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FACTORS INFLUENCING THE AT-SEA DISTRIBUTION OF CASSIN'S AUKLETS (*PTYCHORAMPHUS ALEUTICUS*) THAT BREED IN THE CHANNEL ISLANDS, CALIFORNIA

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Abstract.—We used radiotelemetry to evaluate at-sea habitat use by Cassin's Auklets (*Ptychoramphus aleuticus*) that bred at Prince Island, off southern California, from 1999 through 2001. We used logistic regression to compare paired radiotelemetry (presence) with random (pseudo-absence) location-associated habitat variables derived from (1) satellite remote-sensing of sea surface temperature and chlorophyll-*a* concentration and (2) bathymetry. Compared with random locations within their foraging area and after controlling for distance to colony, odds ratios indicated that Cassin's Auklets with dependent young occurred in relatively shallower, warmer, and chlorophyll-rich water associated with chlorophyll fronts near the insular shelf break. These oceanographic features characterize habitats that support key euphausiid prey (e.g., *Thysanoessa spinifera*) and also other krill predators. Radiotelemetry combined with satellite remote-sensing of the ocean provides an alternative to vessel-based surveys for evaluating seabird foraging habitats. In the absence of information on the actual distribution, abundance, and, hence, availability of zooplankton prey for seabirds, environmental factors can serve as proxies to help elucidate distributional patterns of seabirds at sea. *Received 10 September 2008, accepted 27 December 2009.*

Key words: California Bight, California Current, Cassin's Auklet, logistic regression, *Ptychoramphus aleuticus*, radiotelemetry, southern seabird foraging habitat.

Factores que Influencian la Distribución Marina de Individuos de *Ptychoramphus aleuticus* que Anidan en las Islas del Canal en California

Resumen.—Utilizamos radiotelemetría para evaluar el uso de hábitat marino de individuos de *Ptychoramphus aleuticus* que anidan en la isla Prince, en el sur de California entre los años 1999 y 2001. Usamos regresión logística para comparar las localizaciones de hábitat de forrajeo obtenidas con telemetría (presencias) con puntos escogidos al azar (pseudo-ausencias) asociadas a tres variables medioambientales obtenidas a partir de imágenes satelitales, concentración de clorofila-a y temperatura de superficie, y de datos de batimetría. Después de controlar por el efecto de la distancia a la colonia, el análisis reveló que los individuos de *P. aleuticus* con crías ocupaban las aguas menos profundas, más calientes y con concentraciones de clorofila más altas. Estas características, que identifican las zonas de frentes oceanográficos al borde de la plataforma peri-insular, tembién definen los hábitats de los eufausidos que son presas clave (e.g., *Thysanoessa spinifera*) y de otros depredadores de krill. En comparación con los métodos de muestreo que utilizan embarcaciones, el uso conjunto de radiotelemetría con datos obtenidos de imágenes satelitales proporcionó una forma alternativa para el estudio los hábitats de forrajeo de las aves marinas. Este método es especialmente útil en situaciones donde la falta de información sobre la distribución y abundancia del zooplancton imposibilita la evaluación de la disponibilidad de recursos para las aves marinas. En estos casos, el uso de variables medioambientales obtenidas indirectamente a través de imágenes satelitales puede facilitar el estudio de la distribución de las aves en el mar.

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Most habitat-use and resource-selection studies have been conducted on terrestrial species with well-defined home ranges where landscape features are fixed in space and do not change appreciably throughout the study (Manly et al. 2002). In marine environments, habitats used by seabirds and marine mammals include both static (e.g., colony location, bathymetry) and dynamic features (e.g., sea-ice conditions, temperature fronts, upwelling plumes, turbidity fronts, and phytoplankton blooms) that change through time (Skov and Prins 2001, Spear et al. 2001, Hyrenbach et al. 2002, Chapman et al. 2004, Yen et al. 2004, Ainley et al. 2005). Furthermore, these features influence distribution and abundance of key prey, including krill (Huntley et al. 2000, Ainley et al. 2009) and larval fishes (Bjorkstedt et al. 2002). In the absence of information regarding the actual distribution, abundance, and, hence, availability of zooplankton prey, certain environmental factors can serve as proxies to help elucidate seabird distributions at sea. For example, physical oceanographic forcing (i.e., winds or currents) can rapidly modify nutrient fluxes, sea surface temperature (SST), phytoplankton blooms (Lynn et al. 2003), and spatial distribution of zooplankton prey (Huntley et al. 2000).

