XANTUS'S MURRELET BREEDING RELATIVE TO PREY ABUNDANCE AND OCEANOGRAPHIC CONDITIONS IN THE SOUTHERN CALIFORNIA BIGHT

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Received 18 May 2005, accepted 19 January 2006

SUMMARY

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.

We investigated the effects of temporal variability in prey abundance and oceanographic conditions on Xantus's Murrelet *Synthliboramphus hypoleucus* breeding on Santa Barbara Island, California, USA, from 1983 to 2001. We used estimates of prey abundance from California Cooperative Oceanic Fisheries Investigations surveys. We focused on known murrelet prey, including larval Northern Anchovy *Engraulis mordax,* larval Pacific Saury *Cololabis saira,* larval rockfish *Sebastes* spp., and mesozooplankton (including euphausiids). We obtained data on upwelling and sea-surface temperature (SST) from the National Oceanic and Atmospheric Administration to characterize oceanographic conditions. Average clutch initiation date was earlier in years with abundant mesozooplankton, stronger upwelling, and lower SST. Average clutch size was higher in years with abundant larval saury and mesozooplankton and lower SST. These results suggest that murrelets in the Southern California Bight are influenced by "bottom-up" processes in which variability in oceanographic conditions affects breeding through effects on prey abundance.

Key words: Xantus's Murrelet, breeding biology, prey abundance, oceanographic conditions, Santa Barbara Island, Southern California Bight

INTRODUCTION

Many seabird studies have documented earlier breeding and higher reproductive success in years when prey is abundant (Cairns 1987, Croxall & Rothery 1991, Phillips *et al.* 1996). An increasing number of studies have focused on seabird responses to variability in oceanographic conditions (Ainley *et al.* 1995, Gaston & Smith 2001, Abraham & Sydeman 2004). Ocean productivity along the west coast of the United States is enhanced in the spring and summer by an influx of cool, nutrient-rich water from the north and localized upwelling that brings nutrients to the surface (Chelton *et al.* 1982, Schwing *et al.* 2000). Low sea-surface temperature (SST) and strong upwelling are, therefore, associated with high primary and secondary productivity in the region and can show substantial interannual variation (Chelton *et al.* 1982). Seabird studies have documented earlier breeding and higher reproductive success in years of stronger upwelling and lower SST, demonstrating the importance of "bottom-up" processes to higher trophic levels (Gaston & Smith 2001, Abraham & Sydeman 2004).

Relatively little is known about the effects of variability in prey abundance and oceanographic conditions on Xantus's Murrelet *Synthliboramphus hypoleucus* breeding. Early diet studies indicated that murrelets fed exclusively on larval fish, including larval Northern Anchovy *Engraulis mordax,* larval Pacific Saury *Cololabis saira,* and larval rockfish *Sebastes* spp. (Hunt *et al.* 1979). A more recent diet study indicated that murrelets feed on a wider variety of prey than previously thought, including subadult and adult anchovy, juvenile Bluefin Driftfish *Psenes pellucidus* or Medusafish *Icichthys lockingtoni,* and euphausiids *Thysanoessa spinifera* (Hamilton *et al.* 2004). The only previous study of the relationship between murrelet breeding and prey abundance focused on larval anchovy and found that murrelets delayed breeding when larval anchovies were unavailable until late in the season (Hunt & Butler 1980). However, larval anchovy abundance has declined since that study was conducted (Smith 1995). The effect of the decline on murrelet breeding is unknown. The effects of variation in other prey species abundances and oceanographic conditions on murrelet breeding are also unknown, though a study of the closely related Ancient Murrelet *Synthliboramphus antiquus* found that breeding success was higher in years of lower SST (Gaston & Smith 2001).

We used 19 years of data (1983–2001) to examine the influence of variability in prey abundance and oceanographic conditions on Xantus's Murrelet breeding. Our first objective was to evaluate the effect of variation in prey abundance on clutch initiation date, clutch size and hatching success. We focused on known murrelet prey, including larval anchovy, larval saury, larval rockfish, and mesozooplankton (including euphausiids). We expected that clutch initiation date would be earlier and clutch size and hatching success higher in years of higher prey abundance. Our second objective was to evaluate the effects of variation in upwelling and SST on clutch initiation date, clutch size and hatching success. We used Bakun's upwelling index (described in Schwing *et al.* 1996) and SST from a local buoy. We expected that clutch initiation date would be earlier and clutch size and hatching success higher in years of stronger upwelling and lower SST.

