

Distribution of Xantus' Murrelet *Synthliboramphus hypoleucus* at sea in the Southern California Bight, 1995–97

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We radiomarked 153 Xantus' Murrelets *Synthliboramphus hypoleucus* captured at sea near Santa Barbara Island (SBI), the largest murrelet colony in the California Channel Islands, USA. We tracked these radiomarked murrelets in the Southern California Bight (SCB) off coastal southern California during the 1995–97 breeding seasons. In 1995 during mild El Niño conditions, the murrelets were distributed in non-upwelling areas. In 1996–97, they were distributed in dense patches, aggregating in cool upwelled waters near the northern Channel Islands or south of San Nicolas Island. Murrelets flew longer distances from SBI to foraging areas in 1997 ($\bar{x} = 111 \pm 44$ km) than in 1996 ($\bar{x} = 62 \pm 25$ km), but the distances they travelled did not differ between months (Apr and May) within years. Mean foraging distances from SBI were similar for 'incubating' murrelets (determined on the basis of repeated visits to SBI) and 'non-incubating' murrelets during the colony attendance period. We attributed the low return rate of radiomarked murrelets to SBI to the capture and marking of a large proportion of birds that were not actively incubating rather than to any adverse effects of radio attachment. We believe changes in murrelet foraging patterns between the 1970s and 1990s are associated with changes in prey resources in the SCB. Flexibility in the foraging strategies of these murrelets may be related to the highly variable marine environment at the southern end of the California Current Upwelling System.

The Xantus' Murrelet *Synthliboramphus hypoleucus* (hereafter murrelet) is one of the rarest seabirds in the world, having an estimated population of fewer than 10 000 breeding individuals (Drost & Lewis 1995). Murrelets may be considered for listing under the US Endangered Species Act in the near future because of their small world population size, narrow range, and population threats on nesting islands and at sea. Their

breeding range is restricted to islands and offshore rocks from central Baja California, Mexico to southern California, USA (AOU 1983). After the breeding season, they disperse offshore along the Pacific coast from southern Baja California, Mexico to southern British Columbia, Canada.

Murrelets are small alcids ($\bar{x} = 167$ g) and vulnerable to a variety of introduced and native predators at the colony (McChesney & Tersky 1998). Their colony visits are strictly nocturnal, and their nests are concealed in rock crevices, sea caves and under low shrubs on

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steep slopes and cliffs (Murray *et al.* 1983, Carter *et al.* 1992). They forage at sea during the eight-day interval between laying the two eggs that comprise a normal clutch and during the two- to four-day period between incubation shifts. Their incubation period averages 34 days but is variable (range 27–44 days; Murray *et al.* 1983). Chicks are precocial and leave the nest within three days of hatching, moving quickly away from the colony with their parents (Murray *et al.* 1983). Although murrelets are among the most pelagic of the Alcidae, there is little information concerning their ecology and distribution at sea.

Researchers first investigated the at-sea distribution of marine birds through shipboard observations or aerial surveys, but these techniques have provided little information about patterns in the movements of individual birds. Radiotelemetry is now a widely accepted tool for determining such individual movements of free-ranging birds, but it has been used in relatively few studies of alcids at sea (Wanless *et al.* 1990, Duncan & Gaston 1990, Kuletz *et al.* 1995). Logistic difficulties (capture of adequate sample sizes, transmitter retention problems, adverse reaction to handling and marking, and prohibitive expense) have limited the use of radiotelemetry in the past.

We developed capture and radiomarking techniques (Whitworth *et al.* 1997a; Newman *et al.* 1999) to study the distribution of murrelets at sea in the Southern California Bight (SCB; Fig. 1) during the 1995–97 breeding seasons. There is little information on their distribution at sea since aerial (Briggs *et al.* 1987) and shipboard surveys (Hunt *et al.* 1979) documented aggregations near Santa Barbara Island during the 1975–78 breeding seasons. Yet distribution information is critical for assessing population threats at sea (Carter *et al.* in press) and for studying the effects of the significant changes which have occurred in the marine environment of the SCB since the mid-1970s.

STUDY AREA AND METHODS

Capture area

Santa Barbara Island (SBI; 33°28'N, 119°02'W) is 65 km southwest of Los Angeles in the California Channel Islands (Fig. 1). SBI (2.6 km²) is within the Channel Islands National Park and Channel Islands National Marine Sanctuary and supports about 1500 pairs of murrelets, the largest breeding colony in California (Carter *et al.* 1992). We captured murrelets offshore from the east side of the island during April

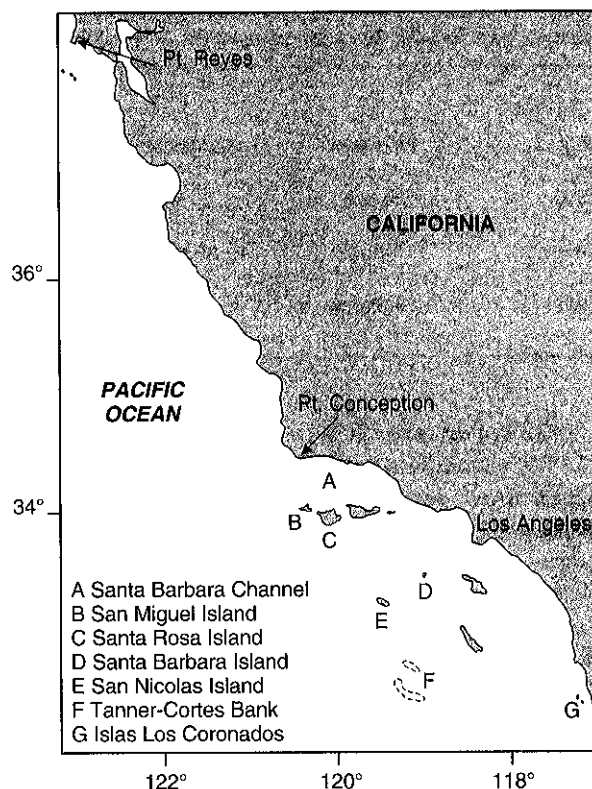


Figure 1. Central California coast and the Southern California Bight (area with islands) study areas.

and May 1995–97, preceding and following peak nest initiation at the colony (Table 1).

