AT-SEA DISTRIBUTION, ABUNDANCE AND HABITAT AFFINITIES OF XANTUS'S MURRELETS

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SUMMARY

KARNOVSKY, N.J., SPEAR, L.B., CARTER, H.R., AINLEY, D.G., AMEY, K.D., BALLANCE, L.T., BRIGGS, K.T., FORD, R.G., HUNT, G.L. Jr, KEIPER, C., MASON, J.W., MORGAN, K.H., PITMAN, R.L. & TYNAN, C.T. 2005. At-sea distribution, abundance and habitat affinities of Xantus's Murrelets. *Marine Ornithology* 33: 89–104.

We used shipboard and aerial surveys at sea to study distribution, abundance and habitat affinities of Xantus's Murrelets *Synthliboramphus hypoleucus* within their range, including waters from British Columbia to southern Baja California, and to 500 km offshore. We recorded 1628 murrelets during strip-transects conducted in most years from 1975 to 2003. Densities were highest over the continental slope (depths 200–1000 m) at distances 25–150 km offshore. Murrelets were most numerous in warmer waters of lower salinity, a pattern consistent each year regardless of El Niño–Southern Oscillation or Pacific Decadal Oscillation anomaly fluctuations. During the breeding season, murrelets concentrated in the Southern California Bight (SCB), with lower densities off Baja California and from Point Conception to Bodega Bay, California. During the nonbreeding period, they dispersed north as far as northern Vancouver Island, British Columbia, although densities were highest from central Baja California to central Oregon. We used generalized additive models to estimate the abundance of this species at sea. We observed no trends in abundances across years, 1975–2001 (SCB), and 1985–2003 (central California). After adjustment for biases in survey data, our estimate for the total number of Xantus's Murrelets in North America during the nonbreeding season (1975–2003) is 39 700 birds, consisting of an estimated 17 900 breeding birds (95% confidence interval = 13 900 to 21 000) and 21 800 subadults/nonbreeders.

Key words: At-sea behavior, distribution, ocean habitat, population size, *Synthliboramphus hypoleucus,* Xantus's Murrelet

INTRODUCTION

Xantus's Murrelet *Synthliboramphus hypoleucus* is endemic to the Pacific coast of North America, ranging at sea from 52°N off British Columbia to 23°N off Baja California, Mexico, and to about 500 km offshore (Drost & Lewis 1995, Carter *et al.* 2005). Waters frequented by this murrelet encompass *c.* 1 665 000 km². The global population is divided into two subspecies: *S. h. hypoleucus* (hereafter *hypoleucus*), which breeds almost entirely on Guadalupe Island (with some at the San Benito Islands) off central western Baja California, Mexico; and *S. h. scrippsi* (hereafter *scrippsi*) which breeds primarily on the Channel Islands and Coronado Islands within the Southern California Bight (SCB), but also as far south as the San Benito Islands where it overlaps with *hypoleucus* (Jehl & Bond 1975, Carter *et al.* 2005, Keitt 2005, Wolf *et al.*

2005; Fig. 1). The pelagic distributions of both subspecies overlap to a great extent during post-breeding dispersal in late summer and autumn, when both move primarily northward (Whitworth *et al.* 2000). In addition, Craveri's Murrelet (*S. craveri,* hereafter *craveri*), difficult to distinguish from Xantus's Murrelet in the field and an endemic breeder in the Gulf of California, Mexico, also disperses northward and co-occurs with Xantus's Murrelets along the coasts of Baja California and California during the nonbreeding season (Howell & Webb 1995, Carter *et al.* 2005).

In December 2004, the California Fish and Game Commission listed Xantus's Murrelet as a State Threatened species. It is among the least numerous of alcids and has been adversely affected from predation by rats *Rattus* sp., cats *Felis catus,* Deer Mice *Peromyscus maniculatus* and Barn Owls *Tyto alba* at islands where it nests

(Murray *et al.* 1983, Drost & Lewis 1995, McChesney & Tershy 1998, Keitt 2005). However, because of difficulties in censusing murrelets at their colonies, population estimates and trends for this species are only roughly known. Estimates of the breeding population at the primary Channel Islands colony (on Santa Barbara Island) during 1975–1977 ranged from 1500 to 10 000 birds (Hunt *et al.* 1979, 1980; Sowls *et al.* 1980; Murray *et al.* 1983), although estimates during 1991–2002 (with allowance for censusing difficulties) indicated that the global breeding population was 10 000 to 20 000 birds (Drost & Lewis 1995; Carter *et al.* 1992, 2000; Keitt 2005). Springer *et al.* (1993) estimated the global population to be 16 000 to 30 000 birds, but that estimate used historical 1970s estimates for the Channel Islands.

Xantus's Murrelets nest in crevices and under bushes on steep rocky slopes, cliffs and boulder talus. Many nesting areas are not accessible. Estimates of colony size have been derived from

- nest-site counts in accessible areas,
- at-sea counts near colonies,
- extrapolations using available breeding habitat,
- at-sea nocturnal vocalization surveys, and
- at-sea nocturnal spotlight transects (summarized in Burkett *et al.* 2003).

Fig. 1. Breeding range of Xantus's Murrelets. Islands where murrelets breed are shown in italics (from Whitworth et al. 2003b).

None of these methods have been validated, and estimates lack confidence intervals. Yet, a measurement of estimated precision (reliability) is of considerable importance for effective management and conservation.

Because of these difficulties censusing colonies, Xantus's Murrelet is a good candidate for the use of an alternative method of estimating population size—at-sea surveys during the nonbreeding season. Use of at-sea surveys to estimate population size of seabirds has received much attention recently (reviewed in Clarke *et al.* 2003). The primary concerns have been development of standardized at-sea survey protocols (reviewed in Tasker *et al.* 1984), reduction in biasing factors (e.g. Spear *et al.* 1992, 2005), and development of a statistical method that can deal with biases hampering analyses of at-sea survey data and that provides reasonable 95% confidence intervals for such estimates (Clarke *et al.* 2003).

These primary biases are encountered during at-sea surveys:

- Bird movement relative to that of the ship ("flux")
- Varying survey platforms (e.g. boat vs. plane)
- Varying survey methods (strip vs. snapshot)
- Variation in observer ability (see "Methods")

Primary problems encountered when analyzing survey data (aerial and shipboard) have been the use of sample-based procedures on data that are often collected using a nonrandom survey design, and the patchiness of seabird distributions at sea. The former condition results in estimate inaccuracies (for example, if areas of high seabird density are surveyed in greater proportion than are areas having a lower density, abundance is overestimated), and the latter leads to lack of precision (high variances) and unwieldy confidence intervals, rendering the estimates themselves of little use.

The development of generalized additive models (GAMs; Hastie & Tibshirani 1990) and their subsequent use to estimate seabird population size and trend from at-sea surveys, has alleviated both of these concerns (Clarke *et al.* 2003). Unlike inference from sample-based methods, inference from model-based methods is not dependent on a random survey design. In addition, as compared with stratified methods, GAMs provide substantial improvements in precision (e.g. Borchers *et al.* 1997, Augustin *et al.* 1998), because GAMs capture nonlinear trends in density while using only a few parameters. GAMs also provide a method for smoothing time series of abundance estimates to estimate underlying trends (e.g. Buckland *et al.* 1992). Relevant to these advances, it is fortunate that the Xantus's Murrelet has been intensively surveyed by seabird biologists within its entire range during the past three decades.

For this paper, our objectives were

- to assemble as much available at-sea survey data as possible to provide good coverage of all parts of the range of Xantus's Murrelets during the breeding and nonbreeding periods.
- to describe the birds' oceanographic habitat affinities.
- to estimate the abundance of the species within its at-sea range during the breeding and nonbreeding seasons.
- to compare estimated pelagic population size in the SCB averaged over the breeding seasons of 1975–1978 versus population size averaged for the 1999–2001 period.

- to estimate the annual trend in population size of murrelets occurring off central California during the breeding season using survey data collected each year from 1985 to 2003.

We amassed data from 11 at-sea studies that, together, provided thorough coverage throughout the pelagic range of this species. The total area surveyed was 65 180 km^2 of ocean, or about 9% of the total pelagic range of Xantus's Murrelets. This amount of survey coverage of a population's pelagic range is more than adequate for the purpose of providing an accurate estimate of population size when using GAMs (Clarke *et al.* 2003, Spear *et al.* 2003).

METHODS

Study area

We conducted surveys in waters from 16.8°N to 54.5°N, from the coast to well beyond 600 km offshore. However, we recorded no Xantus's Murrelets north of 52.46°N (132.71°W), south of 24.14°N (113.18°W), or beyond 555 km offshore. We therefore confined our analyses to surveys conducted from 23°N to 53°N, and to about 600 km offshore (Fig. 2). This species' range is not known to extend beyond those latitudes or distance offshore.
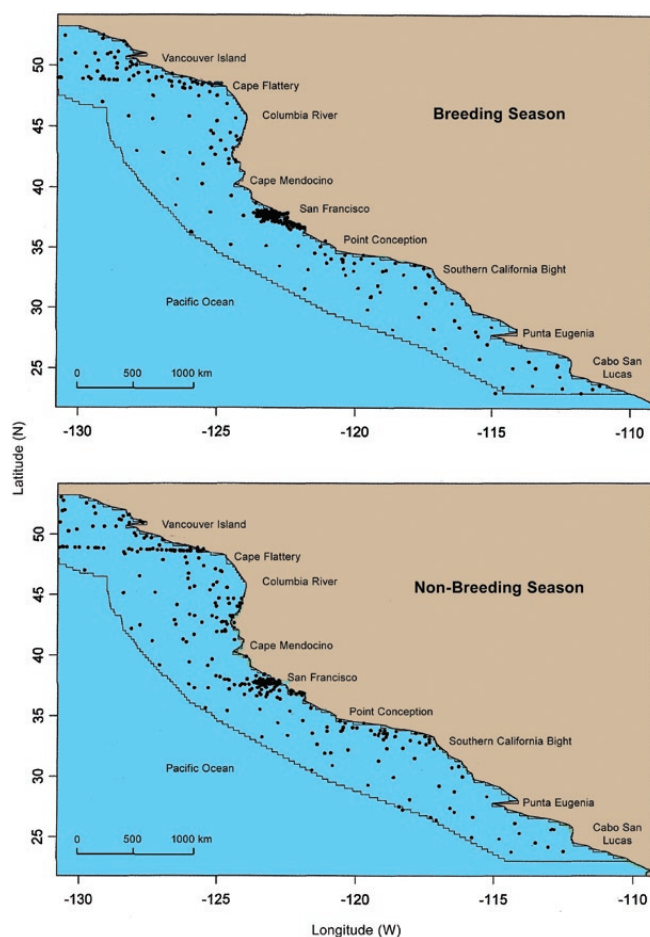

Fig. 2. Study area and survey effort for breeding season and nonbreeding season surveys off the Pacific coast of North America (53°N to 23°N). Each dot represents one noonday position. Many positions were repeatedly sampled in different years; see "Methods" for number of survey transects.

