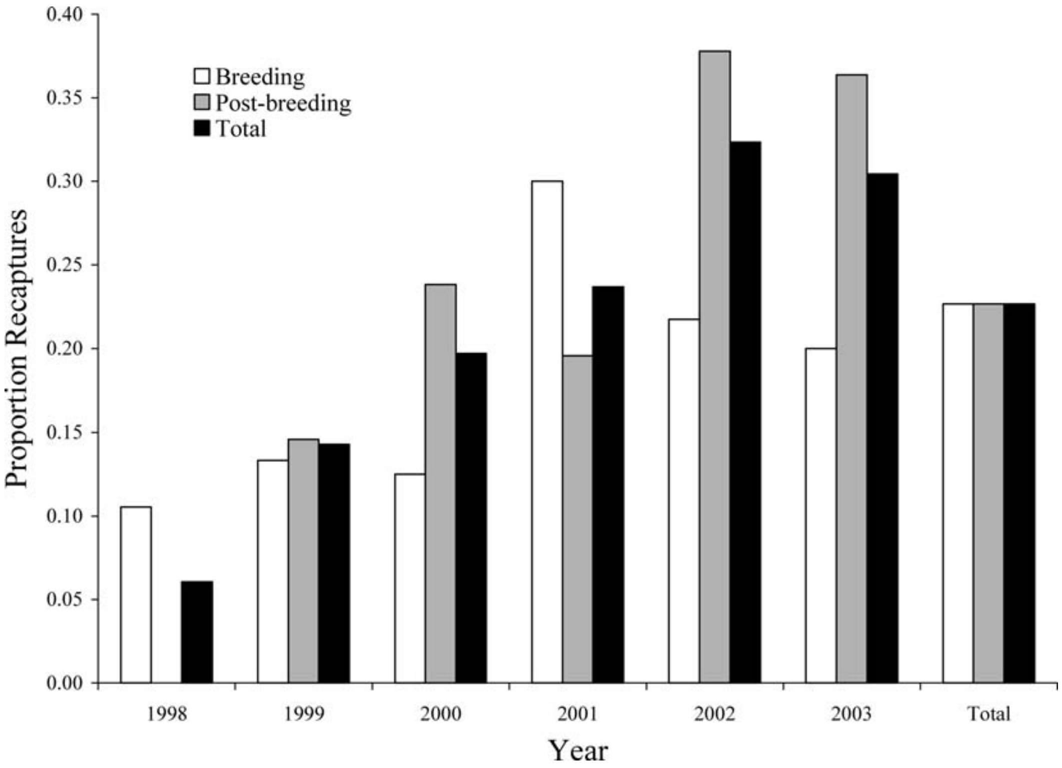

Figure 2. Proportion of marbled murrelets (*Brachyramphus marmoratus*) captured that were recaptures (i.e., originally captured in a previous year) in central California from 1997–2003.

and comparing deviances between simulated and actual data sets. Model Φ_t, p_t fit the capture data adequately as its deviance was less than 23% of the simulated deviances and we therefore assumed that the capture data were not overdispersed and did not require adjustment by a variance inflation factor ($\hat{c}$; Anderson et al. 1994).

Models were ranked in terms of how well they explained the capture data using Akaike's Information Criterion corrected for small sample sizes (AIC_c [Burnham and Anderson 1998]), which was calculated as

$$AIC_c = -2\ln(L) + 2K + 2K(K+1)/(n-K-1),$$

where $\ln(L)$ was the natural log-likelihood of the model, K was the number of parameters in the model, and n was the number of individuals. Models were also evaluated using AIC-weights (w) which provided an estimate of the relative likelihood of each model and summed to 1.0 (Burnham and Anderson 1998). To account for uncertainty in model selection, we conducted model averaging where mean parameter estimates were calculated across models using AIC_c weights as weighting factors (Burnham and Anderson 1998).