Aerial survey area

We conducted aerial telemetry surveys from Islas Los Coronados (32°25'N, 117°17'W), Baja California Norte, Mexico, north to Point Reyes (38°00'N, 123°00'W), Marin County, California (Fig. 1). The California Current Upwelling System is the dominant oceanographic feature of the region. The high productivity of this eastern boundary current results from transport of relatively cool, nutrient rich water from the north along with further nutrient inputs from seasonal upwelling. Periodic natural perturbations in current flow and upwelling intensity, such as those caused by El Niño events, cause decreased primary productivity (Chelton *et al.* 1982) and variable breeding success for many seabirds in the region (Ainley & Boekelheide 1990).

During the breeding season (including pre-breeding, incubation and early chick rearing at sea) our main survey area was south of Point Conception (34°27'N,

Table 1. Xantus' Murrelet breeding phenology at monitored sites on Santa Barbara Island, 1995–1997. Data from Channel Islands National Park Seabird Monitoring project (Pt. Reyes Bird Observatory unpubl. data).

Year	First nest	Peak initiation	Spread	Capture dates	Brood patches	
					Y	N
1995	10 May	25 May	≈30 days	26–28 April	1	34
				19–20 May	0	25
1996	9 April	19 April–9 May	≈40 days	15–18 April	0	116
				13–16 May	7	79
1997	15 March	19 April	≈70 days	10–11 April	0	47
				5–7 May	10	60

120°28'W) in the SCB and extended seaward to 121°W, encompassing about 80 000 km². The continental shelf south of Point Conception broadens considerably and is traversed by a series of basins and ridges, resulting in a relatively shallow region of complex hydrography and water circulation. The Santa Rosa-Cortes Ridge, a narrow and shallow ridge which extends south from Point Conception to the Tanner-Cortes Bank (Fig. 1) normally marks the boundary between cool California Current waters and warmer subtropical waters intruding from the south into the SCB (Owen 1980). This transition zone between water masses delimits the northern or southern breeding ranges for eight seabird species, including murrelets (Carter *et al.* 1992). During the periods of chick rearing at sea and colony dispersal (mid-May to June), we extended surveys to central California seaward as far as 140 km from the coast.

Capture and marking

Two- to four-day capture sessions were conducted in April and May each year (Table 1). We scheduled our April capture efforts prior to peak egg-laying to track incubating murrelets as they attended the colony and foraged at sea. Capture efforts were also scheduled about one month later in May to track late-incubating murrelets and follow family groups as they left the colony.

We captured murrelets in dip-nets with a night-lighting technique developed in 1995 (Whitworth *et al.* 1997a). During the breeding season, murrelets congregated at night on staging area waters adjacent to the nesting colony. Three-person capture crews searched the staging area waters with high-intensity spotlights in 4-m inflatable boats powered by 15 or 25 hp outboard motors. We transported murrelets in cardboard boxes to our research vessel anchored nearby.

All murrelets were fitted with US Fish and Wildlife Service stainless steel rings and weighed. We selected heavier murrelets (> 160 g) or murrelets with brood patches for radiomarking, but only a small proportion of our captured sample displayed brood patches (see Discussion). Two radio attachment techniques were used: (1) a suture and epoxy method employed in 1995 and April 1996; and (2) a subcutaneous anchor method used in 1996 and 1997 (Newman *et al.* 1999). An inhalation anesthetic, isoflurane, was used in 1996 and 1997. Transmitters (model PD-2, Holohil Systems Ltd, Woodlawn, Ontario) weighed approximately 3.5 g (< 2.5 % of murrelet body-weight) and were equipped with a 15-cm external whip antenna and front and rear suture channels. Transmitters had pulse rates of about 40 beats/min and an expected lifespan of 12 weeks in 1995, and six weeks in 1996 and 1997. Transmitter range depended on ambient conditions but was about 15 km from the air and up to 8 km from a receiving station on SBI.

Aerial telemetry surveys

We conducted aerial telemetry surveys in twin-engined aircraft equipped with paired 'H' antennae (1995) or four-element Yagi antennae (1996–97) mounted on wing struts or underwing mounting brackets. Observers wearing headphones scanned each frequency at 2 s intervals with R-4000 receivers (Advanced Telemetry Systems, Inc., Isanti, Minnesota) connected by coaxial cables and a left-right switch box to the antennae. We determined signal location by assessing the signal direction and relative distance from the aircraft.

We conducted 11 aerial surveys (45 h) between 1 May and 27 June 1995; 24 surveys (109 h) between 18 April and 24 June 1996; and 37 surveys (171 h) between 12 April and 12 June 1997. Surveys were conducted during daylight hours (07:00–18:00 h Pacific Standard Time). Aerial survey coverage

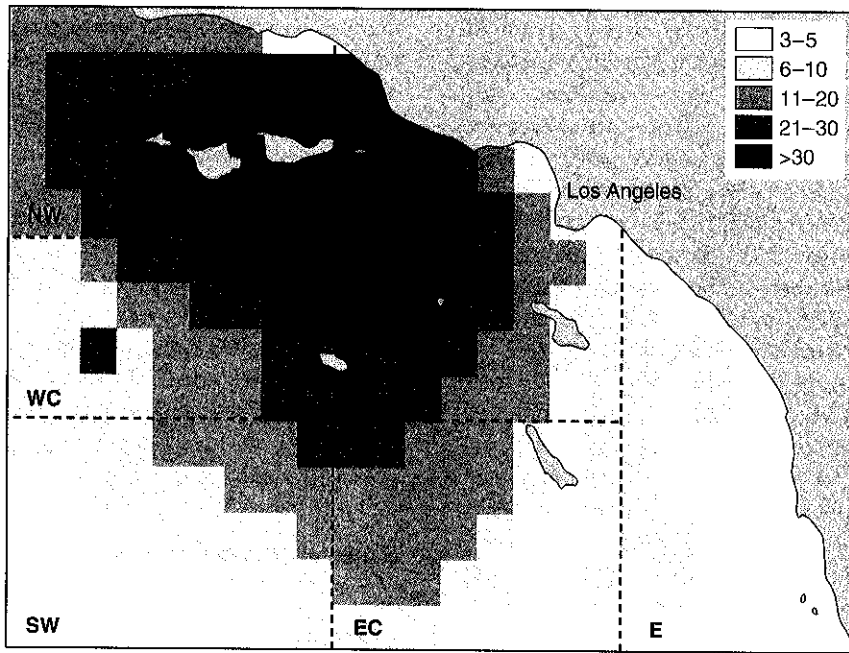


Figure 2. Aerial survey coverage by 10' (latitude × longitude) grid blocks in the Southern California Bight, 1995–97. Boundaries indicate sector groups for analyses of grid block densities.

encompassed the entire SCB, but coverage was not uniform (Fig. 2). Flights were often restricted by weather conditions and military operations. We usually adjusted flight paths to locate the maximum number of marked murrelets on the basis of previous survey results, but searches of less frequently surveyed areas were regularly conducted.