Factors biasing survey data

Primary biases potentially problematic in this study are these:

1) Effects of bird movement relative to that of the ship

2) Varying survey platforms

3) Variation in observer ability

4) Undercounting birds that dive ahead of the ship or plane, especially when ship or plane surveys were conducted using only one observer on watch

5) Overcounting because of inclusion of *craveri* in counts of *hypoleucus/scrippsi*

We avoided the first bias by using the "vector" method (Spear *et al.* 1992) during central California, GLOBEC (global ocean ecosystems dynamics), and EPOCS (Eastern Pacific Ocean Climate Study) studies (41% of total survey effort; Table 1) and by applying the correction factor found in those studies to data from studies for which the vector method could not be used (details below). The vector method has been validated with favorable results (Clarke *et al.* 2003). Although two survey platform types were used (boat and plane), the second bias was not a problem because similar abundance estimates are obtained by each (Briggs *et al.* 1985).

The best way to reduce the third and fourth biases is to use multiple observer teams (Verner 1985). Indeed, apart from reducing the effect of observer differences, the use of multiple observers on watch simultaneously is required to detect 95% of the birds in a survey quadrant. This is true especially for smaller species such as murrelets for which a single observer detects, on average, 26% fewer birds than two observers on watch together (Spear *et al.* 2005). Bias from undercounting diving birds can also be reduced by use of multiple observer teams. Multiple observer teams were used in central California, GLOBEC, and EPOCS studies, but single observers were used in other studies. An exception was aerial surveys in which two observers were often on watch simultaneously. However, each aerial observer scanned a different strip, one on each side of the plane. See "Discussion" for qualifications regarding negative bias caused by diving birds and use of single observers, and positive bias caused by inclusion of *craveri* in count data.

Survey protocol

All surveys were conducted as strip surveys. During studies conducted from ships (Table 1), we conducted continuous strip-surveys from the flying bridge while the ship was underway. Xantus's Murrelets seen within a 90-degree quadrant of known width (300–600 m wide depending on height of the ship's flying bridge) off one forequarter were counted. An exception was the Canadian Wildlife Service (CWS) surveys, most of which were used a 300-m strip width, but with two 150-m strips surveyed simultaneously, one off each of the boat's quarters centered on the bow. For aerial surveys (MMS [Minerals Management Service] II, MMS III, and USGS/HSU [US Geological Survey/Humboldt State University]), all birds were counted within 50-m strips on one or both sides of the aircraft (one observer per side) flying at a 60-m elevation (Briggs *et al.* 1987, Mason *et al.* 2004). By noting ship or plane speed, we calculated surface area of ocean surveyed.

Information recorded for each sighting during the GLOBEC, SFDODS (San Francisco Deep Ocean Disposal Site), EPOCS, Rockfish I, and Rockfish II studies (Table 1) were number of birds and behavior (sitting on water or flying in transit). During those

surveys we also recorded flight direction to the nearest 10 degrees. For all other studies, we did not record flight direction; only number of birds and behavior were recorded.

For nearshore shipboard surveys (GLOBEC, SFDODS, Rockfish I, Rockfish II, SWFSC [Southwest Fisheries Science Center], CWS; Table 1) survey effort was divided into 15-minute "transect" periods, with ship speed at about 18 km/h. For the offshore EPOCS study (where environmental variables changed over a larger spatial scale), survey effort was binned into 30-minute transects with ship speed at about 28 km/h. Aerial surveys, including inshore and offshore regions, were flown at about 165 km/h, with survey effort binned into 5- to 6-minute transects. Data recorded at the beginning of each transect during all studies included date, position, ship or plane speed, and course. The average ocean area surveyed for 15-minute and 30-minute boat and aerial transects was 1.33 ± 0.74 km^2 ($n = 35\,206$ transects; unless noted otherwise, this paper presents means ± 1 standard deviation [SD]—6.53 ± 1.80 km^2 ($n = 1015$) and 0.38 km$^2 \pm 0.14$ ($n = 30\,400$), respectively. Respective transect line lengths were 4.4, 13.1, and 4.7 km.

During GLOBEC, SFDODS, Rockfish I, Rockfish II, and EPOCS studies, we also recorded these variables for each transect:

- Sea-surface temperature (degrees Celsius) and salinity (ppt)
- Thermocline depth (m) and strength (degrees Celsius change at 20 m below thermocline; details below)
- Wind direction (nearest 10 degrees) and speed (km/h)
- Ocean depth (m)
- Distance to mainland (km)

Environmental data were not available for other studies listed in Table 1. Thermocline depth and strength (i.e. indices of mixing in the water column) were monitored using expendable bathythermographs (XBTs) or conductivity–temperature–depth profilers (CTDs), generally producing a temperature profile to at least 200 m below the ocean surface (except in shallower waters). Values of thermocline depth and strength were extrapolated for survey transects that occurred between XBTs or CDTs. Thermocline depth (in meters) is the point where the warm surface layer meets cooler water below, which we identified as the strongest of the shallower inflection points determined from data printouts in which temperature was plotted as a function of depth. Exceptions occurred where there was no inflection point, and in that case the thermocline was considered to be at the ocean surface. Inflection points (warm to cold) near the surface were ignored because these reflect the warming of the ocean surface by the sun instead of mixing in the water column. We measured thermocline strength as the temperature difference (nearest 0.1°C) between the thermocline and a point 20 m below it. A region with strong upwelling or a strong front has a shallow, weak thermocline; the reverse is true where little mixing is occurring.

For survey data in which flight direction was recorded (see above), we used vector analysis (Spear *et al.* 1992) to adjust observed counts to correct for movement of flying birds relative to the ship (flight speeds as related to wind speed were taken from Spear & Ainley 1997). This adjustment is required when estimating abundance from shipboard surveys because the use of observed counts generally results in density overestimation, particularly for fast fliers such as murrelets. However, because of the high

TABLE 1
Summary of studies of at-sea seabird distribution along the Pacific coast of North America which contributed data on Xantus's Murrelets between 23°N and 53°N and within 560 km of the mainland

Study	Period	Years	Latitude	Area surveyed (km^2)	Murrelets (n)	Investigators
Southern California Bight (SCB)						
SCB I	75–78	4	32.5–34.0	5 371.8	293	Hunt/Ford
SCB II [a]	75–78	4	32.3–34.4	1 638.5	174	Briggs/Ford
USGS/HSU [a]	99–02	4	32.5–35.5	1 885.8	184	Carter/Mason
Central California						
Rockfish I	85–94	10	36.3–38.5	9 908.0	288	Ainley/Spear
SFDODS	95–02	7	36.8–38.0	4 586.3	96	Ainley/Spear
Rockfish II	97–03	7	37.0–38.1	4 025.8	22	Keiper/Ainley
British Columbia to Baja California						
MMS [a]	80–90	6	34.4–48.4	8 160.5	170	Briggs/Ford
EPOCS	79–95	12	26.5–48.5	6 629.6	32	Ainley/Spear
CWS	82–01	13	47.0–54.5	10 938.9	15	Morgan/Amey
SWFSC	88–01	8	16.8–48.0	10 380.2	344	Ballance/Pitman
GLOBEC	00–02	2	41.9–44.7	1 654.2	10	Tynan/Ainley
Total	75–03	77	16.8–54.5	65 179.6	1 628	

USGS = US Geological Survey; HSU = Humboldt State University; SFDODS = San Francisco Deep Ocean Disposal Site; MMS = Minerals Management Service; EPOCS = Eastern Pacific Ocean Climate Study; CWS = Canadian Wildlife Service; SWFSC = Southwest Fisheries Science Center; GLOBEC = global ocean ecosystems dynamics.
[a] Study conducted aerially; all others were conducted shipboard.

proportion of observations of stationary murrelets (87%) in studies for which behavior was available, adjustment for movement in those data resulted in a reduction (correction for flux) of only 8.4% from recorded counts. We used that value to adjust counts of murrelets recorded in shipboard studies when flight direction was not recorded. However, we considered that adjusting murrelet counts for the effect of movement was unnecessary for aerial survey data because of the low proportion of murrelets recorded in flight, and because murrelet flight speed is much slower than survey aircraft, thus vastly reducing the effect of bird movement on count accuracy (Spear *et al.* 1992).

We used the data from GLOBEC, SFDODS, EPOCS, Rockfish I and Rockfish II studies to examine distribution of birds in relation to ocean depth and distance to land. We did not include SCB surveys in such analyses because those data may be confounded with colony attendance. That is, birds seen during daylight within 100 km of colonies may reflect a restricted foraging range related to nocturnal colony attendance during the breeding season (Whitworth *et al.* 2000).

Habitat affinities
To understand how murrelet density is related to habitat variables, we used Rockfish I and II and SFDODS data. These surveys were conducted throughout the year (5 January to 27 December). Habitat variables included sea-surface temperature and salinity, thermocline depth and strength, wind speed, ocean depth and distance to mainland. We also considered temporal effects by plotting densities relative to Julian dates and year. The sample unit in these analyses was one survey transect; average transect length was 4 km. Transect densities were weighted by surface area of ocean surveyed to control for differences in survey effort.

To examine murrelet densities off central California (1985–2003) in relation to El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO), we used ENSO and PDO anomaly indices from ftp://ftpprd.ncep.noaa.gov/pub/cpc/wd52dg/data/indices/sstoi.indices and http://jisao.washington.edu/pdo/PDO latest respectively. The ENSO index is the average sea-surface temperature (SST) anomaly equatorward of 5 degrees latitude (north and south) in the tropical Pacific (120°W to 170°W). Annual anomaly values are averaged monthly values for each year. The PDO index reflects standardized values derived as the leading principal component (PC) of monthly SST anomalies in the North Pacific, poleward of 20°N. Monthly mean global average SST anomalies are removed to separate this variability from any "global warming" signal in data. For this analysis we also calculated an annual murrelet density anomaly by subtracting murrelet density averaged across all years from murrelet density observed in each year.