Estimating Survival with Radiotelemetry.—For comparison with the mark–recapture analysis, we estimated annual local survival rates for radiomarked birds using the tracking histories of individual birds (i.e., a known fates analysis). Radiomarked murrelets were tracked from fixed-wing aircrafts and trucks following Peery et al. (2004*a,b*), and intensive searches for carcasses were made when we suspected that an individual had died. We divided the number of dead birds for which carcasses were recovered within 2, 3, and 4 months of tagging by the total number of radiomarked birds to estimate mortality rates (White and Garrott 1990). Monthly mortality rates were then extrapolated to estimate annual survival rates. Mean realized radio-life was approximately 60 days and it was not possible to determine if

Table 1. The *m*-array and number of radiotransmitters deployed for after-hatch-year marbled murrelets (*Brachyramphus marmoratus*) captured from 1997 to 2003 in central California. R_{t-1} = number murrelets released in year *t*, r_t = number of murrelets radiomarked in year *t*, m_t = number of individuals captured for the first time in year *t* that were released in year *t* – 1, and Σm_t = total number of individuals released in *t* – 1 that were eventually recaptured.

						m_t			
Year	R_{t-1}	r_t	**98**	**99**	**00**	**01**	**02**	**03**	Σm_t
1997	41	28	2	3	7	2	1	3	18
1998	33	19		6	3	1	0	0	10
1999	63	7			10	8	4	1	23
2000	73	24				7	7	5	19
2001	76	24					10	5	15
2002	68	20						8	8

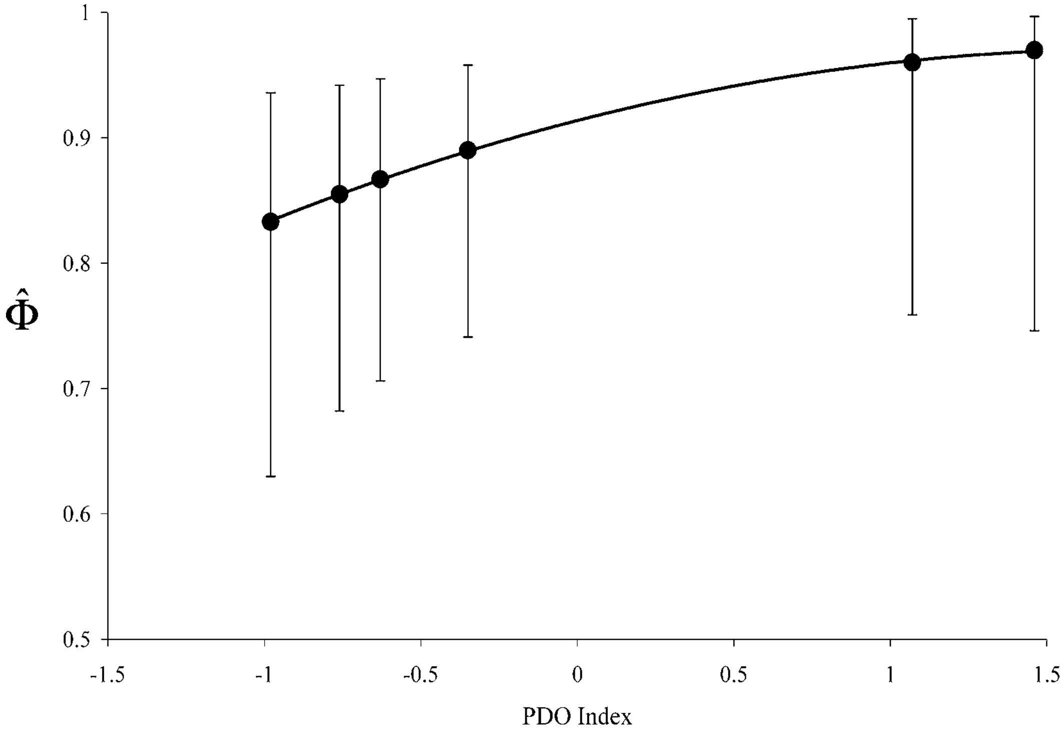

Figure 3. Relationship between estimates of annual survival ($\hat{\Phi}$) of marbled murrelets (*Brachyramphus marmoratus*) and the Pacific Decadal Oscillation Index in central California from 1997 to 2003 based on model $\Phi_{PDO+radio}$, p_{effort}. Positive values for the PDO index indicate warm-water conditions and negative values indicate cold-water conditions.

most individuals without functioning transmitters died, so some murrelets may have died and not been detected. We did not use more complex modeling approaches because mean radio-life was considerably less than expected radio-life (120 days), which would have led to subjective decisions about censoring individuals and potentially large biases in estimates (White and Garrott 1990:223–224).