METHODS

Study area

Santa Barbara Island, California, USA (33°28′N, 119°02′W), part of Channel Islands National Park (CINP), is located within the Southern California Bight (SCB). The island supports the largest murrelet breeding population in the United States, including 1000–2500 birds (Burkett *et al.* 2003). The SCB extends along the coast from Point Conception, California, to Cabo Colonet, Baja California, Mexico (Daily *et al.* 1993; Fig. 1). The California Current flows in a southeasterly direction offshore of the Channel Islands and marks the western edge of the SCB. The California Current moves inshore just south of the border between California and Mexico. We selected the area between Point Conception and San Clemente Island as our study area because it encompasses the primary foraging range of murrelets associated with Santa Barbara Island (Fig. 1; Hunt *et al.* 1979, Whitworth *et al.* 2000).

Murrelet breeding

We used murrelet data from CINP's Seabird Monitoring Program. Seabird biologists checked individual nest sites in two study plots on Santa Barbara Island each year and recorded information on clutch initiation date, number of eggs laid and number of chicks hatched at each site. To minimize disturbance, they did not check sites every day or handle birds during visits to the sites. We used data from individual nest sites to calculate average clutch initiation date (Julian date) for first nesting attempts over 13 years during 1983–2001 (1983, 1985, 1986, 1989, 1992–1998, 2000/01). We were not able to include all years because nest monitoring started after the start of breeding in some years. We excluded years if more than 20% of nests were found on the first nest check of the season, and we excluded observations in all years if more than 14 days passed between surveys. The exclusions ensured that dates were within two weeks of actual clutch initiation dates. We calculated average clutch size and average hatching success (chicks hatched per eggs laid) for first nesting attempts in each year from 1983 to 2001. We used hatching success as our measure of productivity, because chicks leave the nest site shortly after hatching and the remainder of the chick-rearing period occurs at sea (Murray *et al.* 1983, Drost & Lewis 1995).

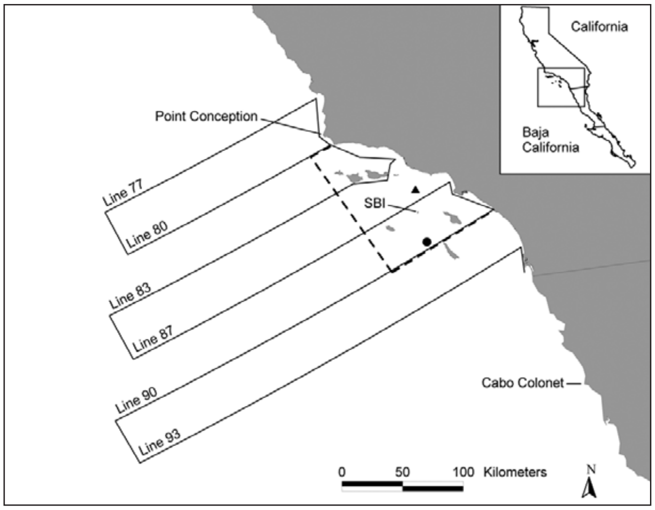

Fig. 1. Map showing the location of Santa Barbara Island (SBI), California, USA. The Southern California Bight extends from Point Conception, California to Cabo Colonet, Baja California, Mexico. The solid lines represent the California Cooperative Oceanic Fisheries Investigations transects. The dashed lines represent the boundaries of the study area. The triangle indicates the location of sea-surface temperature measurements. The circle indicates the location of upwelling index measurements.

Prey abundance

We used larval fish and zooplankton data from quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys (Paul Smith, National Marine Fisheries Service, pers. comm.). We used prey abundance data from Quarter 1 (January–March) to represent the prebreeding season and from Quarter 2 (April–June) to represent the breeding season (Table 1). We used data from a survey conducted in late March to represent Quarter 2 in 1983, and we excluded Quarter 2 in 1991 from our analyses because CalCOFI did not conduct any surveys during Quarter 2 in either of those years.

We used data from stations along Lines 80, 83, 87, and 90 (Fig. 1). Line 80 extends offshore from Point Conception; we used it to define the northern boundary of our presumed murrelet foraging ambit from Santa Barbara Island. Line 90 extends offshore north of San Clemente Island; we used it to define the southern boundary. We used data collected at stations inshore of Station 60 along all of the lines. This cutoff ensured that we were not including the offshore (blue water) domain in our analyses (Hayward & Venrick 1998). We excluded extra surveys conducted in some quarters, lines that were not sampled every year and stations that were sampled more than once during a single survey.