Generalized additive models
GAMs were used to estimate population size from at-sea survey data. GAMs are an extension of generalized linear models (GLMs; McCullagh & Nelder 1989). One advantage of GLMs and GAMs over linear models is their ability to cope with errors that are not normally distributed. Linear models can be expressed as

$$E[y] = \beta_0 + \sum_k \beta_k x_k$$

where y is the response variable, $E[y]$ represents the expected value of y, x_k is the kth explanatory variable (covariate) and the βs are constants estimated from data. The right-hand side of the equation

is the linear predictor. GLMs allow the linear predictor to be a nonlinear function of expected observations,

$$g(E[y]) = \beta_0 + \sum_k \beta_k x_k$$

where g(·) is the link function defining the relationship between the response and the linear predictor. The principal strength of additive models is their ability to fit complex smooth functions in the predictor rather than being constrained by the linearity implicit in GLMs. A GAM is expressed as

$$g(E[y]) = \beta_0 + \sum_k S_k(x_k).$$

The right-hand side of the equation is the additive predictor. β_0 is an intercept term and S_k is a one-dimensional smoothing function for the kth spatial covariate, x_k. The degree of smoothing is determined by the degrees of freedom (df) associated with the smoothing function. Larger dfs have less smoothing with more flexible functions. A GAM in which all the smoothing functions have one df is equivalent to a GLM. An offset (a linear covariate whose coefficient is 1) can also be included in the predictor. This is useful when a transformation of the response variable can be modeled using a standard distribution. For example, rather than modeling density, we could model numbers, with area surveyed as an offset.

Modeling spatial distributions
GAMs were fitted using observed murrelet counts during each survey transect as the response variable. Transects outside study areas were excluded. Explanatory variables considered for each model were latitude, longitude, shortest distance to mainland, ocean depth and distance to breeding colony. Ocean depth and distance to mainland were calculated for each transect using transect position along with coastline and bathymetry data obtained respectively from http://rimmer.ngdc.noaa.gov/ coast/ and http://ingrid.ldgo.columbia. edu/SOURCES/WORLDBATH. The northernmost, primary colony on Santa Barbara Island (*c.* 33.45°N, 119.02°W; Fig. 1) was the designated colony location. GAMs are constrained to use a single colony position. The fact that other large Xantus's Murrelet colonies exist at the Coronado Islands and Guadalupe Island, with smaller ones at Santa Cruz, Anacapa, and San Benito Islands was not a problem because the density relationship with colony location was modeled as nonlinear. High densities in association with other distant colonies are readily modeled with GAMs even with multiple colony locations (see below).

Count data are often modeled using a Poisson error structure, with variance equal to the mean (McCullagh & Nelder 1989). However, when birds occur in clusters, variance of counts is more dispersed than is implied by a Poisson distribution. Therefore, we modeled those data using the Poisson variance function and estimating a dispersion parameter, which we incorporated into model selection procedures (e.g. Venables & Ripley 1997). Observed counts must be adjusted for bird movement, and they depend on area surveyed within the transect, so we used the logarithm of area surveyed multiplied by the bird-movement adjustment factor (which varies for each data point) as an offset. The logarithm was used because we used a log link function.

Model selection with GAMs involves choosing explanatory variables and their degree of smoothing. Forward stepwise selection was used to select covariates for each model on the basis of Akaike's (1973) information criterion. Each covariate was included as a linear term or smooth (curvilinear) term with 4 df. Residual plots

were examined to ensure that model fits were adequate. Because bird clusters could overlap adjacent survey transects, counts were not necessarily independent. Thus, current model-selection methods, which assume observations are independent, could result in overfitting. However overfitting should not bias the population size estimate, although its variance will increase (Augustin 1999), and the choice of a maximum of 4 df in the smooths reduced the possibility of overfitting.

Estimation of population size and temporal trend

Once fitted, a GAM provides a smooth average density surface over the area of interest, including unsampled areas. Population size was estimated by integrating numerically under this surface. First, we created a fine grid across the study area (grid cell size for each GAM given in figure captions for each distribution plot). The fitted surface was then used to predict the average number of birds in each grid square. Finally, population size was estimated as the sum of the predicted numbers over all grid squares within the study area.

Variance estimation

Confidence intervals for population size were obtained using bootstrapping. Bootstrapping involves creating many new data sets from the original sample, and analyzing these new samples in the same way as the original. The distribution of the statistic of interest is then estimated from its empirical distribution among the bootstrap samples.

To control for correlation between counts from survey transects close in space and time, we used an adaptation of a moving-blocks bootstrap (Efron & Tibshirani 1993). In this bootstrap technique, data are resampled with replacement from all possible contiguous blocks of some specified length. Block lengths are determined by accounting for strength of the autocorrelation between observations. The block must be long enough so that observations further than one block length apart are independent.

Because counts from survey transects within a day could be correlated, day was used as the sampling unit (block). The "length" of each day was measured as the number of transects surveyed. The resampling algorithm works through the data set, recreating each day's data in turn. Generating data for a day involved randomly selecting a day from survey data and randomly selecting a transect to start from within that day. Counts for survey transects in the original day were then recreated in turn from survey transects in the new day using the semi-parametric bootstrap procedure (e.g. Davison & Hinkley 1997) described below. If the end of a day was reached before enough transects had been resampled, resampling was continued at the start of the next day. For data from the breeding season, there were an average of 22 transects per day. A bootstrap count b_i for transect i was generated from transect j, $b_i = \hat{f}_i + \hat{s}_i \, \varepsilon_j$ where $\hat{f}_i = E[y_i]$ is the fitted value for count i, $\hat{s}_i$ is the estimated standard deviation for count i and ε_j is the deviance residual of count j. For overdispersed Poisson errors, $\hat{s}_i$ is defined by $\hat{s}_i^2 = \hat{\phi} \, \hat{f}_i \, (1 - h_i)$ (Davison & Hinkley 1997), where h_i is the leverage of count i (McCullagh & Nelder 1989), and $\hat{\phi}$ is the estimate of the dispersion parameter ϕ.

A total of 199 bootstrap resamples were generated for each data set being modeled. The model was refitted to each bootstrap resample and a new population size estimate obtained. However, as is common with bootstrap resamples obtained from GAMs, these estimates were slightly biased. To adjust for this, they were rescaled by multiplying by the ratio of the original estimate to the mean of bootstrap estimates. The coefficient of variation (CV) of the population size estimate was calculated by dividing the sample standard deviation of scaled bootstrap estimates by the original estimate of population size. Confidence intervals (95% CIs) were estimated using the percentile method (e.g. Davison & Hinkley 1997).

Population size estimates

Southern California Bight: 1975–1978 versus 1999–2002

To standardize survey protocols, we restricted analyses of the SCB to two studies conducted using aerial surveys between Point Conception and the US–Mexico border, and to data collected only during the central part of the colony attendance period (Fig. 3, 15 March–15 June; Murray *et al.* 1983, Drost & Lewis 1995, Whitworth *et al.* 2005a, Wolf *et al.* 2005). At that time, most breeding adults have returned from wintering areas (Whitworth *et al.* 2000), although some adults also may have dispersed back to wintering areas during this period because of high rates of nest failure (reviewed in "Discussion"). However, timing of breeding is about one month earlier in central Baja California than in the SCB
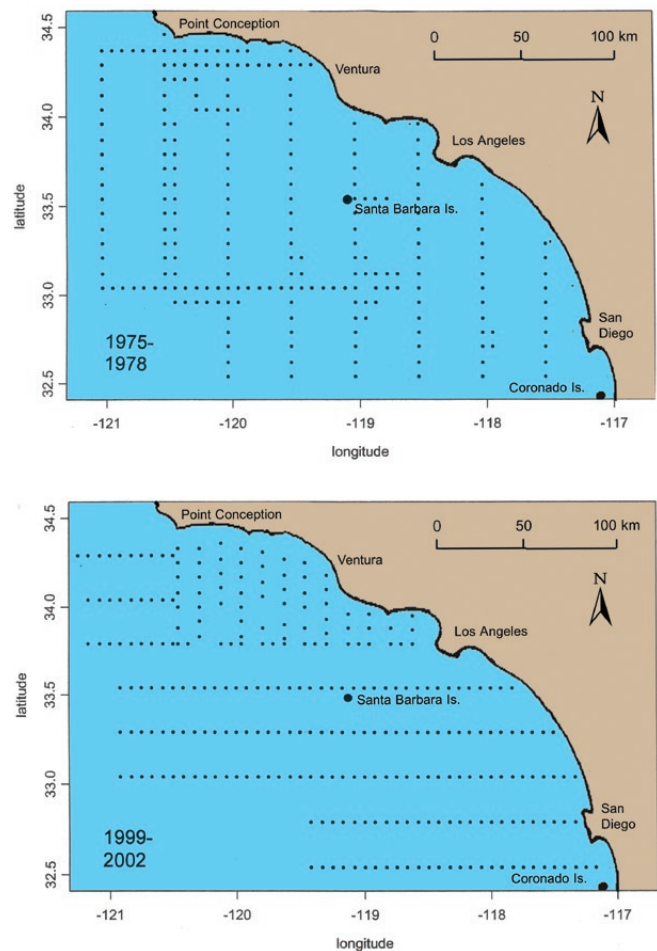

Fig. 3. Study area and survey effort for breeding season surveys in the Southern California Bight during MMS *(Minerals Management Service)* II aerial surveys (1975–1978; top) and USGS/HSU (US Geological Survey/Humboldt State University) surveys (1999–2001; bottom). Dots denote transect positions, many sampled repeatedly during different surveys and years; see "Methods" for number of survey transects.

(Wolf *et al.* 2005), such that some birds likely disperse northward from central Baja California colonies into the SCB before 15 June. After excluding data outside of the March–June period, and from north of Point Conception in 1999–2002, data for 1975–1978 (MMS II) included 336.7 km^2 (n = 756 survey transects) of survey effort, and that for 1999–2002 (USGS/HSU) included 502.4 km^2 (n = 837) of effort (Fig. 3). No surveys were conducted in the southern portion of the SCB within northern Baja California in either study.

Central California: 1985–2003
For consistency across years, we confined analyses of central California to data from surveys in waters within 80 km of Southeast

Farallon Island (SEFI). Because numbers of murrelets recorded in some years were too low to allow a GAM to perform adequately when analyzing each year separately, we grouped the data into three periods: 1985–1990, 1991–1997, and 1998–2003. To standardize data seasonally, we included only data collected during the breeding season from 15 March to 15 June. Survey effort for the breeding season within each period was 3278 km^2 (n = 2904 survey transects), 2380 km^2 (n = 1682), and 4114 km^2 (n = 3348).

Pacific coast of North America
We pooled data from 11 studies conducted from 1975 to 2003 within the pelagic range of Xantus's Murrelets (Table 1). We conducted two GAMs, one to estimate population size for the SCB breeding period (15 March to 15 June, see above), and the other for the remainder of the year, denoted here as the "nonbreeding" period. These periods accounted for major differences in distribution due to colony attendance during the breeding season. However, variation in timing of breeding between colonies and years likely resulted in some overlap between seasons (see "Discussion" for qualifications). Areas surveyed during breeding and nonbreeding periods were 21 844 km^2 (n = 23 604 survey transects) and 43 336 km^2 (n = 44 475 transects) respectively (Fig. 2).