Island monitoring

We monitored radiomarked murrelets from a remote receiving station on North Peak (elevation 171 m), the highest point on the north end of SBI. The system consisted of an R-4000 receiver and D5041 data logger (Advanced Telemetry Systems, Inc., Isanti, Minnesota), four antennae (4-element Yagi), a four-way multiplexer and a 4-m sectional tower. Each transmitter frequency was monitored every 15–30 min. Monitoring duration depended on whether a signal was detected. Each antenna was monitored separately for 10 s if a signal was detected, but monitoring ceased after 3 s if no signal was present. The data logger recorded the frequency, date, time, antenna, number of pulses and signal strength. The system was powered by two 12-volt marine batteries connected in parallel. All electronic equipment was stored in a watertight container at the base of the antenna tower. We main-

tained the station and retrieved stored data (program GETDATA) every 2–4 weeks.

Data analyses

We assumed that individual murrelet aerial locations were independent of previous or subsequent locations because the time between locations was sufficient for a murrelet to cross its entire range (White & Garrott 1990). Location coordinates were plotted to determine distance and direction relative to SBI. Murrelet densities in the SCB (south of 34°30'N and east of 121°00'W) were estimated by grouping aerial locations within 10 min grid blocks (about 275 km²) which were then grouped into regions containing 40–45 blocks (Fig. 2). Average murrelet densities for each block were calculated as the number of aerial locations per survey. We tested for differences in mean murrelet densities among blocks grouped by regions and years (1996 and 1997) using two-way ANOVA tests. When ANOVA results were significant ($P < 0.05$), multiple comparisons were examined with Tukey's honestly significant difference (HSD) test (Zar 1996).

We limited our distance comparisons to locations at sea within the SCB where survey coverage was more consistent, and excluded 1995 data from comparisons because of small sample size. A two-factor ANOVA test

was used to examine month and year effects relative to distance from SBI. Several murrelets returned to SBI at least once; movements that were consistent with murrelet incubation patterns. These are hereafter referred to as 'incubating' murrelets, although we could not confirm the breeding status of any of the radiomarked birds. Murrelets which were not detected at the colony two or more days after release are referred to as 'non-incubating', but may have included pre-, non-, and failed breeding adults as well as subadults (see Discussion). We used a *t*-test to compare mean foraging distances from SBI between the incubating and non-incubating murrelets during the period incubating murrelets returned to the colony. Mann-Whitney *U* tests were used to compare the distances that murrelets were found from SBI (concurrent locations during individual surveys) for the April and May 1997 marked samples. We report means and standard deviations ($\bar{x} \pm \text{sd}$) for all estimates. ANOVA and *t*-tests were performed with Statistica for Windows (Statsoft Inc., Tulsa, Oklahoma). Test results were deemed significant when $P < 0.05$.

RESULTS

Marking and radiotracking

In total, 153 murrelets were captured at sea and radiomarked in April and May 1995 ($n = 38, 8$), 1996 ($n = 25, 23$) and 1997 ($n = 30, 29$). We located 134 of the 153 (88%) radiomarked murrelets; 85% in 1995, 79% in 1996 and 97% in 1997. Combining aerial surveys and island monitoring, we recorded 86 locations in 1995 ($\bar{x} = 1.9 \pm 1.7$ locations per murrelet), 185 in 1996 ($\bar{x} = 3.9 \pm 3.2$ locations per murrelet) and 460 in 1997 ($\bar{x} = 7.8 \pm 6.2$ locations per murrelet). In 1995, we detected a large proportion of murrelets near SBI by island monitoring but tracked most murrelets for only short periods and found only 14 murrelets (19 locations) during aerial surveys ($\bar{x} = 1.7$ locations per survey). We obtained 113 locations for 48 murrelets ($\bar{x} = 4.7$ locations per survey) during expanded aerial surveys in 1996, and 365 locations (including 40 outside the SCB and three on SBI) for 55 murrelets ($\bar{x} = 9.9$ locations per survey) in 1997.

Unfortunately, the limitations of the island monitoring station complicated our assessment of whether murrelets returned to SBI. Signals may have been obscured in some areas (e.g. birds in deep crevices) and we could only scan for each radio every 15–30 min. Radio interference probably obscured many valid signals and may have generated false signals. Although

many island detections were recorded, we were very conservative and discarded over 75% of the monitoring station detections. Our analysis resulted in 67 island locations in 1995, 72 in 1996, and 95 in 1997.

We were unable to determine exact transmitter retention times, but mean tracking duration increased from 6.5 ± 10.2 days per murrelet in 1995 using the suture and glue attachment, to 11.4 ± 10.4 days in 1996, when both attachment techniques were used, and 18.2 ± 15.4 days in 1997 when only the subcutaneous anchor attachment was used (Newman *et al.* 1999). We located 85 (56%) murrelets for one week or more after release. Maximum tracking duration was 51 days for the subcutaneous anchor and 41 days for the suture and epoxy attachment.

Murrelet distribution in the SCB

Distribution by year and marking period

Radiomarked murrelets were not distributed uniformly in the SCB (Fig. 3) and were patchily distributed during individual surveys (e.g. Fig. 4). Murrelets marked in 1995 provided little evidence of aggregation but were not regularly located because of limited survey coverage and less effective tracking antennae. Murrelets marked in April 1996 were patchily distributed north of SBI from the mainland west to Santa Rosa Island, with a few scattered in the Santa Barbara Channel. In contrast, murrelets marked in May 1996 were densely concentrated south of San Nicolas Island, with sparser locations along the Santa Rosa-Cortes Ridge south to the Cortes Bank. The murrelets marked in April and May 1997 were found along the northern Channel Islands, with densest concentrations south of San Miguel and Santa Rosa Islands and infrequent locations south to the Cortes Bank. Except for one individual found near Los Angeles in 1995, murrelets were not located in the eastern or southwestern SCB.