TABLE 1
Dates of California Cooperative Oceanic Fisheries Investigations surveys for Quarters 1 and 2 from 1983–2001

Year	Quarter 1		Quarter 2	
	Date range	Stations sampled (n)	Date range	Stations sampled (n)
1983	2/9–3/6	17	3/22–3/28[a]	17
1984	1/4–1/12	18	4/9–4/17	18
1985	2/25–3/1	18	5/6–5/16	18
1986	1/25–2/17	18	5/13–5/18	19
1987	3/7–3/13	17	5/5–5/11	19
1988	1/24–1/30	19	5/4–5/10	19
1989	1/25–1/31	19	4/21–4/28	19
1990	3/10–3/17	19	4/22–4/29	19
1991	1/13–1/19	19	No survey	N/A
1992	2/3–2/9	19	4/18–4/27	19
1993	1/17–1/23	19	4/4–4/11	19
1994	1/26–2/3	19	4/30–5/7	15
1995	1/10–1/17	18	4/11–4/18	19
1996	2/4–2/11	19	4/21–4/28	18
1997	2/3–2/10	19	4/7–4/15	16
1998	1/28–2/7	18	4/7–4/15	19
1999	1/14–1/22	18	4/6–4/13	19
2000	1/12–1/20	19	4/12–4/19	19
2001	1/13–1/20	19	4/11–4/20	19

[a] Late March survey used to represent Quarter 2.

CalCOFI researchers collected larval fish and zooplankton at each station by towing paired Bongo nets with 505 μm mesh at a 45-degree angle from 210 m to the surface. Researchers identified and counted larval fish and standardized the data to n/10 m^2 at each station. They measured zooplankton wet displacement volumes, and standardized the data to mL/1000 m^3 strained. We used mesozooplankton data in our analyses. Mesozooplankton species are those with a wet displacement volume of less than 5 mL and include euphausiids. We averaged station data to obtain abundance estimates for each season in each year. We log transformed (log10 + 1) individual station data before calculating averages to stabilize the variance (Zar 1999). We examined all species that are known murrelet prey and that are found in the CalCOFI dataset. Our final analyses included larval anchovy, larval saury, larval rockfish and mesozooplankton.

Upwelling and SST

We used Bakun's upwelling index (described in Schwing *et al.* 1996) and SST to characterize oceanographic conditions in the study area. We obtained monthly upwelling indices ($m^3 \times s^{-1}$/100 m coastline) for the study area at 33°N, 119°W from the National Oceanic and Atmospheric Administration's (NOAA's) Pacific Fisheries Environmental Laboratory (Fig. 1; www.pfeg.noaa.gov). We averaged monthly values to obtain one value for each season in each year to match quarterly CalCOFI surveys. We obtained SSTs (degrees Celsius) for Station 46025 at 33°44′42″N, 119°05′02″W from NOAA's National Data Buoy Center (Fig. 1; www.ndbc.noaa.gov). The station is a 3-m discus buoy that measures water temperature at 0.6 m below sea level once every hour. We averaged hourly values to obtain one value for each season in each year to match quarterly CalCOFI surveys.

Statistical analyses

We used two-tailed Spearman rank correlations to evaluate the relationships between clutch initiation date, clutch size and hatching success, and each prey abundance or oceanographic variable for the prebreeding and breeding seasons (Zar 1999). We used rank correlations to establish the significance of relationships because of the robustness of this technique. We report linear regression equations and r^2 values for significant relationships. We considered relationships significant at $P < 0.1$ because of the exploratory nature of these analyses. (See tables for more details on significance levels.) We conducted all analyses in Stata 8.0 (Stata Corporation 2003).

TABLE 2

Spearman rank correlation coefficients between average clutch initiation date, prey abundance and oceanographic conditions in the Southern California Bight during 1983–2001

Parameter	Prebreeding season	Breeding season
	(n=13 years)	(n=13 years)
Prey species		
Northern Anchovy	–0.25	0.32
Pacific Saury	0.00	–0.08
Rockfish spp.	–0.24	0.56[a]
Mesozooplankton	–0.80[b]	–0.51[c]
Oceanographic conditions		
Upwelling	–0.55[a]	–0.55[c]
Sea-surface temperature	0.57[a]	0.02

[a] $P < 0.05$.
[b] $P < 0.01$.
[c] $P < 0.10$.