RESULTS

Habitat affinities
In waters beyond foraging areas used by birds attending breeding colonies (see "Methods" for rationale regarding exclusion of waters within colony foraging range), the average ocean depth at which Xantus's Murrelets were recorded was 1528 m (SE = 55 m; n = 448 birds; range: 26–4589 m). Highest densities of Xantus's Murrelets were found over the upper continental slope (depth: 200–1000 m; Fig. 4[A]). Densities were moderately high over the outer slope (depth: 1001–3000 m), but were low over pelagic waters (depths > 3000 m), as well as over the continental shelf (depth < 200 m).

The average distance from the mainland at which murrelets were recorded was 83 km (SE = 2.5 km; n = 290 birds; range: 2–251 km). Densities of murrelets were highest at distances of
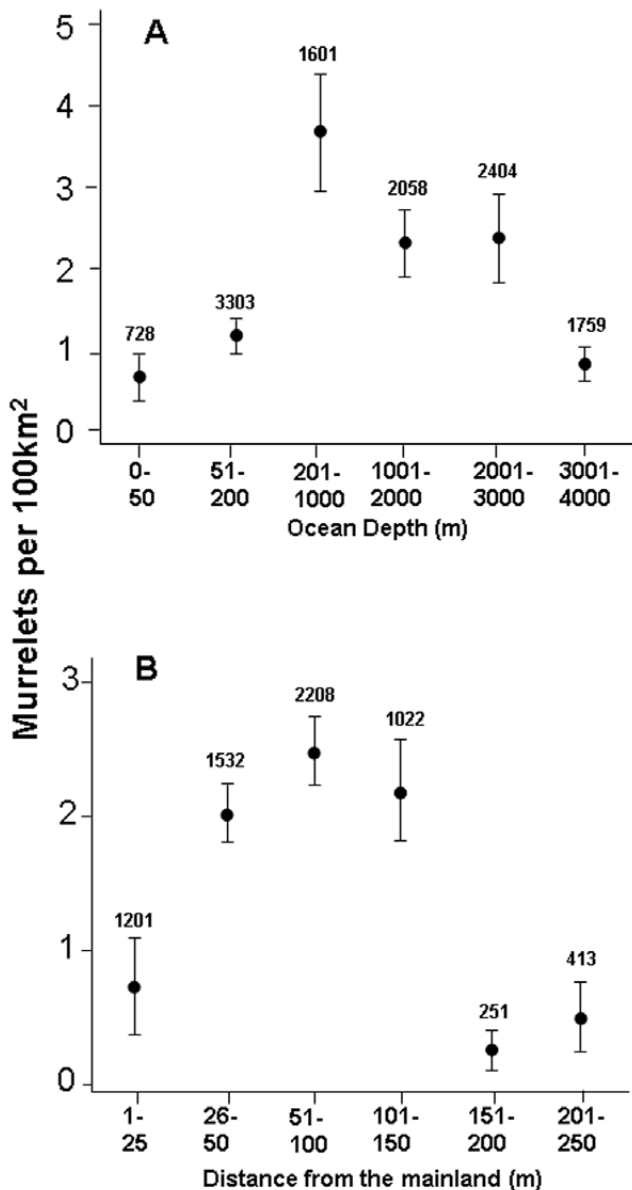

Fig. 4. Occurrence of Xantus's Murrelets (mean density ± 1 standard error [SE]) in relation to ocean depth (A) and distance to the mainland (B). Only data for birds not associated with breeding colonies were analyzed. Sample sizes adjacent to means are numbers of transects.
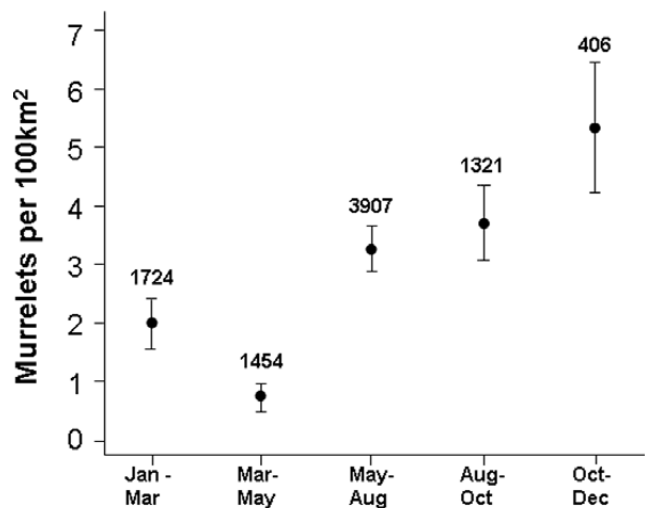

Fig. 5. Occurrence of Xantus's Murrelets (mean density ± 1 standard error [SE]) in relation to time of year within waters off central California. Sample sizes adjacent to means are numbers of transects.

26–150 km from shore, but were low at distances < 26 km and > 150 km (Fig. 4[B]).

For the entire Pacific coast data set in the nonbreeding season, including SCB surveys, mean ocean depth was 1053 m (SE = 42 m; n = 810 sightings; group size: not distinguished), and mean distance to land was 70 km (SE = 2.7 km, n = 810 sightings). Our most distant records were sightings of seven birds more than 300 km from the mainland, including two birds at 42.15°N (302 km), one bird at 27.48°N (334 km), two birds at 47.25°N (432 km) and two birds at 27.72°N (555 km).

In central California waters, murrelet densities increased with Julian date (Fig. 5). Murrelet densities also increased with SST and thermocline strength; densities decreased with increases in sea-surface salinity and thermocline depth (Fig. 6). Thus, murrelet densities in that region were highest late in the year and were also associated with high SST, low salinity, and a shallow but highly stratified thermocline. However, habitat variables were also highly correlated with each other and with Julian date. For example, Julian date was positively correlated with SST, salinity, thermocline strength and wind speed, and was negatively correlated with ocean depth, distance to land and thermocline depth (Table 2).

Relationship of ENSO and PDO to murrelet occurrence in central California

Although highest murrelet densities occurred during the warm-water ENSO years of 1992, 1997 and 1998 (Fig. 7), the relationship between density and the ENSO anomaly index was nonsignificant ($r = 0.176$, n = 19 years, $P = 0.5$). A similar relationship between density and the PDO anomaly index was also nonsignificant ($r = 0.201$, n = 19 years, $P = 0.4$, not shown; note that ENSO and PDO indices were highly correlated: $r = 0.553$, n = 19, $P < 0.02$). Interestingly, densities also were high during cool-water La Niña years (1989 and 2003).
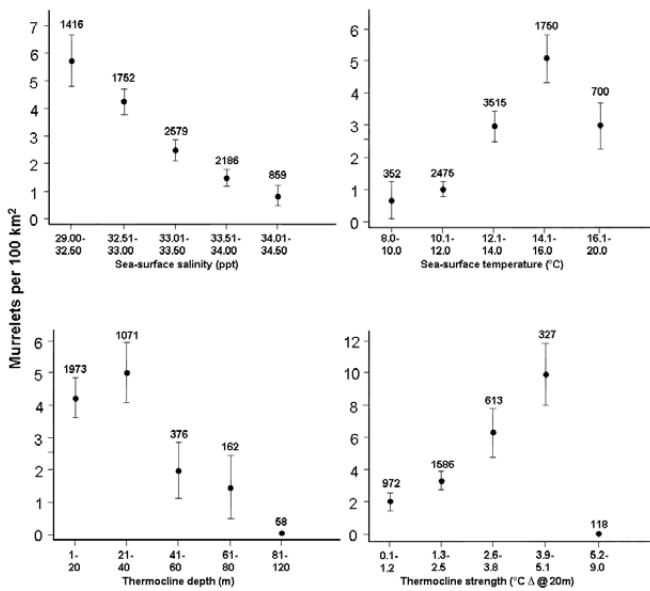

Fig. 6. Occurrence of Xantus's Murrelets (mean density ± 1 standard error [SE]) in relation to four oceanographic variables within waters of the Gulf of the Farallones. Sample sizes adjacent to means are numbers of transects.
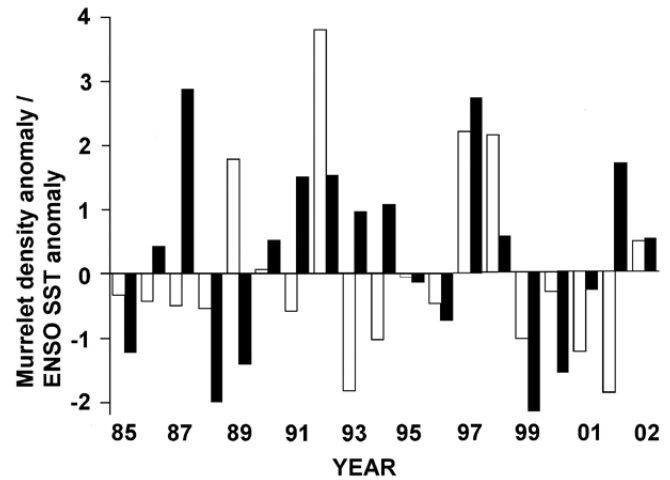

Fig. 7. Mean Xantus's Murrelet density anomaly (birds per 100 km^2; white bars) and El Niño–Southern Oscillation (ENSO) sea-surface temperature anomaly (multiplied by 2; black bars) with respect to year. See "Methods" for details on calculation of anomaly values.

TABLE 2
Relationships (*r* values) between nine environmental and temporal habitat variables
using Pearson correlation (n = 3 616 survey transects)

	SST	SAL	TDPT	TSTR	WSP	LAND	DEPTH	JD
SAL	–0.615[a]							
TDPT	0.017	–0.181[a]						
TSTR	0.407[a]	–0.226[a]	0.152[a]					
WSP	–0.131[a]	0.061[a]	0.135[a]	0.229[a]				
LAND	0.176[a]	–0.372[a]	0.230[a]	0.016	0.034			
DEPTH	0.279[a]	–0.248[a]	0.418[a]	0.222[a]	0.147[a]	0.657[a]		
JD	0.126[a]	0.239[a]	–0.305[a]	0.362[a]	0.267[a]	–0.272[a]	–0.027	
YEAR	0.496[a]	–0.400[a]	0.447[a]	0.490[a]	0.174[a]	0.101[a]	0.539[a]	0.175[a]

[a] Significant correlation (P < 0.05).
SST = sea-surface temperature; SAL = sea-surface salinity; TDPT = thermocline depth; TSTR = thermocline strength; WSP = wind speed; LAND = distance to mainland; DEPTH = ocean depth; JD = Julian date.

Geographic distribution and population size estimates

CVs for the population size estimates indicated that GAMs generally performed well in modeling murrelet distributions at sea, particularly for the SCB during 1999–2001 and the entire population during the nonbreeding season (Table 3). Selected models included most or all covariates, although longitude was chosen least; distance to land and to Santa Barbara Island were chosen by each model (Table 4). Ocean depth and latitude were chosen in all models except in the GAM for the entire population during the breeding season.