Table 2. AIC$_c$ scores for the 10 best Cormack-Jolly-Seber mark–recapture models (of 33 total models) based on 331 after-hatch-year marbled murrelets (*Brachyramphus marmoratus*) captured in central California from 1997–2003 (Φ = survival probability and p = recapture probability). ΔAIC$_c$ scores represent the difference between the AIC$_c$ score of the model in question and the highest ranked model (Burnham and Anderson 1998). AIC$_c$-weights (w) provided an estimate of the relative likelihood of each model and sum to 1.0 (Burnham and Anderson 1998). Models with ΔAIC$_c$ $\leq$ 2 were considered as closely competing models and models with ΔAIC$_c$ $\geq$ 4 and $\leq$ 7 received some support from the capture data.

Model[1]	K	AIC$_c$	ΔAIC$_c$	*w*
$\Phi_{PDO+radio}$, p_{effort}	5	596.74	0.00	0.339
Φ_{radio}, p_{effort}	4	597.81	1.07	0.199
$\Phi_{sex+radio}$, p_{effort}	5	597.97	1.23	0.184
$\Phi_{sex*radio}$, p_{effort}	6	599.65	2.92	0.079
$\Phi_{DA+radio}$, p_{effort}	5	599.78	3.05	0.074
$\Phi.$, p_{effort}	3	603.02	6.29	0.015
Φ_{sex}, p_{effort}	4	603.27	6.53	0.013
Φ_{sex}, p_{radio}	4	603.85	7.11	0.010
Φ_{sex}, p_{EN}	4	603.91	7.17	0.009
$\Phi.,p.$	2	604.04	7.30	0.008

[1] Additional models tested were as follows: Φ_{sex},$p.$; Φ_{sex}, $p_{sex+effort}$; Φ_{DA}, p_{effort}; Φ_{EN}, p_{effort}; Φ_{PDO}, p_{effort}; Φ_t, p_{EN}; $\Phi_{sex+PDO}$, p_{effort}; Φ_{sex}, $p_{EN\text{-}LN}$; Φ_{sex}, $p_{radio+effort}$; Φ_{sex}, $p_{sex+radio}$; Φ_{sex}, p_{sex}; $\Phi_{EN\text{-}LN}$, p_{effort}; Φ_t, $p_{sex+effort}$; Φ_t, $p_{EN\text{-}LN}$; Φ_t, p_{effort}; Φ_{sex}, $p_{sex*radio}$; Φ_{sex}, p_t; Φ_t, $p_{sex+radio}$; Φ_t, p_{radio}; Φ_t, $p.$; Φ_t, $p_{sex+radio}$; Φ_t, p_{radio}; Φ_t, p_t .

Identifying Causes of Mortality.—We compiled information pertaining to the causes of death for all known murrelet mortalities between Point Reyes and Point Conception, California, from 1994 to 2003. Information was obtained from a variety of sources including necropsies of radiomarked and nonradiomarked birds that died and were recovered, anecdotal observations of predation events, and recoveries of oiled birds. Only when direct evidence for a cause of death was available did we attribute the mortality to a particular factor (e.g., if oiling was evident on a carcass or a carcass was recovered below a raptor nest).

Results

Capturing and Marking Murrelets

We captured 331 individual after-hatch-year murrelets from 1997–2003 (Table 1). Of 416 total captures, 145 (34.9%) were in the breeding period and 271 (65.1%) were in the postbreeding period. Greater than 95% of all individual captures occurred in Año Nuevo Bay as this area harbored much greater nighttime densities of murrelets than the other 4 locations (Fig. 1). We deployed 122 radiotransmitters on 117 individuals (35.3%), as 5 birds were radiomarked more than once (Table 1). Most (80.6%) radiotransmitters were deployed during the breeding period to locate nests and identify breeding individuals as part of other studies (Peery et al. 2004*a,b*). The proportion of captured birds that had been banded previously (i.e., recaptures) increased as the study progressed (Fig. 2). By 2002 and 2003, >30% of captured individuals had been banded in previous years, indicating that we had marked a significant portion of the population. Murrelets initially captured in the breeding period and later recaptured (n =

Table 3. Annual survival estimates (±1 SE) for marbled murrelets (*Brachyramphus marmoratus*) for the 3 most highly ranked Cormack-Jolly-Seber mark–recapture models and model-averaged estimates from all models considered. Survival parameters for all 3 models were estimated using a recapture rate that differed between 1998 and 1999–2003 due to differences in capture effort. Survival rates for radiomarked murrelets are for the year following radiotagging only and survival rates for murrelets that were not radiomarked include radiomarked individuals in years in which they were not radiotagged. Estimates for model $\Phi_{PDO+radio}$ were derived from the mean of annual estimates.