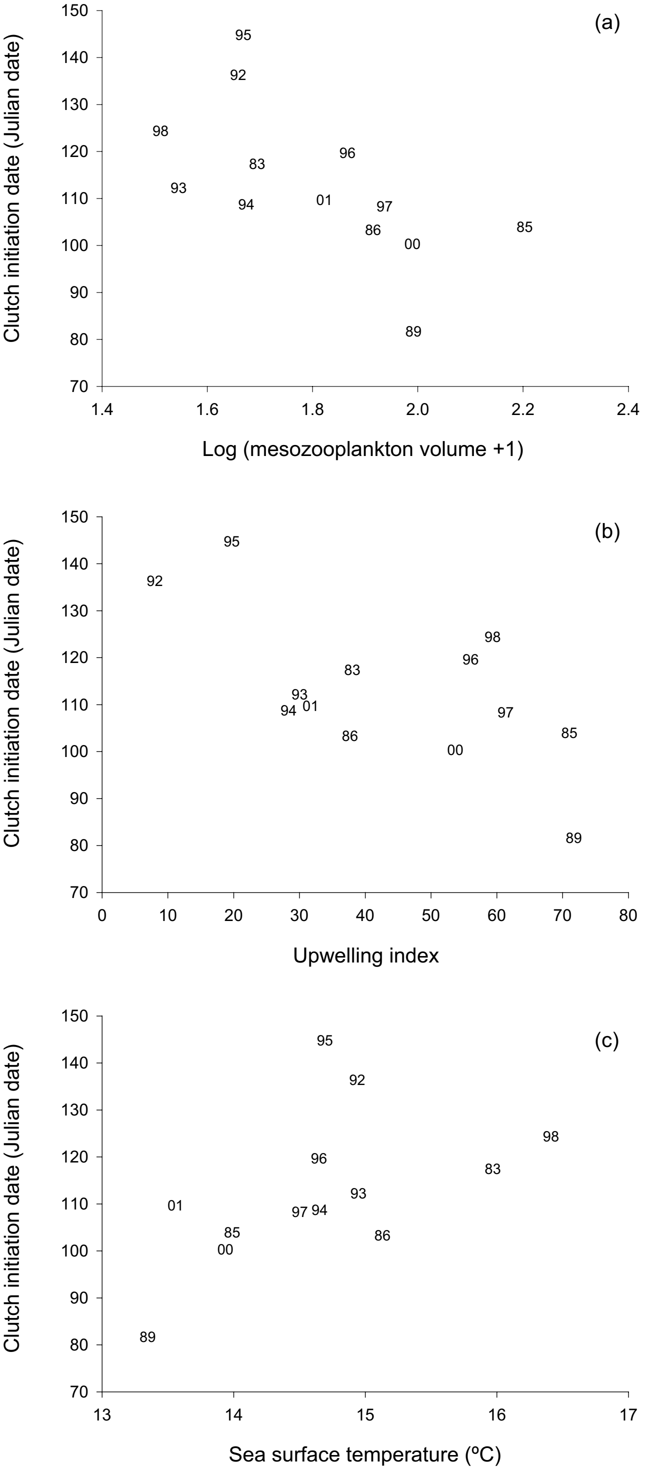

Fig. 2. Relationships between Xantus's Murrelet clutch initiation date and (a) mesozooplankton volume, (b) upwelling index and (c) sea-surface temperature during the prebreeding season over 1983–2001.

RESULTS

Clutch initiation date was negatively correlated with mesozooplankton volume and upwelling and positively correlated with SST during the prebreeding season [Table 2; Fig. 2(a–c)]. The corresponding regression equations were

$y = 202.724 - 49.512 \times \log$ (mesozooplankton volume + 1) $(r^2 = 0.38)$,
$y = 136.060 - 0.523 \times$ upwelling index $(r^2 = 0.42)$, and
$y = -30.774 + 9.797 \times$ SST $(r^2 = 0.28)$.

During the breeding season, clutch initiation date was negatively correlated with mesozooplankton volume and upwelling and positively correlated with larval rockfish abundance (Table 2). The corresponding regression equations were

$y = 143.534 - 14.556 \times \log$ (mesozooplankton volume + 1) $(r^2 = 0.13)$,
$y = 170.840 - 0.243 \times$ upwelling index $(r^2 = 0.34)$, and
$y = 108.831 + 4.011 \times \log$ (larval rockfish abundance + 1) $(r^2 = 0.02)$.

Clutch size was positively correlated with larval saury abundance and mesozooplankton volume and negatively correlated with SST during the prebreeding season [Table 3; Fig. 3(a–c)]. The relationship between clutch size and larval saury abundance was dependent on two (1999 and 2001) of the 19 years. The corresponding regression equations were

$y = 1.548 + 2.652 \times \log$ (larval saury abundance + 1) $(r^2 = 0.31)$,
$y = 1.195 + 0.201 \times \log$ (mesozooplankton volume + 1) $(r^2 = 0.14)$, and
$y = 2.382 - 0.055 \times$ SST $(r^2 = 0.16)$.

During the breeding season, clutch size was positively correlated with mesozooplankton volume and negatively correlated with SST (Table 3). The corresponding regression equations were

$y = 1.361 + 0.096 \times \log$ (mesozooplankton volume + 1) $(r^2 = 0.08)$ and
$y = 2.579 - 0.061 \times$ SST $(r^2 = 0.18)$.

There were no significant relationships between hatching success and prey abundance or oceanographic variables during either the prebreeding or breeding seasons (Table 4).

TABLE 3
Spearman rank correlation coefficients between average clutch size, prey abundance and oceanographic conditions in the Southern California Bight during 1983–2001

Parameter	Prebreeding season (n=19 years)	Breeding season (n=18 years)
Prey species		
Northern Anchovy	–0.19	–0.39
Pacific Saury	0.47[a]	0.18
Rockfish spp.	–0.12	0.22
Mesozooplankton	0.43[b]	0.42[b]
Oceanographic conditions		
Upwelling	0.24	0.01
Sea-surface temperature	–0.46[a]	–0.41[b]

[a] $P < 0.05$.
[b] $P < 0.10$.