Pacific coast of North America

During the breeding season, murrelets occurred from 44°N to 25.5°N, but were concentrated in the SCB (Fig. 8). During the nonbreeding season, they were more dispersed, occurring from southern Baja California to Vancouver Island, British Columbia, with the bulk between central Oregon and central Baja California. The area of

highest concentration during the nonbreeding season was off northern Baja California from about 28°N to 31°N (Fig. 8).

The CV of the population size estimate for the nonbreeding season was low (11.1%) and that for the breeding season was moderately high (19.3%; Table 3). The reason for the better fit of the former GAM was the more uniform distribution of murrelets over their pelagic range during the nonbreeding period, as compared with the highly clumped distribution in the vicinity of the SCB during the breeding period (Fig. 9). Population size estimates for breeding and nonbreeding seasons were about 24 500 and 36 100 birds, respectively (Table 3). As noted in the "Introduction," these estimates include *hypoleucus* and *scrippsi,* and a small proportion of *craveri* (see qualifications in "Discussion"). Using 95% CIs, no fewer than 16 600 birds and no more than 35 500 birds were present during the breeding season, and no fewer than 28 100 birds and no more than 43 700 birds were present during the nonbreeding season (Table 3).

Southern California Bight: 1975–1978 versus 1999–2001

The SCB distribution of murrelets during the breeding season differed between the 1975–1978 and 1999–2001 surveys (Fig. 9). During 1975–1978, there were two areas of high density: one near the California–Mexico border just to the northwest of the Coronado Islands, and the other in the vicinity of Santa Barbara Island. During 1999–2001, murrelets were present only in very low numbers in the southern area, and a more northern extension of the area of high density was seen in the Santa Barbara Island region.

Moderately low CVs for the two SCB population estimates (13%–15%) indicated that models were successful in fitting survey data (Table 3). Population size estimates for the number of murrelets occurring at sea in SCB waters during the breeding seasons of 1975–1978 and 1999–2001 were very similar at about 11 350 and 12 600 birds, respectively. Using 95% CIs, pelagic population sizes were not less than about 7500 birds and not more than about 14 200 birds in 1975–1978 and not less than 9150 birds and not more than 15 500 birds in 1999–2001.

Central California, 1985–2003

In central California, murrelets were concentrated over the mid-to-upper continental slope in all three periods (Fig. 10). However,

TABLE 3
Estimates of population size of Xantus's Murrelet for different areas, seasons and years, derived from generalized additive models (GAMs) using at-sea surveys, 1975–2003

Area	Birds (n)	95% CI	Coefficient of variation
Pacific coast of North America (23°N to 53°N), 1975–2003			
Breeding season	24 537	16 598–35 533	19.3
Nonbreeding season	36 098	28 103–43 699	11.1
Southern California Bight (32.5°N to 34.5°N), breeding season			
1975–1978 (aerial)	11 351	7 505–14 244	14.9
1999–2002 (aerial)	12 620	9 147–15 539	12.7
Central California (36.5°N to 38.5°N), breeding season			
1985–1990	261	128–367	22.9
1991–1997	517	331–702	17.9
1998–2003	293	182–366	17.5

CI = confidence interval.

TABLE 4
Covariates chosen by the generalized additive models when modeling distributions and estimating population sizes of Xantus's Murrelets

Population	Latitude	Longitude	Ocean depth	Distance to	
				Mainland	Colony
Pacific Coast of North America					
Breeding season	[a]	Smooth	[a]	Smooth	Smooth
Nonbreeding season	Smooth	[a]	Smooth	Smooth	Smooth
Southern California Bight (breeding season)					
1975–1978	Smooth	[a]	Smooth	Smooth	Smooth
1999–2001	Smooth	Smooth	Smooth	Linear	Smooth
Central California (breeding season)					
1985–1990	Smooth	[a]	Smooth	Smooth	Smooth
1991–1996	Smooth	Smooth	Smooth	Smooth	Linear
1997–2003	Smooth	Smooth	Smooth	Smooth	Smooth

[a] Covariate was nonsignificant in the model.

distribution in 1985–1990 was more uniform than in 1991–1996 or 1997–2003. During the 1991–1996 period, murrelets were more concentrated near Guide Seamount and Pioneer Canyon, and along the 1000-m depth contour. In the 1997–2003 period, they were found over the 500-m depth contour with two concentrations (50 km south of SEFI and over Cordell Bank).
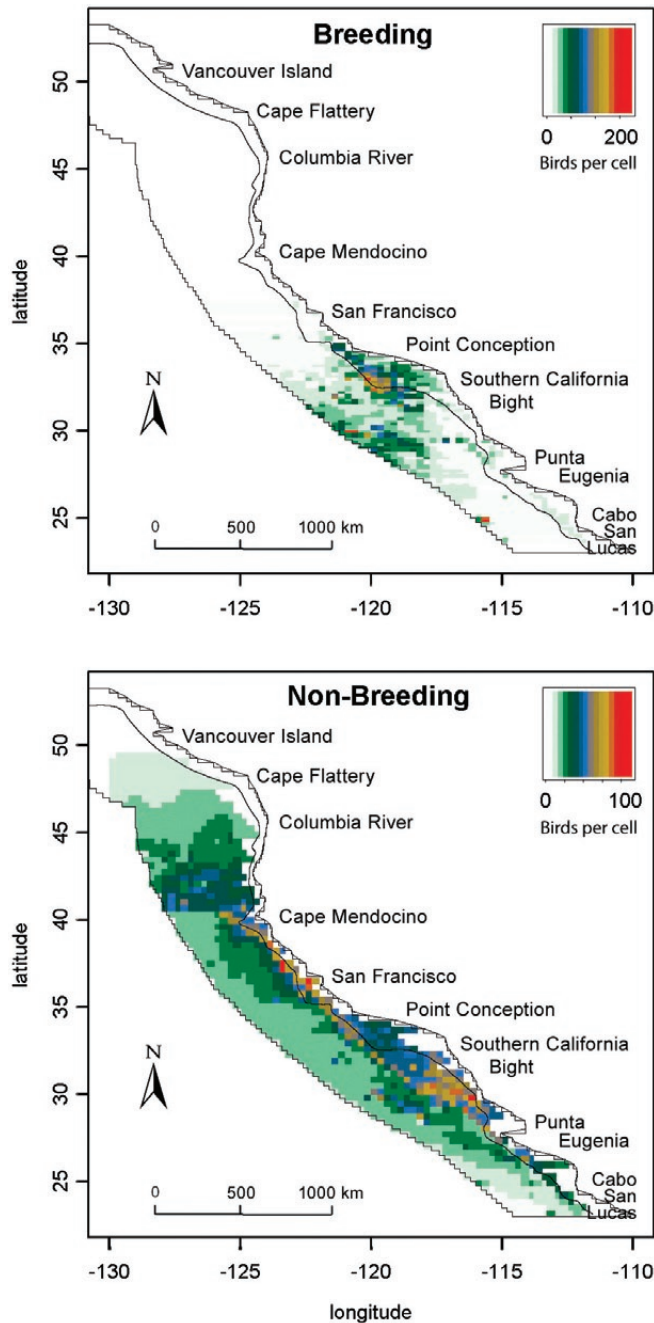
CVs for population estimates of murrelet abundance during the three periods ranged from 17.5% to 22.9% (Table 3). Somewhat larger variances for the Central California estimates as compared with SCB estimates were attributable to the relative scarcity of these birds in the former location, resulting in a large proportion of zero densities per sample period.

Population size estimates (which represent the average for each year included within each of the three periods) ranged from 261 to 517 birds and did not show a significant linear trend ($P > 0.05$) across periods (Table 3). However, a curvilinear trend ($P < 0.05$) was observed because of higher numbers recorded mid-study. Using
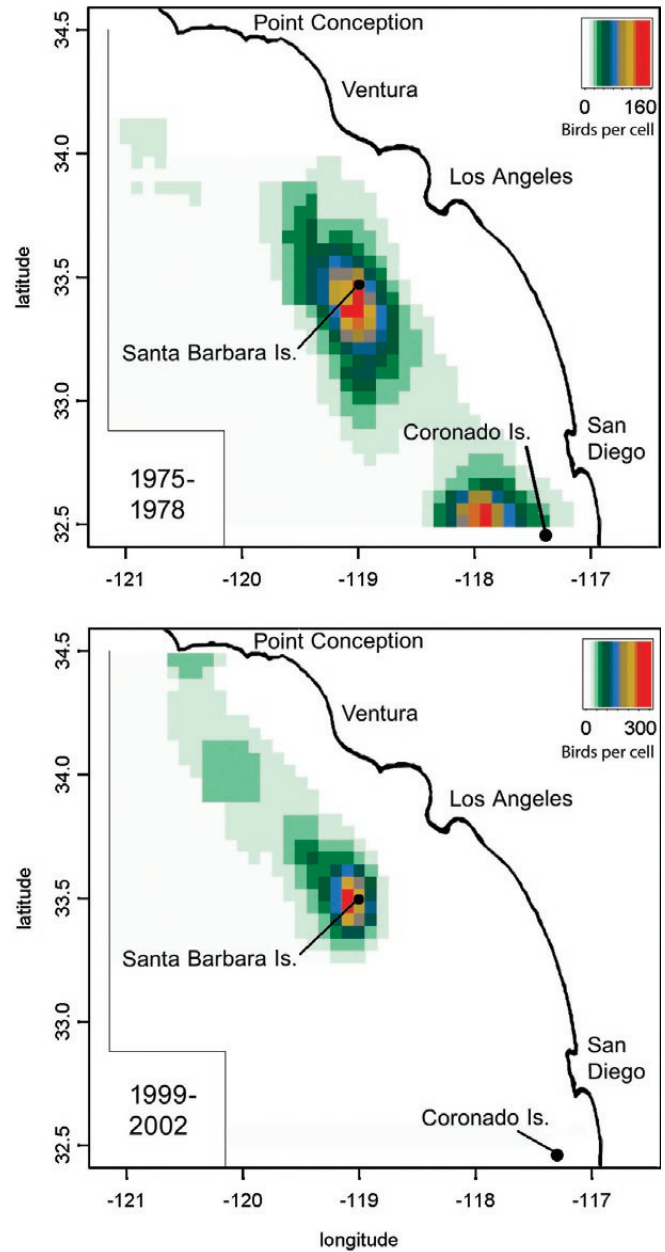

Fig. 8. Xantus's Murrelet distribution off the Pacific coast of North America (birds per 0.5×0.5–degree cell) estimated from aerial and ship surveys during breeding and nonbreeding periods, 1975–2003. Number of birds per cell are smoothed values predicted and plotted using generalized additive models (GAMs). The total population estimate for each season is the sum of numbers across all blocks. Note that numerical scales represented by shading differ between the two periods. The dark line running offshore of the coast is the 200-m isobar, but the outer boundary is the limit of the study area.