	Not radiomarked		Radiomarked	
Model	**Males**	**Females**	**Males**	**Females**
$\Phi_{PDO+radio}$	0.896 (0.054)	0.896 (0.054)	0.493 (0.141)	0.493 (0.141)
Φ_{radio}	0.882 (0.058)	0.882 (0.058)	0.520 (0.105)	0.520 (0.105)
$\Phi_{radio+sex}$	0.846 (0.067)	0.912 (0.053)	0.443 (0.116)	0.599 (0.125)
Model-averaged	0.868 (0.074)	0.896 (0.069)	0.531 (0.175)	0.572 (0.181)

26) were equally likely to be recaptured in the breeding (50.0%) and postbreeding periods (50.0%), while birds initially captured in the postbreeding ($n = 59$) period were more likely to be recaptured in the postbreeding period (71.2%) than in the breeding period (28.8%).

Estimating and Modeling Survival Rates with Mark–Recapture Models

Of 33 competing CJS models, model $\Phi_{PDO+radio}$, p_{effort} had the lowest AIC$_c$ score (Table 2) and indicated that (1) survival rates were related to the PDO index and affected by radiotagging, and (2) recapture rates differed between 1998 and 1999–2003. Survival in year t could be expressed using a logit link function as

$$\hat{\Phi}_t = \frac{1}{1 + \exp(0.767*PDO_t - 2.350*RADIO + 2.360)}, \qquad (1)$$

where PDO_t was the PDO index for year t and $RADIO$ was a dummy variable for radiotagging status (zero for radiomarked individuals and 1 for individuals that were not radiomarked). The negative parameter estimate for the RADIO term indicated that radios reduced the probability of survival in the year following radiotagging. The positive parameter estimate for the PDO term indicated that, contrary to our expectation, survival was lower in cold-water years and higher in warm-water years (Fig. 3). Two models were within 2 AIC$_c$ values and were considered to be closely competing models: 1) model Φ_{radio}, p_{effort} indicated that survival was lower in the year following radiotagging (Table 3) and could be expressed as

$$\hat{\Phi}_i = \frac{1}{1 + \exp(-1.931*RADIO + 2.013)} \qquad (2)$$

and 2) model $\Phi_{sex+radio}$, p_{effort} indicated that survival rates were greater for females than for males, were affected by radiotransmitters in the year following tagging (Table 3), and could be expressed as

$$\hat{\Phi}_i = \frac{1}{1 + \exp(-0.633*SEX - 1.931*RADIO + 2.334)} \qquad (3)$$

where SEX was a dummy variable for gender (zero for males and 1 for females). Based on AIC$_c$ weights, model $\Phi_{PDO+radio}$, p_{effort} was 1.70 and 1.84 times more likely than models Φ_{radio}, p_{effort} and $\Phi_{sex+radio}$, p_{effort}, respectively, and models $\Phi_{sex+radio}$, p_{effort} and Φ_{radio}, p_{effort} were essentially equally likely (Table 2). Model $\Phi_{PDO+radio}$, p_{effort} was more than 4 times more likely than all other models, although 4 of these were within 7 AIC$_c$ values (Table 2) and therefore received some support from the data (Burnham and Anderson 1998).

Model-averaged survival estimates for birds that were not radiomarked were greater than for birds that were radiomarked in the year following tagging and females survived at a slightly higher rate than males (Table 3). Model-averaged recapture rates for both sexes were 0.068 (SE = 0.046) in 1998 and 0.166 (SE = 0.029) from 1999–2003, respectively.

Estimating Survival with Radiotelemetry

We recovered 12 dead individuals within 4 months of radiomarking 122 murrelets, 10 of which died within 2 months of radiomarking (Table 4). Of the 12 mortalities, 7 occurred in years without a domoic acid bloom and 5 occurred in the year with a domoic acid bloom. Annual survival of radiomarked birds in years with no domoic acid bloom ranged from 0.742 to 0.810 (Table 4), compared to only 0.160 to 0.400 in the year with the domoic acid bloom (Table 4).

Identifying Causes of Mortality

We obtained information on the deaths of 25 murrelets and were able to determine the cause of mortality in 17 cases (Table 5). Almost half ($n = 8$) were attributable to predation by raptors, most notably peregrine falcons ([*Falco peregrinus*] $n = 7$). Oiling was also an important cause of mortality as 5 oiled murrelets were recovered during this period. Two radiomarked birds recovered in

Table 4. Estimates of annual survival (Φ) of radiomarked marbled murrelets (*Brachyramphus marmoratus*) in central California, 1997–2003. Survival rates were estimated by dividing the number of radiomarked individuals that died (n_{died}) by the total number of radiomarked individuals ($n_{radioed}$) in 3 different intervals following radiomarking and extrapolating over 1 year.