Relative density in the SCB

Densities of murrelets in 10-min blocks during individual surveys ranged from 0–8 murrelets. As many as 32 locations were recorded in individual blocks, with a mean block density of 0.06 ± 0.11 locations per survey (range = 0–0.91 locations; Fig. 5). We found significant year effects ($F_{1,526} = 9.15, P < 0.003$), region effects ($F_{5,526} = 15.78, P < 0.0001$) and year–region interactions ($F_{5,526} = 10.05, P < 0.0001$) on mean block densities (Table 2). Multiple comparisons (Tukey HSD) for region–year interactions indicated densities were

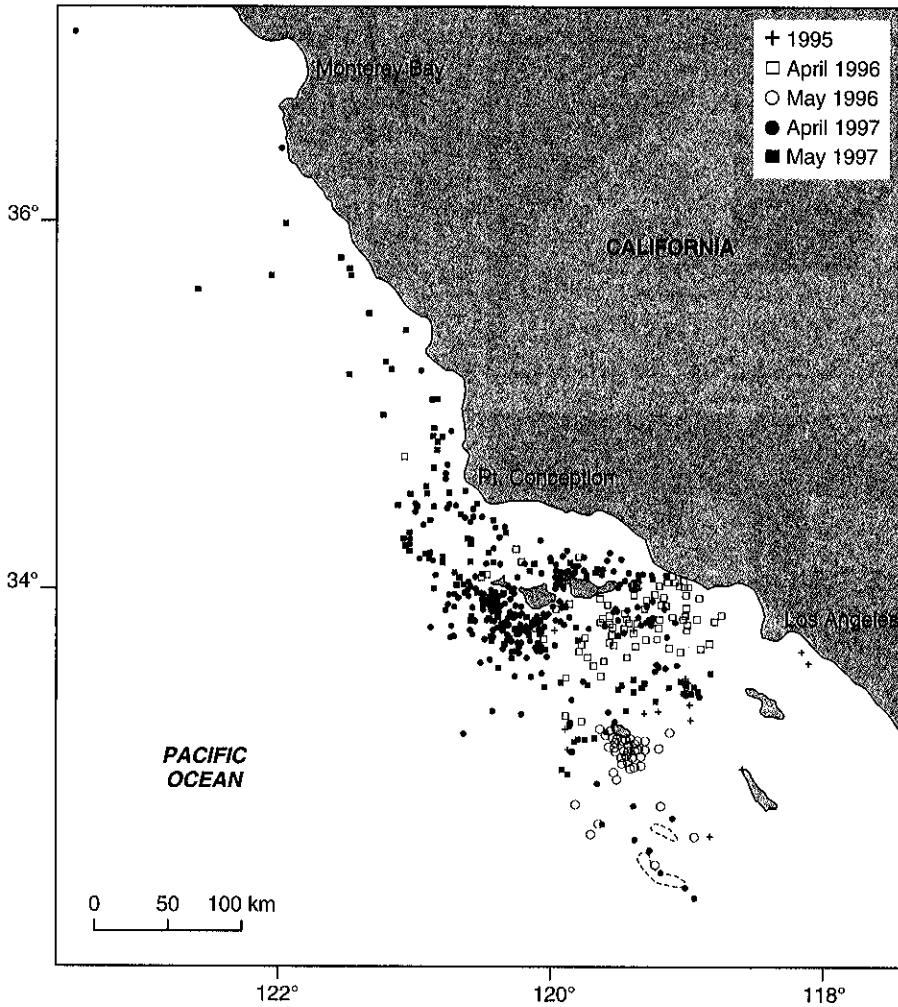


Figure 3. Locations of radiomarked murrelets in the Southern California Bight and along the central California coast, 1995–97, from aerial surveys. Locations are grouped by marking period.

higher (all $P < 0.0001$) in the northwest region in 1997 than in any other area in either year, while no other multiple comparisons among region and year differed significantly.

Distance from SBI

The overall mean distance of radiomarked murrelets from SBI was 110 ± 67 km ($n = 505$; range 2–567 km). Comparison of distance data among all years was not

Table 2. Mean (\pm sd) Murrelet density (number of locations per 10' block per survey) and total number of locations for grid blocks grouped by geographic sector and year in the SCB. All aerial locations at-sea in the SCB in 1996 and 1997.

Sector	1996		1997		Overall sector mean	
Northwest	0.037 ± 0.087	22	0.214 ± 0.243	220	^a 0.126 ± 0.202	242
West central	0.066 ± 0.193	36	0.080 ± 0.108	39	^b 0.073 ± 0.155	75
North central	0.055 ± 0.102	46	0.044 ± 0.096	53	^{bc} 0.050 ± 0.099	99
South central	0.014 ± 0.049	3	0.024 ± 0.054	7	^{cd} 0.019 ± 0.052	10
Southwest	0.026 ± 0.087	6	0.009 ± 0.037	3	^{cd} 0.017 ± 0.067	9
East	0.000	0	0.000	0	^d 0.000	0
Year mean	0.033 ± 0.103	113	0.062 ± 0.138	322		435

^{a–d}Different superscripts designate significantly different overall sector means (Tukey HSD test, $P < 0.05$).

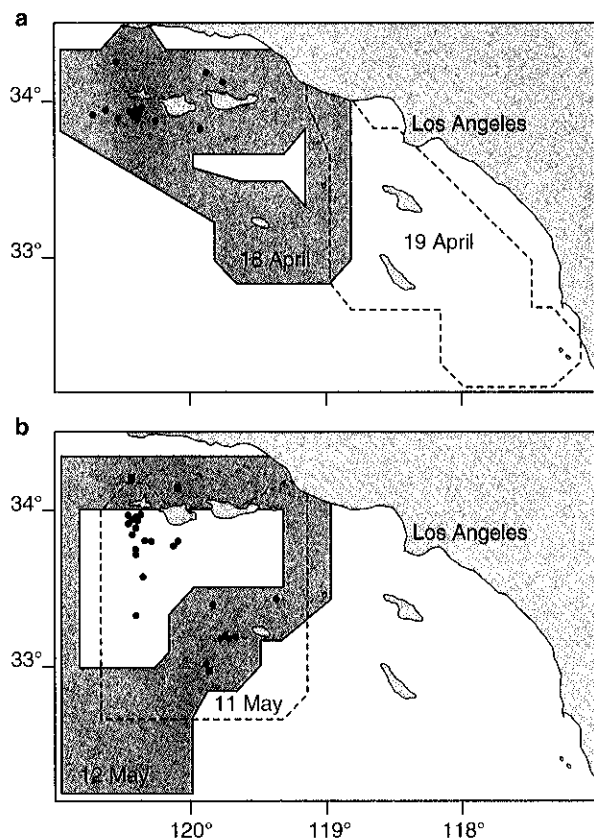


Figure 4. Murrelets detected during consecutive aerial surveys in the Southern California Bight performed on (a) 18–19 April and (b) 11–12 May 1997. Dotted outline indicates single survey coverage area while shading indicates areas covered during both surveys. Locations on 18 April (●), 11 May (●), and 12 May (■) are identified by symbols.