Fig. 9. Xantus's Murrelet distribution in the Southern California Bight (birds per 0.5×0.5–degree cell) estimated from aerial surveys in 1975–1978 and 1999–2001. Estimates were output from generalized additive models (GAMs); shown as birds per grid block. See Fig. 8 for other format details.
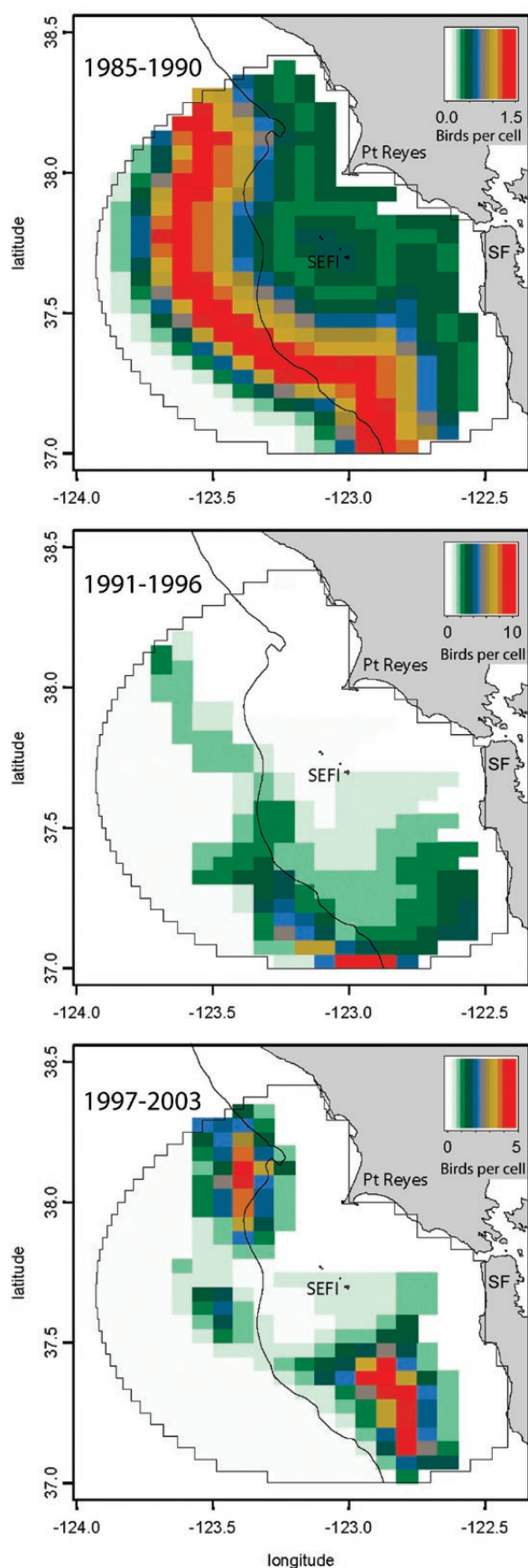
Fig. 10. Xantus's Murrelet distribution off central California (birds per 0.5 × 0.5–degree cell) estimated from ship surveys in three periods between 1985 and 2003. See Figs. 8 and 9 for format details.

95% CIs, no fewer than 128–331 murrelets were present in the area during any given year (Table 3).

DISCUSSION

Although previous at-sea studies provided much information on at-sea occurrence and distribution of Xantus's Murrelets (Hunt *et al.* 1979, Briggs *et al.* 1987, Whitworth *et al.* 2000, Mason *et al.* 2004), this is the first study to provide a detailed analysis of these subjects for the entire pelagic range, plus habitat affinities and, in particular, an analysis of at-sea survey data to estimate global population size.

Survey caveats
As noted in "Methods," two factors that we could not account for during surveys could have negatively biased our count data:

- Birds that dive ahead of the approaching ship or plane before they are within the survey strip
- Use of single observers during 59% of our surveys.

Regarding the latter factor, Spear *et al.* (2005) found that a single observer detects about 26% fewer birds than two observers on watch simultaneously. A 20% deficit also was recorded for single (as compared with paired) observers conducting line transect surveys of Marbled Murrelets *Brachyramphus marmoratus* (Evans Mach *et al.* 2002). The potential effect of the former factor has not been quantified. However, in surveys to estimate population size of another alcid, the Common Murre *Uria aalge* (which dive for up to 112 s [Piatt & Nettleship 1985], much longer than averages of 18–24 s for Xantus's Murrelet [Hamilton *et al.* 2005]), this problem was essentially eliminated through the use of two observers on watch together (Clarke *et al.* 2003). Working in pairs allows one person to frequently scan the water to 0.5 km ahead, recording birds that could potentially dive before being counted within the 300 m strip-width usually being surveyed (reviewed in Spear *et al.* 2005). Nevertheless, in the present study, multiple observer teams were used during only 41% of surveys. Based on our experience during at-sea surveys, we estimate that the effect of murrelets diving ahead of survey craft resulted in a 5%–10% reduction in number of birds detected. When adjustments for use of single observers are applied to 59% of survey data, we estimate that Xantus's Murrelets were undercounted by about 16%.

A third biasing factor unaccounted for in our analyses was the potential overcounting effect of including unknown numbers of *craveri* with *hypoleucus/scrippsi*. To our knowledge, the only information available on the proportion of *craveri* to *hypoleucus/scrippsi* off the Pacific coast is from pelagic surveys in Monterey Bay, California, indicating that *craveri* make up about 7% of the total number of the two species during the nonbreeding season (S. Terrill, pers. comm.). Although Monterey Bay is in the northern part of the *craveri* nonbreeding range, we have assumed that the 7% value represents a rough average for the entire study area and applies throughout the nonbreeding season. In the nonbreeding season, the number of *craveri* is very low to zero from northern California to central British Columbia, but possibly greater in the SCB and off central Baja California than in Monterey Bay. During the breeding season, *craveri* are rare off central California (LBS & DGA, pers. obs.), but regular off the west coast of Baja California. Therefore, we have assumed that *craveri* accounted for 7% of murrelets surveyed on the Pacific coast of North America during the nonbreeding

season and 5% during the breeding season. Considering negative and positive biases, we believe that our counts of Xantus's Murrelets were underestimated by about 10% during both seasons.

Distribution at sea

During the breeding season, Xantus's Murrelets occurred from northern Oregon to southern Baja California, although they were concentrated in the SCB (Fig. 8). During the nonbreeding season, they were more uniformly dispersed from southern British Columbia to southern Baja California, with the largest concentration off northern Baja California and Point Conception to Cape Mendocino. Moderate densities occurred off Oregon, and low densities occurred off western Washington and the west coast of Vancouver Island, British Columbia. Our northernmost at-sea observation was at 52.5°N (132.7°W, 10 August 2000), similar to latitudes in other northernmost records (Carter *et al.* 2000, 2005; K. Morgan, unpubl. data). During the breeding season, densities of Xantus's Murrelets were low south of Punta Eugenia, Baja California (*c.* 28°N), slightly north of southernmost breeding colonies at San Roque and Asunción Islands (Drost & Lewis 1995). However, in the nonbreeding season, at-sea observations increased south of Punta Eugenia. Although those observations indicated some dispersal to the south, occurrence of these murrelets off southern Baja California is infrequent. The most southern historical records (Howell & Webb 1995, Carter *et al.* 2005) are from Cabo San Lucas (23°N) and Magdalena Bay (24°N), and our most southern record was a pair 35 km off Alijos Rocks (240 km west of Magdalena Bay; 24°N).

Relatively high densities in the inner part of the SCB during the breeding season match known foraging areas from southern California colonies (Whitworth *et al.* 2000, Mason *et al.* 2004). However, relatively high densities of murrelets in offshore waters of the SCB and northern Baja California during the breeding season (Fig. 8) have not previously been documented, and murrelet distribution likely extends further offshore beyond surveyed areas. Oceanographic features and prey resources associated with this concentration need to be better studied. High offshore densities in the region may reflect

- extensive offshore foraging at distances of 150–500 km from Guadalupe Island or other Baja California colonies, given low densities near Baja California colonies;
- early northward dispersal movements of some birds from central Baja California colonies before flightless molt in June–August;
- offshore movements of murrelets from southern California and Baja California shortly after departure from colonies, especially during the at-sea chick-rearing period.

Murrelets attending SCB colonies do not forage more than 100–150 km from colonies (Whitworth *et al.* 2000, Mason *et al.* 2004). Localized high densities near Alijos Rocks (*c.* 25°116′N; Fig. 8) in the breeding season may reflect localized foraging conditions or undocumented breeding by a few pairs at these little-visited small offshore rocks.

In the nonbreeding season, the concentration of murrelets between Point Conception and Cape Mendocino has been recognized for some time (Briggs *et al.* 1987). Northward dispersal of murrelets after breeding likely reflects use of abundant prey resources on the continental shelf, although diet during this time of year and in this region has not been examined (Whitworth *et al.* 2000, Hamilton *et*

al. 2004). The large concentration of murrelets off northern Baja California in the nonbreeding season (Fig. 8) has not been noted previously. Oceanographic features and prey resources associated with this concentration need to be better studied. This concentration also may partly reflect variation in timing of movements of birds from Baja California colonies. Delayed northward movements for some murrelets may occur after breeding and after flightless molt, which occurs between June and August (Drost & Lewis 1995). Early southward movements to attend central Baja California colonies prior to breeding typically occurs before 15 March (Keitt 2005, Wolf *et al.* 2005). Thus, we suspect that this concentration may be less distinct in the middle of the nonbreeding season. The occurrence of substantial numbers of murrelets off Oregon, Washington and British Columbia in late summer and fall has previously been recognized, although poorly described in earlier studies (Wahl *et al.* 1993, Nehls 2003). This study clearly shows that the nonbreeding range of the Xantus's Murrelet regularly extends north from California to central British Columbia.

Habitat affinities and ENSO effect

Xantus's Murrelets were most abundant over the upper continental slope (see also Briggs *et al.* 1987). When dispersed away from breeding areas, murrelets were associated with warmer, lower-salinity waters characteristic of the main flow of the California Current. This pattern was consistent within any given year regardless of larger-scale oceanographic conditions. For example, murrelet densities off central California were highest during the ENSO years of 1992 and 1997–1998, but their tendency to disperse north was not significantly related to the ENSO anomaly index. This lack of a relationship is surprising because more birds might be expected to disperse north during warm-water ENSO years, when lower breeding effort and success leads to earlier dispersal from colony areas (Hunt & Butler 1980, Drost & Lewis 1995, Whitworth *et al.* 2000, Roth *et al.* 2005). However, effects of ENSO conditions in any one year often differ between different parts of the California Current, and murrelets seem able to find adequate prey in more southern waters (although not necessarily within foraging distance of colonies) during most years through wide-ranging generalist foraging behavior (Whitworth *et al.* 2000, Hamilton *et al.* 2004, Roth *et al.* 2005).