	2 months			3 months			4 months			
Years	**Φ**	**SE**	n_{died}	**Φ**	**SE**	n_{died}	**Φ**	**SE**	n_{died}	$n_{radioed}$
Domoic acid (1998–1999)	0.160	0.036	5	0.295	0.045	5	0.400	0.048	5	19
Not domoic acid (1998–1999 excluded)	0.742	0.043	5	0.787	0.040	6	0.810	0.039	7	103
All Years	0.599	0.044	10	0.685	0.042	11	0.733	0.040	12	122

Table 5. Causes of mortality for 25 after-hatch-year marbled murrelets (*Brachyramphus marmoratus*) in central California from 1994 to 2003.[a]

Cause of mortality	Radiomarked $n = 117$	Banded only $n = 214$	Not radioed or banded
Raptor Predation[b]	2	0	6
Domoic acid	2	0	0
Oil Spills	0	1	4
Physical Injury or Trauma	1	1	0
Unknown	7	1	0

[a] Sources include this study, E. Burkett (California Department of Fish and Game, unpublished data), S. Hampton (California Department of Game, personal communication), and D. Suddjian (personal communication).

[b] Includes 7 predation events by peregrine falcons (*Falco peregrinus*) and 1 predation event by a red-shouldered hawk (*Buteo linneatus*). One predation event by peregrine falcons was probable, rather than confirmed, based upon remains of carcass.

1998 had pathological lesions associated with poisoning by domoic acid.

Discussion

We provided the second estimate of survival rates for murrelets based upon marked individuals, and the first estimate in the southern and endangered/threatened portion of the murrelet's range (Washington to California). Model-averaged survival estimates for murrelets in central California without radiotransmitters (males: 0.864, 95% CL = 0.642–0.967; females: 0.893, 95% CL = 0.678–0.967) were slightly greater than what was predicted by Beissinger and Nur (1997) for a murrelet-sized alcid based on allometric relationships (0.845, 95% CL = 0.811–0.880), but differences were small relative to the confidence intervals. Survival estimates were also slightly greater than what was estimated by Cam et al. (2003) in Desolation Sound, British Columbia, using similar mark–recapture techniques (0.829, 95% CL = 0.716–0.903). Note that Cam et al.'s (2003) sample included an unspecified number of radiomarked birds that could have artificially reduced survival rates, but a suite of environmental differences between regions such as prey communities and predator guilds could result in differences in survival as well. Differences in local survival between regions could also be due to emigration rates, which depend on the scale of sampling relative to population size and distribution. We believe that a high proportion of individuals within the central California population were available for capture and that permanent dispersal of individuals from the study area reflected a true emigration event because our capture locations encompassed almost all of the areas visited by the radiomarked murrelets at night (M. Z. Peery, University of California, Berkeley, unpublished data). In contrast, Cam et al. (2003) sampled individuals at 2 locations from within a much larger population (both in size and range) and emigration away from capture areas could have represented relatively small scale redistributions of individuals.

Recapture rates were low in this study (0.068 in 1998 and 0.166 in 1999–2003) compared to mark–recapture studies of other wildlife species (e.g., Forsman et al. 1996), which resulted in relatively large confidence intervals for survival estimates. Nevertheless, recapture rates in this study were generally greater than those estimated by Cam et al. (2003) for murrelets in British Columbia (0.038 to 0.134, but <0.06 in all but 2 years), which permitted us to model the effects of oceanographic conditions, radiotagging, and sex. Future demographic analyses of murrelets would be greatly facilitated by the development of unique external markers that could be identified during the daytime without physically capturing individuals.

There was some support for males having lower survival than females (model $\Phi_{sex+radio}$, p_{effort} was within 1.23 AIC$_c$ of the best model), indicating that males may have experienced either greater mortality or emigrated at a higher rate than females. In general, female birds tend to disperse greater distances and at higher rates from their natal and breeding sites or populations than males (Greenwood and Harvey 1982, Clarke et al. 1997). More specifically, gender biases in dispersal in the family Alcidae are ambiguous (e.g., Harris et al. 1996), but most species in the order Charadriformes have evolved a female-biased dispersal pattern (Clarke et al. 1997). Therefore, it is likely that gender differences in local survival of murrelets in this study were due to a higher rate of mortality for males. Although a variety of mortality factors could differ between sexes, a plausible explanation is that males fly inland more to provision nestlings (Bradley et al. 2002) and are therefore more likely to be taken by inland predators such as peregrine falcons. However, caution should be exercised when interpreting gender differences because sampling variances were large relative to the difference between model-averaged estimates of male and female survival (Table 3).