possible because of poor survey coverage in 1995. Survey coverage was more extensive and consistent within the SCB in 1996 and 1997, and we compared distance data in these years. We found highly significant year effects ($F_{1,431} = 113.90$, $P < 0.0001$), but no month effects ($F_{1,431} = 1.27$, ns) or month-year interactions ($F_{1,431} = 0.01$, ns). Murrelet locations in the SCB were almost twice as far from SBI in 1997 ($\bar{x} = 111 \pm 44$ km, $n = 322$) as in 1996 ($\bar{x} = 62 \pm 25$ km, $n = 113$). Long-distance movements were common, and distances between consecutive locations exceeding 75 km were recorded for most (83%) of the murrelets in 1997. Concurrent locations from the April and May 1997 groups were at similar distances (Mann-Whitney U tests; all $P = ns$) from SBI during individual surveys (April: $\bar{x} = 131 \pm 49$ km, $n = 39$; May: $\bar{x} = 117 \pm 56$ km, $n = 102$).

Our efforts to track actively incubating murrelets were hampered by variable nesting phenology among

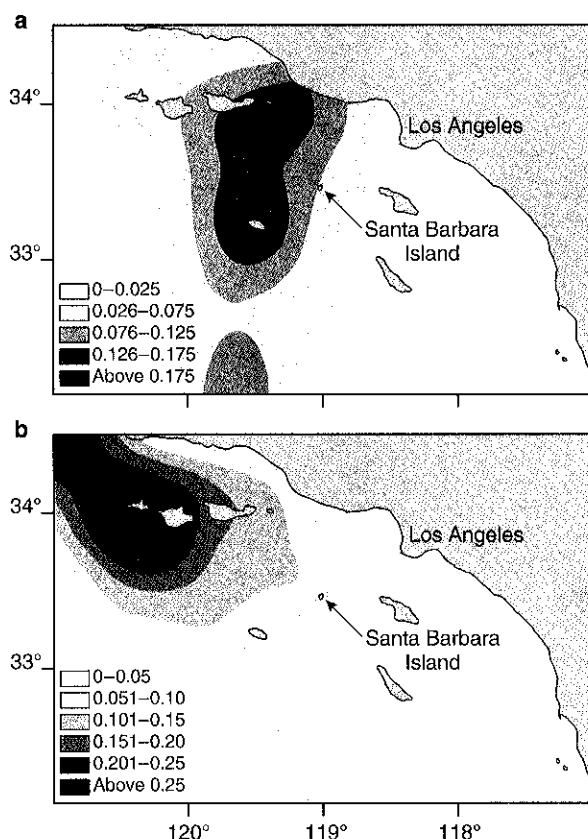


Figure 5. Relative murrelet densities (detections per survey) in the Southern California Bight, 1996 (a) and 1997 (b). Contour intervals are scaled to maximum values for each year.

years, chronic poor nesting success at SBI and possible breeding status biases in the sample captured at sea (see Discussion). At least 17 incubating murrelets, none of which had brood patches when captured, returned to SBI after being located at sea during aerial surveys: two in 1995, nine in 1996 and six in 1997. We found that, while attending the colony in 1996, mean foraging distance for incubating murrelets ($\bar{x} = 51 \pm 13$ km; $n = 9$) was similar ($t_{37} = 1.68$, ns) to non-incubating murrelets ($\bar{x} = 62 \pm 18$ km; $n = 30$). Location distances were much further from SBI in 1997, but again were similar ($t_{51} = 0.91$, ns) between the non-incubating ($\bar{x} = 101 \pm 28$ km; $n = 47$) and incubating ($\bar{x} = 90 \pm 22$ km; $n = 6$) murrelets while they attended the colony.

DISCUSSION

This is one of the first studies to use radiotelemetry to document the distribution at sea and follow the movements of individual alcids. Our results revealed that murrelets were patchily distributed, were highly vari-

Table 3. Number of Murrelet locations at-sea during aerial surveys (excluding locations on SBI) by distance class from SBI. Percentages by distance class are included in parentheses. Total locations by year are reported and include locations north of Point Conception (34°30'N).

Distance (km)	Year			Total
	1995	1996	1997	
0–25	5 (26.3)	2 (1.8)	15 (4.1)	22 (4.5)
26–50	2 (10.5)	31 (27.2)	18 (5.0)	51 (10.3)
51–75	2 (10.5)	63 (55.3)	35 (9.7)	100 (20.2)
76–100	7 (36.8)	6 (5.3)	47 (13.0)	60 (12.1)
101–125	3 (15.8)	6 (5.3)	81 (22.4)	90 (18.2)
126–150	0	4 (3.5)	68 (18.8)	72 (14.6)
151–175	0	1 (0.9)	37 (10.2)	38 (7.7)
176–200	0	0	20 (5.5)	20 (4.0)
> 200	0	0	41 (11.3)	41 (8.3)
Total locations	19	113	362	494

able in their overall distribution both within and between years, and were foraging at much greater distances from the colony during the breeding season than had previously been reported (Hunt *et al.* 1979). While transects used during shipboard surveys (Hunt *et al.* 1979) were limited in range, and may have underestimated the actual distances travelled compared with telemetry (Ostrand *et al.* 1998), extensive aerial surveys (Briggs *et al.* 1987) confirmed that murrelets foraged in the immediate vicinity of SBI (< 25 km) in the mid-1970s. Our telemetry locations were typically 30–90 km from the island in 1996 and 70–160 km away in 1997 and we recorded only 22 locations within 25 km of SBI (Table 3), an area of intense survey effort (Fig. 2). In fact, we had to expand our coverage area because radiomarked murrelets were found further from SBI than we had anticipated. Although our survey coverage may have biased our assessment of murrelet distributions, murrelet densities were consistently higher in the northwestern SCB (Fig. 5) and flights on consecutive days showed that when most murrelets were around the northern Channel Islands or near San Nicolas Island, few or no birds were found near SBI or in other regions of the SCB (Fig. 4).