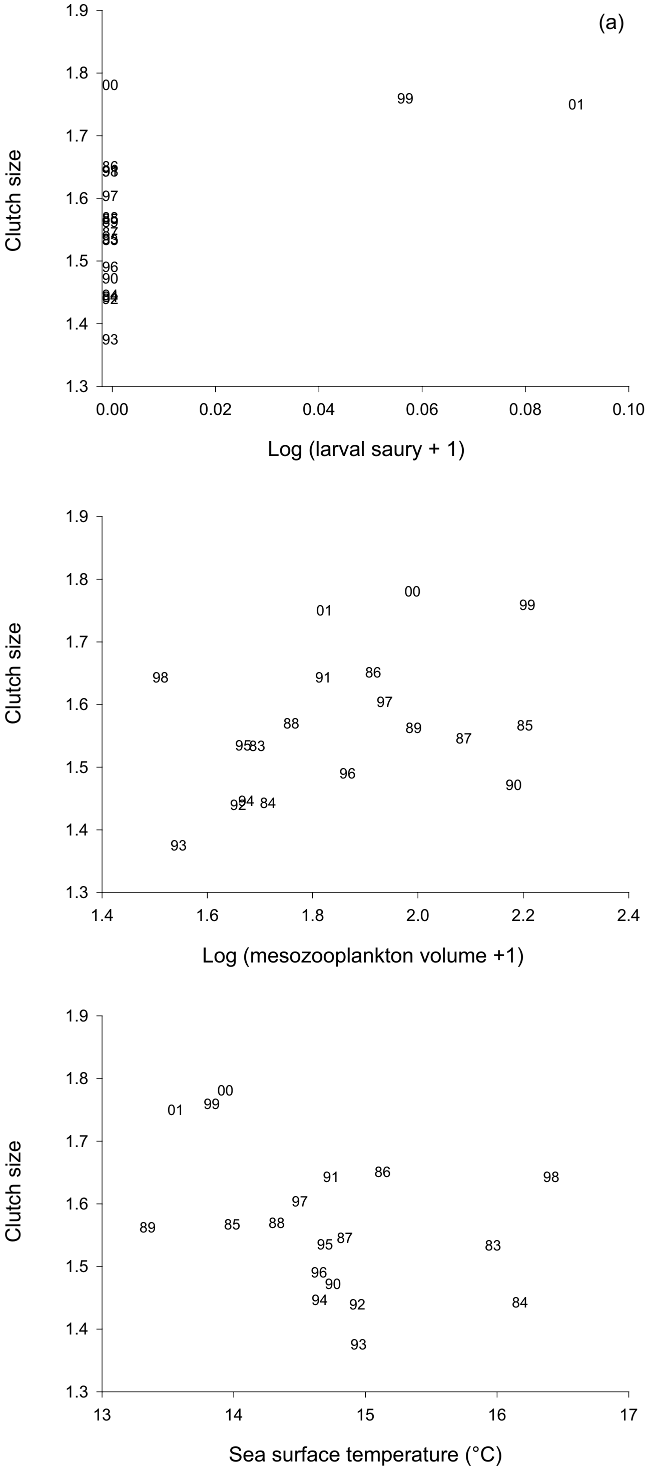

Fig. 3. Relationships between Xantus's Murrelet clutch size and (a) larval saury abundance, (b) mesozooplankton volume and (c) sea-surface temperature during the prebreeding season over 1983–2001.

DISCUSSION

Predator–prey relationships

Average clutch initiation date was earlier in years with abundant mesozooplankton. In addition, average clutch size was higher in years with abundant larval saury and mesozooplankton. We did not find the relationship between clutch initiation date and larval anchovy abundance documented by Hunt & Butler (1980), but our results support their more general conclusion that timing of breeding is influenced by prey abundance. Our results are also consistent with other seabird studies that have documented earlier breeding and increases in breeding parameters (e.g. clutch size, hatching success, productivity) in response to abundant prey (Anderson *et al.* 1982, Schaffner 1986, Monaghan *et al.* 1989, Sydeman *et al.* 1991, Crawford & Dyer 1995, Phillips *et al.* 1996, Suddaby & Ratcliffe 1997, Ratcliffe *et al.* 1998, Nur & Sydeman 1999, Abraham & Sydeman 2004). Larval saury and mesozooplankton (euphausiids) are known murrelet prey species (Hunt *et al.* 1979, Hamilton *et al.* 2004), and our results may indicate that they are specifically important in determining murrelet timing of breeding and clutch size. Alternatively, larval saury and mesozooplankton may be proxies for general prey abundance. The results were similar between the prebreeding and breeding seasons, with the exception of a positive relationship between clutch initiation date and larval rockfish abundance during the breeding season. That relationship does not appear to have any biological relevance and is likely a spurious correlation.