Annual survival rates of murrelets were positively correlated with the PDO index and were higher during El Niño years, indicating that warm-water conditions did not necessarily reduce survival. This result conflicts with increased rates of adult mortality that have been observed for other seabird species during El Niño events, including pigeon guillemots (*Cepphus columbia*; Hodder and Graybill 1985), common murres (*Uria aalge*; Hodder and Graybill 1985), California least terns (*Sterna antillarum browni*; Massey et al. 1992), eared grebes (*Podiceps nigricollis*; Jehl et al. 2002), and Brandt's cormorants (*Phalacocorax penicillatus*; Nur and Sydeman 1999). Several explanations that are not mutually exclusive could explain this apparently contradictory result. First, fewer murrelets fly inland to breed in years when prey is reduced (Peery et al. 2004*b*), which could result in reduced exposure to predation risks, particularly by raptors. Second, murrelet prey may be more affected by near-shore processes than large-scale temperature changes in shelf waters such as those due to El Niños. Murrelets forage to an unknown extent on near-shore fishes, such as smelt (family Osmeridae) that depend on freshwater inflow and small fishes in and around kelp beds whose populations are less impacted by large-scale changes in ocean temperatures than the offshore fishes preyed on by pelagic seabirds (USFWS 1997; H. Carter, U.S. Geological Survey, personal communication). Third, the domoic acid bloom, which peaked during the breeding sampling period of 1998 (Gulland 2000) and resulted in at least 2 mortalities, could have reduced survival in the 1998–1999 interval and negated the potentially positive effects of the strong La Niña that occurred during this period. Finally, recapture probabilities in 1998 were low (0.068), making it difficult to estimate survival for the 1997–

1998 interval and potentially resulting in a spurious relationship between survival and the PDO index.

This study indicated that radiomarked murrelets had a lower probability of surviving the year after they were marked than nonmarked murrelets. This demonstrated an additional potential negative effect on adults as was displayed by reduced reproductive success of radiomarked Cassin's Auklets (Ackerman et al., in press). The effect of radiotransmitters on murrelet survival estimated using mark–recapture models was potentially confounded with seasonal effects because most (80.6%) transmitters were deployed in the breeding period. Individuals that were captured and radiotagged in the breeding period had to survive one more breeding season than individuals that were captured but not radiotagged in the postbreeding period, assuming that they were recaptured at the same time. Nevertheless, it is unlikely that experiencing an additional breeding season resulted in the large difference in rates between birds that were and were not radiomarked (Table 5). If the survival rate of a hypothetical female that was initially captured but not radiomarked in the breeding period of year t and recaptured in the postbreeding period of year $t+1$ is adjusted for the additional time it had to survive (the median difference in capture date between the breeding and postbreeding periods was 124 days), the adjusted survival rate (0.865) is still much higher than the survival of radiomarked females (0.572). Moreover, 71.2% of birds initially captured in the postbreeding period were recaptured in the postbreeding period, indicating that most of these birds were also subject to mortality factors during a breeding season in the survival interval following capture.

Survival rates of radiomarked individuals estimated using known mortality events supported the negative effect of radiotransmitters documented by the mark–recapture analysis. When both domoic acid and non-domoic acid years were included, survival rates from the known-fates analysis were lower than survival rates estimated for birds that were not radiomarked using mark–recapture analysis (Tables 3 and 4). Survival rates from the known-fate approach were very similar (for 2-month interval) or somewhat greater (for the 3- and 4-month interval) than they were for radiomarked birds as estimated with mark–recapture models (Tables 3 and 4). However, survival estimates from the known-fates analysis were likely affected by both positive and negative biases. Estimates may be biased high because it was almost impossible to locate individuals that died without a functioning radiotransmitter and many transmitters failed in less than 4 months (mean radio-life was approximately 60 days). However, mortality rates were likely greatest following radiotagging, which would negatively bias annual survival estimates based on the first few months after radiomarking. Regardless, low survival rates estimated with the known-fates analysis for the 1998–1999 interval, which encompassed the domoic acid bloom, indicate that murrelets were more susceptible to the negative impacts of transmitters when algal blooms occurred than during typical oceanographic conditions. In 1998, 3 of 19 radiomarked birds died within 5 days of marking, one more died within 17 days, and 2 of these birds had pathologic lesions associated with domoic acid. Radiomarking in more typical years had more moderate effects on survival as estimates ranged from 0.742 to 0.810 using the known-fates analysis in years excluding the 1998–1999 interval (Table 4). We were not able to evaluate mark–recapture models that contained a domoic acid effect by radiotagging status interaction because all birds that were not radiomarked were captured after the bloom abated (i.e., in the postbreeding sampling period). Moreover, we may not have detected a domoic acid effect on survival with the mark–recapture analysis if domoic acid primarily affected radiomarked birds because the sample size of radioed birds in this interval was small (19). Although radiotransmitters appeared to affect survival, they may be the only effective way to identify and quantify the importance of mortality factors such as domoic acid or depredation.