Effects of capture and radiomarking

Assessing the effects of capture and radiomarking on murrelets was difficult because little was known about 'normal' murrelet movements, and murrelets captured at sea were of unknown age and breeding status. Although few murrelets had brood patches when captured, adults with brood patches might already have failed or hatched young. Murrelets without brood

patches may have been subadults, or adults captured during courtship or egg formation when brood patches would not be evident.

Some disturbance to normal behaviour is often noted from capture and marking during telemetry studies (Fuller 1987, Wanless *et al.* 1988). However, we found little evidence of long-term physical or behavioural effects on radiomarked murrelets. On the contrary, most evidence suggests murrelets responded relatively well to the attachment procedure and transmitter. Marked murrelets demonstrated flight capability and vigour at release, showed no evidence of mortality, injury or predation (Newman *et al.* 1999), had low recapture rates similar to the unmarked captured sample (Whitworth *et al.* 1997b) and were capable of travelling long distances (up to 570 km from SBI, and over 100 km in less than 4 h). Thirty-eight murrelets were detected at SBI for up to three nights after release and maintained the typical pattern of nocturnal colony attendance. At least 17 other murrelets returned to SBI after they were located far from the island and probably laid eggs after radiomarking. A nesting murrelet marked in 1996 was observed incubating in 1997 with the transmitter still attached (Newman *et al.* 1999).

The only evidence of adverse marking effects was our inability to locate 12% ($n = 153$) of the murrelets, only 41% of the birds later detected at sea ($n = 134$) returned to SBI, and only 31% of birds returning to SBI ($n = 55$) exhibited attendance patterns consistent with incubating. Our difficulties in relocating murrelets at sea or at the island could have resulted from post-release mortality, failure of the transmitter or attachment, poor performance of the island monitoring station, or long-distance dispersal by non-incubating

murrelets. There is no evidence that murrelets were debilitated by marking or were more vulnerable to predation. However, we found a high rate of transmitter failure in a study on Cassin's Auklets *Ptychoramphus aleuticus* recaptured at nests, which used identical marking techniques (J. Takekawa unpubl. data). Transmitter failures, or to a lesser extent attachment failures, may have accounted for a significant proportion of the murrelets not located or located for brief periods. In addition, the island monitoring data were compromised by radio interference for many murrelets. Our conservative analysis of these data probably underestimated the number of murrelets that returned to the colony.

Some murrelets may have dispersed from the study area shortly after marking. We recaptured a few radiomarked murrelets in subsequent years that were not located or located for only brief periods after release. Other murrelets were detected after absences of several weeks. Infrequent colony attendance and early dispersal after initial colony visitation is consistent with the high rate of early nest failure reported at this colony, primarily due to egg predation by Deer Mice *Peromyscus maniculatus* (Murray *et al.* 1983, Martin & Sydeman 1998). However, it is possible that their movements were adversely influenced by the radiomarking.

Sample captured at sea

Although the sample captured at sea may be biased by age and breeding status, we found no sex biases (Whitworth *et al.* 1997a). Only 5% of murrelets captured during radiomarking trips had laid eggs prior to capture, as indicated by presence of brood patches. While we expected a larger proportion of incubating murrelets in our sample captured at sea, deferred sexual maturity, failure to breed in years of poor prey availability (Harris & Wanless 1995) and low reproductive success may have resulted in varying numbers of subadults and non-breeding or failed breeding adults in this murrelet population.

In 1995, we marked all murrelets well before peak egg-laying, which was delayed until late May (Table 1) and reduced because of mild El Niño conditions (Martin & Sydeman 1998). These conditions corresponded with poor tracking success. In April 1996 and 1997, capture efforts occurred just before peak nest initiation, but we still captured no murrelets with brood patches (which are thought to develop between laying of the first and second egg; Murray *et al.* 1983). In May 1996 and 1997, less than 20% of the captured

sample had brood patches during the late incubation and the chick departure period when we observed young on the water. Elevated sea surface temperatures occurred in advance of the severe 1997–98 El Niño, but these conditions did not greatly affect murrelet breeding in 1997 (Point Reyes Bird Observatory unpubl. data).

Nocturnal nest and staging area attendance patterns by incubating or non-incubating murrelets have not been well studied, but Murray *et al.* (1983) noted that incubating murrelets flew ashore shortly after dusk and that more murrelets vocalized on the staging areas during chick departure than during incubation. Gaston (1992) suggested that incubating Ancient Murrelets *Synthliboramphus antiquus* may fly directly from foraging areas to the nest and that most murrelets on the water near the colony were not breeding during the incubation period. Thus, actively incubating murrelets may have attended staging areas briefly or not at all prior to chick departure. Most murrelets at sea near the colony may have been subadults and non-incubating adults, especially later in the night during our capture efforts which extended from 21:00–04:00 h (Whitworth *et al.* 1997a).

If most of the murrelets we marked were subadults and non-incubating adults, we may have decreased our chances of detecting marked birds in the SCB. During the spring and summer, murrelets have been documented in upwelling regions along central and northern California (Karnovsky *et al.* 1996). As there are no known colonies north of the SCB, these murrelets were probably subadults or non-incubating adults that either did not attend or departed early from breeding colonies.

Marking non-incubating murrelets also could have affected our evaluation of foraging areas and ranges, because non-incubating murrelets might forage farther from the colony than incubating murrelets. However, incubating and non-incubating murrelets foraged at similar distances from SBI in both 1996 and 1997. Capture biases are a more likely explanation for the lack of colony attendance by some marked birds, but do not explain the apparent changes in foraging distribution and ranges since the mid-1970s.