Hunt & Butler (1980) found a relationship between timing of breeding and larval anchovy abundance and concluded that larval anchovies were of particular importance to murrelets. We did not find a relationship between these variables in our time series. A decline in larval anchovy numbers may be responsible for the difference between the two studies. Larval anchovy abundance peaked in the mid-to-late 1970s (Ahlstrom 1966, MacCall & Prager 1988), when Hunt & Butler (1980) conducted their study. Anchovy abundance declined during the 1980s and 1990s (Smith 1995) and may be a less prevalent diet item than in the past. The lack of a relationship between murrelet breeding and larval anchovy abundance, significant relationships between murrelet breeding and other measures of prey abundance, and evidence that murrelets are generalists (Hamilton *et al.* 2004) suggest that murrelets exploit a variety of prey species depending on their relative abundances in the environment. Studies of the closely related Ancient Murrelet also support this idea. Ancient Murrelets are generalists (Sealy 1975, Vermeer *et al.* 1985, Gaston *et al.* 1993, Gaston 1994), whose diet composition varies both seasonally and geographically depending on prey abundances (Sealy 1975, Vermeer *et al.* 1985).

TABLE 4
Spearman rank correlation coefficients between average hatching success, prey abundance and oceanographic conditions in the Southern California Bight during 1983–2001

Parameter	Prebreeding season (n=19 years)	Breeding season (n=18 years)
Prey species		
Northern Anchovy	–0.23	–0.17
Pacific Saury	0.26	0.33
Rockfish spp.	0.03	0.13
Mesozooplankton	0.12	0.33
Oceanographic conditions		
Upwelling	–0.24	–0.39
Sea-surface temperature	–0.36	–0.37

Hatching success was not related to prey abundance. The lack of a relationship is likely attributable to the influence of egg predation on hatching success. Sydeman *et al.* (1998) found that approximately 47% of the eggs were preyed upon by native deer mice on Santa Barbara Island from 1983 to 1995. However, it is important to note that prey abundance may have an indirect effect on egg predation. Egg neglect appears to increase in years of low prey abundance (Murray *et al.* 1979). Sydeman *et al.* (1998, 2001) suggested that there may be an interaction between prey abundance and mouse predation that determines hatching success. In that case, increased egg neglect in years of low prey abundance would lead to higher predation and lower hatching success. Blight *et al.* (1999) proposed a similar mechanism for Rhinoceros Auklets *Cerorhinca monocerata* subjected to egg predation by native deer mice.

Predator–oceanographic relationships

Average clutch initiation dates were earlier in years with stronger upwelling and lower SST. In addition, average clutch sizes were higher in years with lower SST. These results, coupled with results of predator–prey interactions, offer evidence for the influence of "bottom-up" processes on murrelet breeding. Annual productivity in the SCB is influenced by the strength of the California Current and seasonal upwelling. The California Current brings cool, nutrient-rich waters into the region from the north (Chelton *et al.* 1982, Daily *et al.* 1993). Coastal upwelling near Point Conception and localized upwelling near headlands and islands replaces surface waters with cool, nutrient-rich waters from below (Daily *et al.* 1993, Schwing *et al.* 2000). The increase in nutrients at the surface leads to increases in primary and secondary (fish and zooplankton) productivity (Chelton *et al.* 1982, Schwing *et al.* 2000) that are beneficial for seabirds. Our results are consistent with seabird studies from other areas that have documented relationships between breeding parameters and oceanographic conditions. For instance, Gaston & Smith (2001) found that Ancient Murrelet breeding success was higher in years with lower SST. In addition, Abraham & Sydeman (2004) found that Cassin's Auklet *Ptychoramphus aleuticus* hatching dates were earlier in years with lower SST and stronger upwelling.

Given the association between murrelets and oceanographic conditions, recent changes in the SCB may have long-term implications for murrelets. The SCB was characterized by relatively warm SST and low productivity between the late 1970s and the late 1990s (McGowan *et al.* 2003), and murrelet reproductive success declined concordantly from 1985 to 1997 (Sydeman *et al.* 2001). In late 1998, there was a rapid shift to lower SST and higher productivity throughout the region (Bograd *et al.* 2000, Schwing *et al.* 2000). This may have marked a shift to a new "regime," characterized by cooler, more productive conditions (Bograd *et al.* 2000, Schwing *et al.* 2000, Peterson & Schwing 2003).