Radiotagging could have increased mortality rates of murrelets by 1) increasing drag underwater, thereby reducing diving speed and foraging efficiency, 2) increasing wing loadings and the energetic cost of flight, 3) disrupting waterproofing and increasing heat loss at the attachment site, 4) leading to infections at radio attachment sites, 5) increasing vulnerability to predators, and 6) increasing handling time and the use of anesthesia. The first mechanism is perhaps the most likely as foraging speeds of African penguins (*Spheniscus demersus*) were inversely related to the cross sectional area of their recording device (Wilson et al. 1986) and external antennas on radiotransmitters increase the duration of foraging trips and reduce chick provisioning rates for common murres, presumably by increasing drag (Wanless et al. 1988). Increased wing-loading is less likely because radiotransmitters only weighed 2.3 grams (about 1% of the average murrelet's body mass) and murrelets undergo large natural fluctuations in body mass as a fully developed egg weighs about 48 grams (22% of mean adult body mass; M. Z. Peery, University of California, Berkeley, unpublished data). Increased aerodynamic drag and reduced flight efficiency are also possible explanations, but murrelets routinely carry relatively large fish in their bill to feed chicks which should affect their flight performance more than the drag from a radiotransmitter. Using glue to attach the bottoms of the transmitters to birds' dorsal feathers may have reduced waterproofing and increased thermoregulatory costs (Bakken et al. 1996), but no feathers were removed or trimmed at the attachment site and recaptured radiomarked murrelets had preened the radio into their plumage and had no loss of waterproofing (S. H. Newman, University of California, Davis, unpublished data). Infections at radio attachment sites was not likely either because many recaptured marbled and Xantus' murrelets had no signs of infection based on visual inspection of radio attachment sites, and necropsies of 5 dead marbled murrelets indicated that infections at the radio attachment sites played no role in mortality (S. H. Newman, University of California, Davis, unpublished data). Increased vulnerability to predators is difficult to assess, but could be important because predation by raptors was common. We consider it very unlikely that handling or the use of anesthesia resulted in lower survival for radiomarked individuals because 1) murrelets were only sedated by exposure to isoflurane gas for less than 2 minutes as opposed to being completely fully anesthetized, 2) murrelets recovered rapidly (<10 min) after isoflurane exposure with no noticeable effects on wing or leg withdrawal or sensory reflexes, vigor, respiratory and heart rate, or body temperature (Newman et al. 1999; S. H. Newman, University of California, Davis, unpublished data), and 3) the median number of days that elapsed before the dead radiomarked individuals in Table 5 died were recovered was 23 days, long after handling and sedation effects should have resulted in problems.

While murrelets appeared to be affected by radiotransmitters, certain biological data is invaluable for conservation and management decisions and telemetry studies will often be necessary despite detrimental effects that may occur. Future radiotelemetry studies of seabirds should carefully consider the benefits of the information gained from telemetered individuals versus potential impacts to individuals and populations. Finally, future demographic studies of marbled murrelets based on radiomarked birds should address the effects of radiotransmitters.