Long-distance foraging flights

Long-distance foraging was common for incubating murrelets in the SCB. This contrasted with earlier murrelet studies (Hunt *et al.* 1979, Briggs *et al.* 1987) and with some other alcid telemetry studies. Radiomarked Marbled Murrelets *Brachyramphus mar-*

moratus in central California and southcentral Alaska generally foraged within 30 km of nest sites (Kuletz *et al.* 1995, E. Burkett unpubl. data), while radiomarked Common Guillemots *Uria aalge*, Razorbills *Alca torda* and an Atlantic Puffin *Fratercula arctica* foraged within 10 km of the colony at the Isle of May, Scotland (Wanless *et al.* 1990). However, a few telemetry studies have shown that long-distance foraging by alcids is not extraordinary. Radiomarked Marbled Murrelets in southeast Alaska made daily flights to foraging areas up to 124 km (\bar{x} = 78 km) from prospective nesting areas (Whitworth *et al.* in press). Breeding Brünnich's Guillemots *Uria lomvia* travelled 10–168 km from their Icelandic colony to foraging areas at sea (Benvenuti *et al.* 1998).

Alcids have high wing-loading coefficients (Pennycuik 1987) which may preclude long-range foraging flights, except when: 1) productive and predictable feeding areas are available which enhance foraging efficiency; and 2) morphological or behavioural adaptations reduce the energetic costs or frequency of long-distance flights (Spring 1971). While morphological adaptations related to long-distance foraging have not been studied in murrelets, they have adopted a breeding strategy with long incubation shifts and precocial chick development (Murray *et al.* 1983) which effectively reduces the frequency of their long-distance foraging flights during incubation and shortens the period of colony attendance.

Variation in prey resources and the marine environment in the SCB

Given the few radiomarked murrelets located near SBI in this study compared with the many murrelets Hunt *et al.* (1979) surveyed in the mid-1970s, we suspect that murrelet foraging patterns have greatly changed over the last two decades. Significant changes in zooplankton and small pelagic fish populations have occurred in the California Current since the mid-1970s (MacCall and Prager 1988, Roemmich & McGowan 1995, McGowan *et al.* 1996). We were unable to relate changes in murrelet distribution at sea directly to prey resources because of the scarcity of information on their diets. However, our results provide strong circumstantial evidence that murrelet foraging patterns were related to patchily distributed prey resources located far from SBI which may explain why distribution shifts in their foraging have occurred.

Murrelet concentrations during April in 1996 and 1997 occurred around the northern Channel Islands

and along the Santa Rosa-Cortes Ridge where the coldest upwelled waters were found within the SCB (Schwing *et al.* 1997). Upwelling zones are known to concentrate seabird prey and promote aggregations (Hunt & Schneider 1987). Larval Northern Anchovies *Engraulis mordax* were the principal prey found in a small sample of murrelets collected in the mid-1970s (Hunt *et al.* 1979), but little or no anchovy spawning occurs in cold upwelled waters (Fiedler 1983) where larval anchovy survival is typically reduced (Lasker 1981). Other potential prey items in the murrelet diet such as larval rockfish *Sebastes* spp. (Hunt *et al.* 1979) are associated with upwelling-based waters. Small pelagic fish species in the California Current are more or less cyclically abundant over periods of several decades (MacCall 1996). Anchovy abundance has declined by as much as 75% since peaking in the mid-1970s (Jacobson *et al.* 1994, L. Jacobson pers. comm.) while Pacific Sardines *Sardinops sagax*, which were virtually non-existent two decades ago, have become one of the most abundant small pelagic fish species in the SCB (Barnes *et al.* 1992, Deriso *et al.* 1996).

Murrelet prey abundance and distribution in the SCB is highly variable (MacCall 1996). We found that murrelets have the flexibility to forage at great distances from their largest California breeding colony at Santa Barbara Island, and that they probably changed their foraging pattern since the 1970s in response to changing prey availability. Thus, flexibility to forage over long distances may be an important adaptation, allowing this small alcid to survive at a major oceanographic boundary between upwelling-based and subtropical waters.