Seabird studies have used telemetry methods to track individuals over periods of weeks or months (rarely years) to measure colony-based foraging areas over large expanses and within a variety of open-ocean environments (Hyrenbach et al. 2002, Ainley et al. 2003, Adams et al. 2004a). At the scale of seabird foraging areas (i.e., hundreds to millions of square kilometers), measurements of dynamic habitat parameters have been facilitated by the increased availability of remotely sensed environmental data measured by satellites (Haney 1989, Hyrenbach et al. 2002, DiGiacomo et al. 2002, Bump and Lovvorn 2004). When combined with marine habitat parameters (e.g., SST, surface chlorophyll-*a* [chl-*a*] concentration), habitat-use patterns of seabirds provide species- and system-specific information to quantify associations.

The Southern California Bight (SCB) supports an abundant and diverse marine avifauna (Briggs et al. 1987, Mason et al. 2007). The abundance and distribution of seabirds and their prey in the SCB fluctuate on annual and decadal scales, and this is often attributed to oscillating ocean climate events (e.g., Pacific Decadal Oscillation, El Niño–Southern Oscillation) that drive ecosystem variability (Mantua and Hare 2002, Miller and Sydeman 2004). For example, off central-southern California during a recent extended warm-ocean climate period characterized by frequent El Niño events (McGowan et al. 1998), cool-water-affiliated seabirds including Cassin's Auklet (*Ptychoramphus aleuticus*) and Sooty Shearwater (*Puffinus griseus*) declined in abundance (Ainley et al. 1995, Viet et al. 1997, Oedekoven et al. 2001, Hyrenbach and Viet 2003). Presumably, the declines resulted in part from long-term increases in surface warming coincident with deepening of the upper mixed layer in the California Current System (CCS; Palacios et al. 2004). Ecosystem effects included reduced nutrient flux to surface waters, negative effects on primary productivity (Barber and Chavez 1983), and altered zooplankton availability and community composition (McGowan et al. 1998).

Cassin's Auklet (hereafter "auklet"; ~160 g) is one of five auklet species (Family Alcidae) endemic to the North Pacific. It has the most extensive breeding range (Bering Sea to central Baja California, Mexico; Manuwal and Thoresen 1993) of the five, and in California, auklet colonies are located on islands within oceanographic areas that are seasonally influenced by wind-driven upwelling of relatively cool (9–12°C), nutrient-enriched water that supports extensive seasonal phytoplankton blooms (Kahru and Mitchell 2001, Lynn et al. 2003) and large macrozooplankton standing stocks (Brinton and Townsend 2003). Breeding by auklets generally coincides with enhanced prey abundance near breeding colonies (Bertram et al. 2000), and clutch initiation occurs when SST, associated with coastal upwelling, decreases abruptly (e.g., annual "spring transition"; Ainley et al. 1990); recent work also highlights the importance of prebreeding diet in determining clutch initiation and subsequent breeding success (Sorensen et al. 2009). Auklets have limited diving ability and depend on prey that aggregate within the upper 10–20 m (Burger and Powell 1990, J. Adams et al. unpubl. data). Throughout their range, chick diets consist of macrozooplankton: copepods (especially off British Columbia), euphausiids, amphipods, and larval–early juvenile fishes (Ainley et al. 1996, Sydeman et al. 2001, Hedd et al. 2002, Adams et al. 2004b).

We combined radiotelemetry data with satellite imagery of the sea surface and digital bathymetry to model habitat use by auklets. The factors that regulate the abundance and availability of auklet prey off southern California are complex (Fiedler et al. 1998, Nishimoto and Washburn 2002). We therefore sought to first identify abiotic and biotic factors that influence foraging distributions of auklets provisioning chicks. We examined three alternative hypotheses related to the spatial distribution of auklet locations: (1) provisioning auklets' at-sea distribution is influenced by SST and/or chl-*a* concentrations, and associations with these parameters are independent of season (early vs. late rearing); (2) provisioning auklets' at-sea distribution is influenced by gradients in SST and/or chl-*a* concentration, and associations with these parameters are independent of season; and (3) provisioning auklets' at-sea distribution is influenced by bathymetry (depth and distance from the shelf break) and/or chl-*a* concentration, and at-sea distribution related to bathymetry is independent of season.