Most habitat variables were interrelated and significantly correlated with Julian date (Table 2). We found that murrelet densities in central California increased with date over much of the annual cycle (Fig. 5). Thus, seasonal movements of the population, as opposed to habitat selection *per se,* probably account in part for the strong relationships to oceanographic conditions depicted in Fig. 6. For instance, murrelet densities increased with increasing SST and thermocline strength, while Julian date was also positively correlated with those variables. Likewise, murrelet density decreased with thermocline depth and Julian date was negatively correlated with thermocline depth. In contrast, murrelet densities were higher in low-salinity waters, whereas salinity and Julian date were positively correlated. The latter outcome supports our conclusion that Xantus's Murrelets actively choose the lower salinity waters of the main California Current (as suggested earlier). Other indications of habitat selection in our study remain hypothetical and further testing is needed.

Population estimates

CVs for population size estimates indicated that GAMs performed well in modeling murrelet distributions at sea, particularly for the SCB

during the 1999–2001 period, and for the entire population during the nonbreeding season. Population size in the SCB during the 1975–1978 and 1999–2001 periods appeared to be relatively stable. Our best, uncorrected, estimate for 1975–1978 was 11 350 and was 12 600 for 1999–2001 (95% CI for both estimates: 7500–15 500). If corrected for a 10% negative bias, respective estimates become 12 500 and 13 900 (95% CI: 8250–17 000). Mason *et al.* (2004) similarly estimated 13 855 ± 3079 birds in May 1999–2001 for the SCB, but found that mean density in April–June 1975–1983 (0.08 ± 0.03 birds/km^2) was 125% lower than in May 1999–2001 (0.18 ± 0.04 birds/km^2). However, differences in transect locations and timing of surveys between studies may account partly for differences.

Although estimates of population size between 1975–1978 and 1999–2002 were similar, distribution in the SCB differed between the two periods. During 1975–1978, murrelets concentrated in two areas (adjacent to Santa Barbara Island and the Coronado Islands), but only the concentration near Santa Barbara Island persisted in 1999–2002 (Mason *et al.* 2004; the present study). Lower numbers associated with the Coronado Islands were balanced by higher numbers associated with Santa Barbara Island. Higher numbers near Santa Barbara Island do not reflect population increase at this colony, which has been declining over the past two decades (Carter *et al.* 1992, Sydeman *et al.* 1998, Whitworth *et al.* 2003b). It is not likely that birds from the Coronado Islands began foraging near Santa Barbara Island during the latter period, because the two islands are 180 km apart and beyond suitable foraging distance from the Coronado Islands (Whitworth *et al.* 2000). Lower numbers near the Coronado Islands also do not reflect population decline at that colony. Although cats had reduced numbers of murrelets at Coronado North Island by 1990 (RLP, pers. comm, in Drost & Lewis 1995), breeding murrelets at the other three Coronado Islands were not affected by cats, and murrelets have likely increased at Coronado North Island since cat eradication in the early 1990s (McChesney & Tershy 1998, Whitworth *et al.* 2003c, Keitt 2005). We suspect that differences in survey timing and variation in use of foraging areas likely led to different distributions between the two periods and may have masked the population decline noted at the relatively large Santa Barbara Island colony. Specifically, 1975–1978 surveys occurred, on average, a month earlier and over a considerably longer part of the breeding season than did 1999–2001 surveys (i.e. 15 April ± 27 days vs. 15 May ± 2 days). In addition, prey availability and distribution in the SBC, especially for the Northern Anchovy *Engraulis mordax,* also has changed (Jacobsen & Barnes 1994). Birds from Santa Barbara Island foraged further from the colony in 1995–1997 than in 1975–1977 (Hunt *et al.* 1979, Whitworth *et al.* 2000), and birds from the Coronado Islands now appear to forage mostly south of the US–Mexico border, in waters outside the SCB survey area (Fig. 8, Mason *et al.* 2004).

Although temporal trends in population size and distribution in the SCB may be confounded by several factors, we found no evidence for a trend among birds during breeding season surveys in central California (1985–2003; see also Hyrenbach & Veit [2003], who found no trend over an 11-year period embedded within our time series). If global breeding populations had declined to a great degree, we would have detected a decline in numbers in central California, assuming that patterns of nonbreeding distribution had not changed. Our results for the SCB and central California are important, not only from localized perspectives (see below), but also when assessing total population size. SCB estimates represent the average across 29 years (1975–2003) in one of two primary breeding areas,

the other being central Baja California (i.e. Guadalupe and San Benito Islands). In the SCB, population decline has been noted at Santa Barbara Island, increase is suspected at the Coronado Islands, and trends at other colonies are poorly known between 1975 and 2001 (Carter *et al.* 1992, unpubl. data; Sydeman *et al.* 1998; Whitworth *et al.* 2003a, 2003b, 2003c, 2005b; Keitt 2005).

Despite the decline at Santa Barbara Island, it is encouraging that the overall SCB population has not declined below 1975–1978 levels. Population increase is expected to occur at Anacapa Island over the next two decades, following rat eradication in 2002 (Whitworth *et al.* 2005a). However, impacts that lead to decline may occur at the Coronado Islands from the planned construction and operation of a liquid natural gas terminal within the next decade (Whitworth *et al.* 2003c, 2005b). Given the difficulty of censusing colonies and the varying conservation issues, the assessment of overall SCB population condition has been problematic, and declines at Santa Barbara Island have been incorrectly considered by some biologists and managers to reflect the entire SCB population. The present study has shown that the SCB Xantus's Murrelet population is relatively stable at present; however, a long-term monitoring program is needed to better assess trends and conditions at each breeding colony.

Our best, uncorrected, estimate for the number of Xantus's Murrelets at sea is 36 100 birds during the nonbreeding period, and 24 500 birds during the breeding period. When corrected for a 10% negative bias in count data, these estimates are 39 700 and 27 000 birds, respectively. Using the same adjustment, 95% CIs for minimum and maximum estimates of numbers of *scrippsi* and *hypoleucus* are about 30 900–48 100 birds and 18 300–39 100 birds during the respective periods. Our estimate for the nonbreeding period (39 700 birds) is about 25% higher than the maximum global population estimate (30 000) derived from colony-based surveys (Springer *et al.* 1993). This discrepancy is likely due to the difficulty of making population estimates based on colony counts of crevice-nesting birds.

Our estimates of the overall population size differed from estimates based on colony counts, but our estimate of the number of breeding birds is similar to that from the colony-based estimates of 10 000–20 000 breeding birds (Carter *et al.* 2000, Burkett *et al.* 2003, Keitt 2005). While the proportion of nonbreeding adults and subadults in at-sea populations of Xantus's Murrelets is not known, we assume 50%–60% for the nonbreeding period, as found in many other species of seabirds: Ancient Murrelet *Synthliboramphus antiquus,* Adélie Penguin *Pygoscelis adeliae,* Western Gull *Larus occidentalis* and Manx Shearwater *Puffinus puffinus* (Ainley 1978, Spear *et al.* 1987, Brooke 1990, Gaston 1992). Using a value of 45% for breeding adults during the nonbreeding period, we estimate a global breeding population of about 17 900 birds. Using ratios from 95% CIs calculated in the present study (Table 3), minimum and maximum estimates are 13 900 and 21 000 birds respectively.

Crevice-nesting seabirds are especially difficult to census at their colonies. The application of GAMs to at-sea survey data to provide accurate population estimates is a powerful way of monitoring such populations. Estimating population levels and trends over time is critical for the conservation of seabirds like Xantus's Murrelets that are highly restricted in range and are faced with threats to their breeding populations at colonies.

ACKNOWLEDGMENTS

REFERENCES

AINLEY, D.G. 1978. Activity and social behavior of non-breeding Adélie Penguins. *Condor* 80: 138–146.

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petran, B.N. & Csaaki, F. (Eds). International symposium on information theory. 2nd ed. Budapest: Akadeemiai Kiadi. pp. 267–281.

AUGUSTIN, N.H. 1999. Spatial and spatio-temporal models with applications in vegetation dynamics and wildlife population estimation [PhD thesis]. St. Andrews, UK: University of St. Andrews.

AUGUSTIN, N.H., BORCHERS, D.L., CLARKE, E.D. & BUCKLAND, S.T. 1998. Spatio-temporal modeling for the annual egg production method of stock assessment using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2608–2621.

BORCHERS, D.L., BUCKLAND, S.T., PRIEDE, I.G. & AHMADI, S. 1997. Improving the precision of the daily egg production method using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2727–2742.

BRIGGS, K.T., TYLER, W.B. & LEWIS, D.B. 1985. Comparison of ship and aerial surveys of birds at sea. *Journal of Wildlife Management* 49: 405–411.

BRIGGS, K.T., TYLER, W.B., LEWIS, D.B. & CARLSON, D.R. 1987. Bird communities at sea off California, 1975 to 1983. *Studies in Avian Biology* 11.

BROOKE, M. 1990. The Manx Shearwater. London: T & AD Poyser.

BUCKLAND, S.T., CATTANACH, K.L. & ANGANUZZI, A.A. 1992. Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific Ocean, using sighting data collected by commercial tuna vessels. *Fishery Bulletin* 90: 1–12.

BURKETT, E.E., ROJEK, N.A., HENRY, A.E., FLUHARTY, M.J., COMRACK, L., KELLY, P.R., MAHANEY, A.C. & FIEN, K.M. 2003. Status review of Xantus's Murrelet (*Synthliboramphus hypoleucus*) in California [unpublished report]. Status report 2003–01. Sacramento, CA: California Department of Fish and Game, Habitat Conservation Planning Branch. 70 pp. plus appendices.

CARTER, H.R., MCCHESNEY, G.J., JAQUES, D.L., STRONG, C.S., PARKER, M.W., TAKEKAWA, J.E., JORY, D.L. & WHITWORTH, D.L. 1992. Breeding populations of seabirds in California, 1989–1991 [unpublished report]. Dixon, CA: US Fish and Wildlife Service, Northern Prairie Wildlife Research Center. 491 pp.

CARTER, H.R., WHITWORTH, D.L., TAKEKAWA, J.Y., KEENEY, T.W. & KELLY, P.R. 2000. At-sea threats to Xantus' Murrelets (*Synthliboramphus hypoleucus*) in the Southern California Bight. In: Browne, D.R., Mitchell, K.L. & Chaney, H.W. (Eds). Proceedings of the Fifth California Islands Symposium; 29 March–1 April 1999; Santa Barbara, CA, USA. Camarillo, CA: US Minerals Management Service. pp. 435–447.

CARTER, H.R., SEALY, S.G., BURKETT, E.E. & PIATT, J.F. 2005. Biology and conservation of Xantus's Murrelet: discovery, taxonomy and distribution. *Marine Ornithology* 33: 81–87.