We do not yet have enough data to quantitatively compare the two "regimes" or to assess murrelet responses to the shift. However, earlier breeding and increased clutch size and hatching success after 1999 suggest that murrelets are responding positively to this ecosystem shift. Several seabird species—including Cassin's Auklet, Pelagic Cormorant *Phalacrocorax pelagicus,* and Pigeon Guillemot *Cepphus columba*—breeding off Central California showed similar increases in reproductive success after 1998 (Schwing *et al.* 2002). The California Current System appears to alternate between warm and cool regimes on multidecadal scales (Chavez *et al.* 2003), and the recent shift to a cooler, more productive ecosystem may have a positive effect on the murrelet population if it persists.

ACKNOWLEDGMENTS

We thank the people and programs that provided data for these analyses. Channel Islands National Park supported collection of the murrelet data. Paul Smith provided data on prey abundance and patiently answered our questions. The National Marine Fisheries Service, Scripps Institution of Oceanography, and California Department of Fish and Game provided support for the CalCOFI surveys. Many field biologists collected data on Santa Barbara Island and during CalCOFI surveys over the years and were crucial to this effort. We also thank Tom Hayward, David Hyrenbach and Larry Jacobson for insightful conversations regarding the oceanography and ecology of the Southern California Bight. Finally, we thank Scott Hatch, John Piatt, Ron Ydenberg and an anonymous reviewer for helpful comments on earlier drafts. This is PRBO contribution No. 1317.

REFERENCES

ABRAHAM, C.L. & SYDEMAN, W.J. 2004. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus. Marine Ecology Progress Series* 274: 235–250.

AHLSTROM, E.H. 1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951–64: a summary. Special Scientific Report, Fisheries No. 534. Washington, DC: United States Fish and Wildlife Service. 71 pp.

AINLEY, D.G., SYDEMAN, W.J. & NORTON, J. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series* 118: 69–79.

ANDERSON, D.W., GRESS, F. & MAIS, K.F. 1982. Brown pelicans: influence of food supply on reproduction. *Oikos* 39: 23–31.

BLIGHT, L.K., RYDER, J.L. & BERTRAM, D.F. 1999. Predation on Rhinoceros Auklet eggs by a native population of *Peromyscus. Condor* 101: 871–876.

BOGRAD, S.J., DIGIACOMO, P.M., DURAZO, R., HAYWARD, T.L., HYRENBACH, K.D., LYNN, R.J., MANTYLA, A.W., SCHWING, F.B., SYDEMAN, W.J., BAUMGARTNER, T., LAVANIEGOS, B. & MOORE, C.S. 2000. The state of the California Current, 1999–2000: forward to a new regime? *California Cooperative Oceanic Fisheries Investigations Report* 41: 26–52.

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. California Department of Fish and Game, Habitat Conservation Planning Branch Status Report 2003-01. Sacramento, CA: California Department of Fish and Game. 96 pp.

CAIRNS, D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.

CHAVEZ, F.P., RYAN, J., LLUCH-COTA, S.E. & ÑIQUEN C.M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299: 217–221.

CHELTON, D.B., BERNAL, P.A. & MCGOWAN, J.A. 1982. Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research* 40: 1095–1125.

CRAWFORD, R.J.M. & DYER, B.M. 1995. Responses by four seabird species to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329–339.

CROXALL, J.P. & ROTHERY, P. 1991. Population regulation of seabirds: implications of their demography for conservation. In: Perrins, C.M., LeBreton, J.D. & Hirons, G.M. (Eds). Bird population studies: relevance to conservation and management. Oxford: Oxford University Press. pp. 272–296.

DAILY, M.D., ANDERSON, J.W., REISH, D.J. & GORSLINE, D.S. 1993. The Southern California Bight: background and setting. In: Dailey, M.D., Reish, D.J. & Anderson, J.W. (Eds). Ecology of the Southern California Bight: a synthesis and interpretation. Berkeley: University of California Press. pp. 1–18.

DROST, C.A. & LEWIS, D.B. 1995. Xantus's 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.

GASTON, A.J. 1994. Ancient Murrelet (*Synthliboramphus antiquus*). In: Poole, A. & Gill, F. (Eds). The birds of North America, No. 132. Philadelphia & Washington, DC: Academy of Natural Sciences & American Ornithologists' Union. 19 pp.

GASTON, A.J., CARTER, H.R. & SEALY, S.G. 1993. Winter ecology and diet of Ancient Murrelets off Victoria, British Columbia. *Canadian Journal of Zoology* 71: 64–70.

GASTON, A.J. & SMITH, J.L. 2001. Changes in oceanographic conditions off northern British Columbia (1983–1999) and the reproduction of a marine bird, the Ancient Murrelet (*Synthliboramphus antiquus*). *Canadian Journal of Zoology* 79: 1735–1742.

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.

HAYWARD, T.L. & VENRICK, E.L. 1998. Nearsurface pattern in the California Current: coupling between physical and biological structure. *Deep-Sea Research II* 45: 1617–1638.