Management Implications

Mortality of after-hatch-year murrelets in central California does not appear to be of immediate concern for population viability because survival rates were not lower than expected based on comparative analyses (Beissinger and Nur 1997). Thus, our estimate of survival supports Peery et al.'s (2004*a*) suggestion that low reproductive success limits population growth in the region and that factors impacting reproduction should be ameliorated. Nevertheless, population growth rates for long-lived species such as murrelets are more sensitive to small changes in survival rates of adults than reproductive success (Sæther and Bakke 2000) and some mortality factors such as predation by raptors and oil spills are amenable to management. The fact that multiple deaths were attributable to predation and oil spills indicates that both of these factors are important sources of mortality and ameliorating their impacts would likely increase population growth. Domoic acid blooms and their effects on murrelet populations also merit further investigation as it is possible that many murrelets die from toxicity and this mortality goes unnoticed due to the difficulty in locating carcasses.

Estimating survival rates for murrelets is a challenging endeavor because individuals must be caught at sea and because effective visible markers have not been developed. Consequently, whether survival estimates from this study can be applied to other regions merits consideration. Our survival rate is most applicable to the murrelet population in northern California because both populations nest in fragmented patches of old-growth redwood forest and are sympatric with known predators such as peregrine falcons and red-shouldered hawks (*Buteo linneatus*). Moreover, both populations forage within the California Current System and experience similar influences due to large-scale oceanographic processes. Although it is premature to apply our survival rate to murrelet populations outside of California because of potential differences in predator guilds and foraging habitat, doing so may ultimately be the best option for exploratory modeling of murrelet populations in Oregon and Washington.

Acknowledgments

We thank the many people who spent long cold nights out on the open ocean catching murrelets, including D. Fiess, R. Steers, J. Meyer, C. Morrison, T. Hausdoerffer, H. Carter, and K. Cramer. We also thank B. Puccinelli and the crew of the Bluefin for providing a platform from which to capture and radiotag birds. B. Becker provided invaluable support throughout the project, while G. Strachan and B. McCrary provided housing and access to capture areas. G. White provided important statistical advice and A. Franklin and A. Burger provided very helpful comments on an earlier draft of this manuscript. Funding was provided by the California Department of Fish and Game, the U.S. Fish and Wildlife Service, Pacific Lumber Company, Big Creek Lumber Company, the Oiled Wildlife Care Network, and the University of California, Berkeley.

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Associate Editor: Smallwood.

APPENDIX A

To model the effect of radiotransmitters on annual survival rates of marbled murrelets in program MARK, we defined 6 individual covariates (Franklin 2001), 1 corresponding to each survival interval (R1-R6 in Table A-1). If an individual was radiomarked in year *t*, the individual covariate corresponding to that year was coded as a 1, otherwise the covariate was coded as a zero (Table A-1). However, it was only possible to model the effect of radiotagging on survival for 1 interval for each bird and 5 murrelets were radiotagged in at least 2 years. To model the survival rate of these individuals in the year following radiotagging separately from previous and subsequent years, we split their capture histories into 2 separate capture histories as shown for individual 3 in Table A-1. This individual was not captured in years 1 to 3, was captured every year from year 4 to 7, and was radiotagged in years 4 and 5. The first capture history was censored, as indicated by the −1 in the Group ID column, and the individual was not considered to be available for capture after the first survival interval following radiotagging (year 4). This individual became available for capture in its second capture history the year after the first survival interval following the first radiotagging (year 5). To construct a model where survival differed in the year following radiotagging from previous and subsequent years and from rates for murrelets that were never radiotagged, we structured the Design Matrix (White and Burnham 1999) in program MARK as shown in Table A-2.

Table A-1. Hypothetical example of how banding data for 3 marbled murrelets (*Brachyramphus marmoratus*) was input into program MARK.

			Program MARK input								
				Group ID		Individual covariates					
Individual	**Sex**	**Year radiotagged**	**Capture history**	**M**	**F**	**R1**	**R2**	**R3**	**R4**	**R5**	**R6**
1	F	1	1100111	0	1	1	0	0	0	0	0
2	M	None	1100000	1	0	0	0	0	0	0	0
3[a]	F	4 and 5	0001100	0	−1	0	0	0	1	0	0
3	F	4 and 5	0000111	0	1	0	0	0	0	1	0

[a] Individual 3 was radiomarked in years 4 and 5 and originally had capture history 0001111.

Table A-2. Design matrix in program MARK (White and Burnham 1999) for model Φ_{radio}, *p*.

Parameter	Intercept for Φ	Slope for Φ	Intercept for P
Φ1	1	R1	0
Φ2	1	R2	0
Φ3	1	R3	0
Φ4	1	R4	0
Φ5	1	R5	0
Φ6	1	R6	0
P1	0	0	1
P2	0	0	1
P3	0	0	1
P4	0	0	1
P5	0	0	1
P6	0	0	1