CLARKE, E.D., SPEAR, L.B., MCRACKEN, M.L., BORCHERS, D.L., MARQUES, F.F.C, BUCKLAND, S.T. & AINLEY D.G. 2003. Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. *Journal of Applied Ecology* 40: 278–292.

DAVISON, A.C. & HINKLEY, D.V. 1997. Bootstrap methods and their application. New York: Cambridge University Press.

DROST, C.A. & LEWIS, D.B. 1995. Xantus' Murrelet (*Synthliboramphus hypoleucus*). In: Poole, A. & Gill, F. (Eds). *The Birds of North America.* No. 164. Philadelphia & Washington, DC: Academy of Natural Sciences & American Ornithologists' Union. 23 pp.

EFRON, B. & TIBSHIRANI, R.J. 1993. An introduction to the bootstrap. London: Chapman and Hall.

EVANS MACH, D., RAPHAEL, M.G. & LAAKE, J.L. 2002. Probability of detecting Marbled Murrelets at sea: effects of single vs. paired observers. *Journal of Wildlife Management* 66: 865–873.

GASTON, A.J. 1992. The Ancient Murrelet: a natural history in the Queen Charlotte Islands. London: T. & D. Poyser.

HAMILTON, C.D., CARTER, H.R. & GOLIGHTLY, R.T. 2004. Diet of Xantus's Murrelets in the Southern California Bight. *Wilson Bulletin* 116: 152–157.

HAMILTON, C.D., GOLIGHTLY, R.T. & TAKEKAWA, J.Y. 2005. Characteristics of diving in radio-marked Xantus's Murrelets. *Marine Ornithology* 33: 155–159.

HASTIE, T. & TIBSHIRANI, R.J. 1990. Generalized additive models. London: Chapman and Hall.

HOWELL, S.N.G. & WEBB, S. 1995. A guide to the birds of Mexico and northern central America. Oxford: Oxford University Press.

HUNT, G.L. & BUTLER, J.L. 1980. Reproductive ecology of Western Gulls and Xantus' Murrelets with respect to food resources in the Southern California Bight. *California Cooperative Oceanic Fisheries Investigations Report* 21: 62–67.

HUNT, G.L. Jr, PITMAN, R.L., NAUGHTON, M., WINNETT, K., NEWMAN, A., KELLY, P.R. & BRIGGS, K.T. 1979. Distribution, status, reproductive biology and foraging habits of breeding seabirds. In: Summary of marine mammals and seabird

surveys of the Southern California Bight area, 1975–1978. Vol. 3. Investigator's reports, Part 3: Seabirds of the Southern California Bight, Book 2 [unpublished report]. Irvine, CA: University of California. 399 pp.

HUNT, G.L. Jr, PITMAN, R.L. & JONES, H.L. 1980. Distribution and abundance of seabirds breeding on the California Channel Islands. In: Powers, D.M. (Ed). California Islands: proceedings of a multidisciplinary symposium. Santa Barbara, CA: Santa Barbara Museum of Natural History. pp. 443–459.

HYRENBACH, K.D. & VEIT, R.R. 2003. Ocean warming and seabird communities of the Southern California Current system (1987–98): response at multiple temporal scales. *Deep-Sea Research II* 50: 2537–2565.

JACOBSEN, L.D., LO, N.C.H. & BARNES, J.T. 1994. A biomass-based assessment model for Northern Anchovy, *Engraulis mordax. Fisheries Bulletin* 92: 711–724.

JEHL, J.R. Jr & BOND, S.I. 1975. Morphological variation and species limits in murrelets of the genus *Endomychura. Transactions of the San Diego Museum of Natural History* 18: 9–23.

KEITT, B.S. 2005. Status of Xantus's Murrelet and its nesting habitat in Baja California, Mexico. *Marine Ornithology* 33: 105–114.

MASON, J.W., MCCHESNEY, G.J., MCIVER, W.R., CARTER, H.R., TAKEKAWA, J.Y., GOLIGHTLY, R.T., ACKERMAN, J.T., ORTHMEYER, D.L., PERRY, W.M., YEE, J.L., PIERSON, M.L. & MCCRARY, M.D. 2004. At-sea aerial surveys of seabirds in the Southern California Bight: 1999–2002. In: Takekawa, J.Y., Carter, H.R., Orthmeyer, D.L., Golightly, R.T., Ackerman, J.T., McChesney, G.J., Mason, J.W., Adams, J., McIver, W.R., Pierson, M.O. & Hamilton, C.D. At-sea distribution and abundance of seabirds and marine mammals in the Southern California Bight: 1999–2003 [unpublished report]. Vallejo, CA & Arcata, CA: US Geological Survey, Western Ecological Research Center & Humboldt State University, Department of Wildlife. pp. 11–109.

MCCHESNEY, G.J. & TERSHY, B.R. 1998. History and status of introduced mammals and impacts to breeding seabirds on the California Channel Islands and northwestern Baja California islands. *Waterbirds* 21: 335–347.

MCCULLAGH, P. & NELDER, J.A. 1989. Generalized linear models. London: Chapman and Hall.

MURRAY, K.G., WINNETT-MURRAY, K., EPPLY, Z.A., HUNT, G.L. Jr & SCHWARTZ, D.B. 1983. Breeding biology of the Xantus' Murrelet. *Condor* 85: 12–21.

NEHLS, H.B. 2003. Xantus's Murrelet. In: Marshall, D.B., Hunter, M.G. & Contreras, A.L. (Eds). Birds of Oregon: a general reference. Corvallis, OR: Oregon State University Press. p. 293.

PIATT, J.F. & NETTLESHIP, D.N. 1985. Diving depths of four alcids. *Auk* 102: 293–297.

ROTH, J.E., SYDEMAN, W.J. & MARTIN, P.L. 2005. Xantus's Murrelet breeding relative to prey abundance and oceanographic conditions in the Southern California Bight. *Marine Ornithology* 33: 115–121.

SOWLS, A.L., DEGANGE, A.R., NELSON, J.W. & LESTER, G.S. 1980. Catalog of California seabird colonies. FWS/OBS-80/37. Washington, DC: US Fish and Wildlife Service.

SPEAR, L.B., PENNIMAN, T.M., PENNIMAN, J.F., CARTER, H.R. & AINLEY, D.G. 1987. Survivorship and mortality factors in a population of Western Gulls. *Studies in Avian Biology* 10: 44–56.

SPEAR, L.B. & AINLEY, D.G. 1997. Flight speed of seabirds in relation to wind speed and direction. *Ibis* 139: 234–251.

SPEAR, L.B., AINLEY, D.G. & WEBB, S.W. 2003. Distribution, abundance, and behaviour of Buller's, Chatham Island, and Salvin's albatrosses off Chile and Peru. *Ibis* 145: 253–269.

SPEAR, L.B., NUR, N. & AINLEY, D.G. 1992. Estimating absolute densities of flying seabirds using analyses of relative movement. *Auk* 109: 385–389.

SPEAR, L.B., AINLEY, D.G., HARDESTY, B.D., HOWELL, S.N.G. & WEBB, S.W. 2005. Reducing biases affecting at-sea surveys of seabirds: use of multiple observer teams. *Marine Ornithology* 32: 147–157.

SPRINGER, A.M., KONDRATYEV, A.Y., OGI, H., SHIBAEV, Y.V. & VAN VLIET, G.B. 1993. Status, ecology, and conservation of *Synthliboramphus* murrelets and auklets. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds). Status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Canadian Wildlife Service Special Publication. pp. 187–203.

SYDEMAN, W.J., NUR, N. & MARTIN, P. 1998. Population viability analyses for endemic seabirds of the California marine ecosystem: the Ashy Storm-Petrel (*Oceanodroma homochroa*) and Xantus' Murrelet (*Synthliboramphus hypoleucus*) [unpublished report]. Stinson Beach, CA: Point Reyes Bird Observatory. 74 pp.

TASKER, M.L., HOPE-JONES, P., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101: 567–577.

VENABLES, W.N. & RIPLEY, B.D. 1997. Modern applied statistics with S-Plus. 2nd edition. New York: Springer.

VERNER, J. 1985. Assessment of counting techniques in current ornithology. New York: Plenum Press.

WAHL, T.R., MORGAN, K.H. & VERMEER, K. 1993. Seabird distribution off British Columbia and Washington. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds). The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Canadian Wildlife Service Special Publication. pp. 39–47.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R., NEWMAN, S.H., KEENEY, T.W. & KELLY, P.R. 2000. Distribution of Xantus' Murrelet *Synthliboramphus hypoleucus* at sea in the Southern California Bight, 1995–97. *Ibis* 142: 268–279.

WHITWORTH, D.L., CARTER, H.R., YOUNG, R.J., CREEL, E., MCIVER, W.R., GRESS, F. & FANGMAN, S. 2003a. Monitoring of at-sea congregations and nest success of Xantus's Murrelets (*Synthliboramphus hypoleucus*) at Anacapa Island, California, in 2000–2002, prior to the eradication of Black Rats (*Rattus rattus*) [unpublished report]. Arcata, CA: Humboldt State University, Department of Wildlife. 47 pp.

WHITWORTH, D.L., CARTER, H.R., YOUNG, R.J., CREEL, E., MCCHESNEY, G.J. & MARTIN, P. 2003b. Change in breeding population size of Xantus's Murrelets (*Synthliboramphus hypoleucus*) at northeastern Santa Barbara Island, California, 1991–2001 [unpublished report]. Arcata, CA & Davis, CA: Humboldt State University, Department of Wildlife, and California Institute of Environmental Studies.

WHITWORTH, D.L., CARTER, H.R., YOUNG, R.J., CREEL, E.M., MCIVER, W.R. & MASON, J.W. 2003c. Status and trends of the Xantus's Murrelet (*Synthliboramphus hypoleucus*) at Islas Los Coronados, Baja California, Mexico [unpublished report]. Arcata, CA: Humboldt State University, Department of Wildlife. 36 pp.

WHITWORTH, D.L., CARTER, H.R., KOEPKE, J.S., YOUNG, R.J., GRESS, F. & FANGMAN, S. 2005. Initial recovery of Xantus's Murrelets following rat eradication on Anacapa Island, California. *Marine Ornithology* 33: 131–137.

WHITWORTH, D.L., CARTER, H.R., KOEPKE, J.S., GRESS, F. & FANGMAN, S. 2005b. Population assessments and monitoring for Xantus's Murrelets at breeding colonies in the Southern California Bight in 2004 [unpublished report]. Davis, CA: California Institute for Environmental Studies. 47 pp.

WOLF, S., PHILLIPS, C., ZEPEDA-DOMINGUEZ, J.A., ALBORES-BARAJAS, Y. & MARTIN, P. 2005. Breeding biology of Xantus's Murrelet at the San Benito Islands, Baja California, México. *Marine Ornithology* 33: 123–129.