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., PITMAN, R.L., NAUGHTON, M., WINNETT, K., NEWMAN, A., KELLY, P.R. & BRIGGS, K.T. 1979. Summary of marine mammal and seabird surveys of the Southern California Bight area, 1975–1978. Final report to the Bureau of Land Management, Volume 3: Investigators' reports. Part 3: Seabirds of the Southern California Bight. Book 2: Distribution, status, reproductive ecology, and foraging habits of breeding seabirds. Irvine, CA: Regents of the University of California. 399 pp.

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. *California Cooperative Oceanic Fisheries Investigations Report* 29: 91–101.

MCGOWAN, J.A., BOGRAD, S.J., LYNN, R.J. & MILLER, A.J. 2003. The biological response to the 1977 regime shift in the California Current. *Deep-Sea Research II* 50: 2567–2582.

MONAGHAN, P., UTTLEY, J.D. & OKILL, J.D. 1989. Terns and sandeels: seabirds as indicators of changes in marine fish populations. *Journal of Fish Biology* 35(Supplement A): 339–340.

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

MURRAY, K.G., WINNETT-MURRAY., K. & HUNT, G.L. 1979. Egg neglect in Xantus' Murrelet. *Proceedings of the Colonial Waterbird Group* 3: 186–195.

NUR, N. & SYDEMAN, W.J. 1999. Survival, breeding probability and reproductive success in relation to population dynamics of Brandt's Cormorants *Phalacrocorax penicillatus. Bird Study* 46(Supplement): S92–S103.

PETERSON, W.T. & SCHWING, F.B. 2003. A new climate regime in northeast pacific ecosystems. *Geophysical Research Letters* 30, 1896, doi:10.1029/2003GL017528.

PHILLIPS, R.A., CALDOW, R.W.G. & FURNESS, R.W. 1996. The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus. Ibis* 138: 410–419.

RATCLIFFE, N., FURNESS, R.W. & HAMER, K.C. 1998. The interactive effects of age and food supply on the breeding ecology of great skuas. *Journal of Animal Ecology* 67: 853–862.

SCHAFFNER, F.C. 1986. Trends in Elegant Tern and Northern Anchovy populations in California. *Condor* 88: 347–354.

SCHWING, F.B., O'FARRELL, M., STEGER, J.M. & BALTZ, K. 1996. Coastal upwelling indices, West Coast of North America, 1946–95. Technical memorandum 231. Pacific Grove, CA: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center. 103 pp.

SCHWING, F.B., MOORE, C.S., RALSTON, S. & SAKUMA, K.M. 2000. Record coastal upwelling in the California Current in 1999. *California Cooperative Oceanic Fisheries Investigations Report* 41: 148–160.

SCHWING, F.B., BOGRAD, S.J., COLLINS, C.A., GAXIOLA-CASTRO, G., GARCIA, J., GOERICKE, R., GOMEZ-VALDEZ, J., HUYER, A., HYRENBACH, K.D., KOSRO, P.M., LAVANIEGOS, B.E., LYNN, R.J., MANTYLA, A.W., OHMAN, M.D., PETERSON, W.T., SMITH, R.L., SYDEMAN, W.J., VENRICK, E. & WHEELER, P.A. 2002. The state of the California Current, 2001–2002: will the California Current System keep its cool, or is El Niño looming? *California Cooperative Oceanic Fisheries Investigations Report* 43: 31–70.

SEALY, S.G. 1975. Feeding ecology of the ancient and marbled murrelets near Langara Island, British Columbia. *Canadian Journal of Zoology* 53: 418–433.

SMITH, P.E. 1995. A warm decade in the Southern California Bight. *California Cooperative Oceanic Fisheries Investigations Report* 36: 120–126.

STATA CORPORATION. 2003. Stata user's guide, release 8. College Station, TX: Stata Press.

SUDDABY, D. & RATCLIFFE, N. 1997. The effects of fluctuating food availability on breeding Arctic Terns (*Sterna paradisaea*). *Auk* 114: 524–530.

SYDEMAN, W.J., PENNIMAN, J.F., PENNIMAN, T.M., PYLE, P. & AINLEY, D.G. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. *Journal of Animal Ecology* 60: 135–149.

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*). Final report to the United States Geological Survey, Biological Resources Division, Species at Risk Program. Stinson Beach, CA: PRBO Conservation Science. 74 pp.

SYDEMAN, W.J., HESTER, M.M., THAYER, J.A., GRESS, F., MARTIN, P. & BUFFA, J. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress in Oceanography* 49: 309–329.

VERMEER, K., FULTON, J.D. & SEALY, S.G. 1985. Differential use of zooplankton prey by Ancient Murrelets and Cassin's Auklets in the Queen Charlotte Islands. *Journal of Plankton Research* 7: 443–459.

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

ZAR, J.H. 1999. Biostatistical analysis. 4th ed. Upper Saddle River, NJ: Prentice Hall.