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REFERENCES

- Ainley, D.G. & Boekeheide, R.J.** 1990. *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community*. Stanford, CA: Stanford University Press.
- AOU (American Ornithologists' Union)** 1983. *Check-list of North American Birds*, 6th edn. Washington, DC: American Ornithologists' Union.
- Barnes, J.T., Jacobson, L.D., MacCall, A.D. & Wolf, P.** 1992. Recent population trends and abundance estimates for the Pacific Sardine (*Sardinops sagax*). *Calif. Coop. Oceanic Fish. Invest. Rep.* **33**: 60–75.
- Benvenuti, S., Bonadonna, F., Dall'Antonia, L. & Gudmundsson, G.A.** 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* **115**: 57–66.
- Briggs, K.T., Tyler, W.B., Lewis, D.B. & Carlson, D.R.** 1987. Bird communities at sea off California: 1975 to 1983. *Avian Biol.* **11**: 1–74.
- 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*, Vol. 1, *Population Estimates*. Unpublished report. Dixon, CA: US Fish and Wildlife Service, Northern Prairie Wildlife Research Center.
- Carter, H.R., Whitworth, D.L., Takekawa, J.Y., Keeney, T.W. & Kelly, P.R.** in press. At-sea threats to Xantus' Murrelets (*Synthliboramphus hypoleucus*) in the Southern California Bight. In Brown, D., Chaney, H. & Mitchell, K. (eds) *Fifth Channel Islands Symposium*. Camarillo, CA: Minerals Management Service.
- Chelton, D.B., Bernal, P.A. & McGowan, J.A.** 1982. Large scale interannual physical and biological interaction in the California Current. *J. Mar. Res.* **40**: 1095–1125.
- Deriso, R.D., Barnes, J.T., Jacobson, L.D. & Arenas, P.R.** 1996. Catch-at-age analysis for Pacific Sardine (*Sardinops sagax*), 1983–1995. *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**: 175–187.
- 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, PA: 24. The Academy of Natural Sciences. Washington, DC: American Ornithologists' Union.
- Duncan, D.C. & Gaston, A.J.** 1990. Movements of Ancient Murrelet broods away from a colony. *Avian Biol.* **14**: 109–113.
- Fiedler, P.C.** 1983. Satellite remote sensing of the habitat of spawning anchovy in the Southern California Bight. *Calif. Coop. Oceanic Fish. Invest. Rep.* **24**: 202–209.
- Fuller, M.R.** 1987. Applications and considerations for wildlife telemetry. *J. Raptor Res.* **21**: 126–128.
- Gaston, A.J.** 1992. *The Ancient Murrelet, a Natural History in the Queen Charlotte Islands*. London: T. & A.D. Poyser Ltd.
- Harris, M.P. & Wanless, S.** 1995. Survival and non-breeding of adult Common Guillemots *Uria aalge*. *Ibis* **137**: 192–197.
- Hunt, G.L. Jr, Pitman, R.L., Naughton, M., Winnett, K., Newman, A., Kelly, P.R. & Briggs, K.T.** 1979. Reproductive ecology and foraging habits of breeding seabirds. In *Summary of Marine Mammal and Seabird Surveys of the Southern California Bight Area 1975–1978*, Vol. 3, *Investigator's Reports*, Part 3, *Seabirds*, Book II, *Final Report*: 399. Washington, DC: Bureau of Land Management, US Department of the Interior.
- Hunt, G.L. Jr & Schneider, D.C.** 1987. Scale-dependent processes in the physical and biological environment of marine birds. In Croxall, J.P. (ed.) *Seabirds: Feeding Ecology and Role in Marine Ecosystems*: 7–41. Cambridge, UK: Cambridge University Press.
- Jacobson, L.D., Lo, N.C.H. & Barnes, J.T.** 1994. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. *Fish. Bull.* **92**: 711–724.
- Karnovsky N.J., Ainley, D.G., Nur, N. & Spear, L.B.** 1996. Distribution, abundance and behavior of Xantus' Murrelets off northern California and southern Oregon. *Pacific Seabirds* **23**: 38.
- Kuletz, K.J., Marks, D.K., Flint, D., Burns, R. & Prestash, L.** 1995. Marbled Murrelet foraging patterns and a pilot productivity index for murrelets in Prince William Sound, Alaska. *Exxon Valdez Oil Spill Restoration Project Final Report*, Project 94102. Anchorage, AK: US Fish and Wildlife Service.
- Lasker, R.** 1981. Factors contributing to variable recruitment of the Northern Anchovy (*Engraulis mordax*) in the California Current: Contrasting years 1975 through 1978. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* **178**: 375–388.
- MacCall, A.D.** 1996. Patterns of low frequency variability in fish populations of the California Current. *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**: 100–110.
- MacCall, A.D. & Prager, M.H.** 1988. Historical changes in abundance of six fish species off southern California, based on CALCOFI egg and larva samples. *Calif. Coop. Oceanic Fish. Invest. Rep.* **29**: 91–101.
- Martin, P.L. & Sydeman, W.D.** 1998. *Seabird Monitoring Channel Islands National Park 1993–1996*. National Park Service Technical Report 98–03. Ventura, CA: Channel Islands National Park.
- 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.
- McGowan, J.A., Chelton, D.B. & Conversi, A.** 1996. Plankton patterns, climate, and change in the California Current. *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**: 45–68.
- Murray, K.G., Winnett-Murray, K., Eppley, Z.A., Hunt, G.L., Jr. & Schwartz, D.B.** 1983. Breeding biology of the Xantus' Murrelet. *Condor* **85**: 12–21.
- Newman, S.H., Takekawa, J.Y., Whitworth, D.L. & Burkett, E.E.** 1999. Subcutaneous anchor attachment increases retention of radio transmitters on seabirds: Xantus' and Marbled Murrelets. *J. Field Ornithol.* **70**: 520–534.
- Ostrand, W.D., Drew, G.S., Suryan, R.M., & McDonald, L.L.** 1998. Evaluation of radio-tracking and strip transect methods for determining foraging ranges of Black-legged Kittiwakes. *Condor* **100**: 709–718.
- Owen, R.W.** 1980. Eddies of the California Current System: physical and ecological characteristics. In Power, D. (ed.) *The California*

- Islands: Proceedings of a Multidisciplinary Symposium*: 237–263. Santa Barbara, CA: Santa Barbara Museum of Natural History.
- Pennycuik, C.J.** 1987. Flights of seabirds. In J. P. Croxall (ed.) *Seabirds: Feeding Ecology and Role in Marine Ecosystems*: 43–62. Cambridge, UK: Cambridge University Press.
- Roemmich, D. & McGowan, J.** 1995. Climatic warming and the decline of zooplankton in the California Current. *Science* **267**: 1324–1326.
- Schwing, F.B., Hayward, T.L., Sakuma, K.M., Murphree, T., Mascarenas, A.S. Jr, Castillo, S.I.L., Mantyla, A.W., Cummings, S.L., Chavez, F.P., Baltz, K. & Ainley, D.G.** 1997. The state of the California Current, 1996–1997: Mixed signals from the tropics. *Calif. Coop. Oceanic Fish. Invest. Rep.* **38**: 22–47.
- Spring, L.** 1971. A comparison of functional and morphological adaptations in the Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*). *Condor* **73**: 1–27.
- Wanless, S., Morris, J.A. & Harris, M.P.** 1988. The effect of radio transmitters on the behavior of Common Murres and Razorbills during chick rearing. *Condor* **90**: 816–823.
- Wanless, S., Harris, M.P. & Morris, J.A.** 1990. A comparison of feeding areas used by individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the breeding season. *Colonial Waterbirds* **13**: 16–24.
- White, G.C. & Garrott, R.A.** 1990. *Analysis of Wildlife Radio-Tracking Data*. San Diego, CA: Academic Press.
- Whitworth, D.L., Takekawa, J.Y., Carter, H.R. & McIver, W.R.** 1997a. Night-lighting as an at-sea capture technique for Xantus' Murrelets in the Southern California Bight. *Colonial Waterbirds* **20**: 525–531.
- Whitworth, D.L., Takekawa, J.Y., Carter, H.R., Newman, S.H., Keeney, T.W. & Kelly, P.R.** 1997b. Foraging distribution and dispersal of Xantus' Murrelets in the Southern California Bight in 1995–1997. Unpubl. report. Vallejo, CA: US Geological Survey, Biological Resources Division.
- Whitworth, D.L., Nelson, S.K., Newman S.H., van Vliet, G.B. & Smith, W.** in press. Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska. *Condor*.
- Zar, J.H.** 1996. *Biostatistical Analysis*, 3rd edn. Englewood Cliffs, NJ: Prentice-Hall.

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