Methods

Study site.—We studied auklets nesting at Prince Island (34°05′N, 120°20′W), the largest auklet colony in the Channel Islands, California (~8,900 breeding birds in 1991; H. Carter et al. unpubl. report, U.S. Fish and Wildlife Service, 1992; Fig. 1). Prince Island is located 2 km northeast of San Miguel Island. The northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) are separated from mainland southern California by the Santa Barbara Channel (SBCH). The SBCH overlies the elliptical (100 × 40 km) Santa Barbara Basin (maximum depth ~600 m). A shallow shelf (<200 m deep; 3–10 km wide) surrounds the islands, which are separated by narrow, shallow passages (40 m deep). North of Point Conception during spring and summer, strong northwesterly winds transport warm surface waters offshore, driving replacement from below by cool, nutrient-enriched deeper waters (i.e., upwelling). Newly upwelled waters enter the SBCH and generally flow southeastward (Harms and Winant 1998; Fig. 2A). The seasonal infusion of nutrients to the euphotic zone fuels dramatic phytoplankton blooms that are well observed by satellite-borne sensors (Fig. 2B). Within the SBCH, dramatic thermal fronts demarcate boundaries between warm waters of the inner SCB and cool waters from north of Point Conception (Breaker et al. 2003; Fig. 2C). Such fronts may

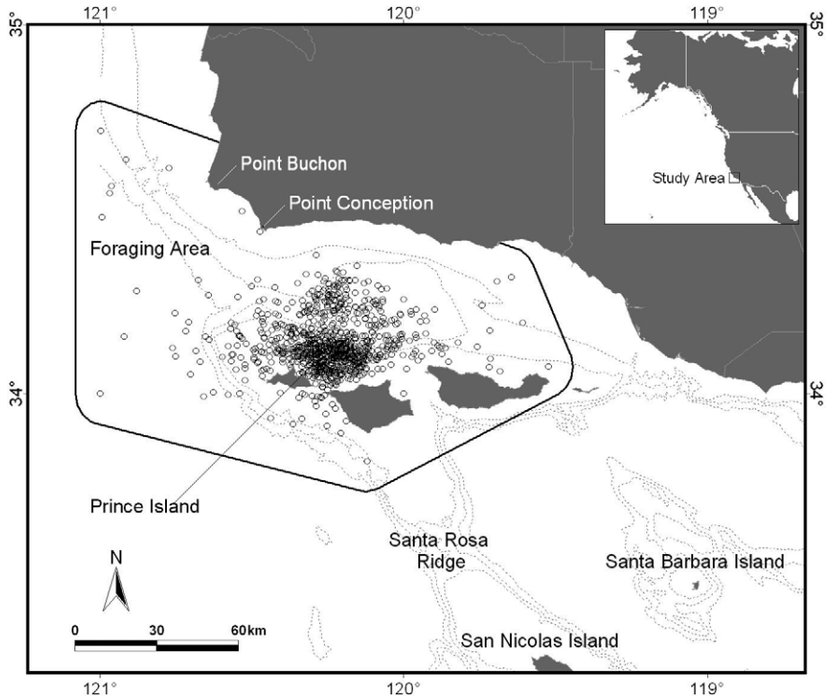

FIG. 1. Foraging area (minimum convex polygon) of radiomarked Cassin's Auklets (*Ptychoramphus aleuticus*) from the Prince Island colony in southern California. Open circles show auklet radiolocations from 1999 to 2001 (N = 930 locations from 80 birds). Bathymetric contour lines are shown at 200, 400, and 600 m.

demarcate zones of elevated productivity where prey are concentrated and seabirds and marine mammals aggregate.

Capture, radiomarking, and telemetry.—During March through June (1999, 2000, and 2001) on Prince Island, we captured breeding adult auklets at night by hand after birds returned to their nest sites. We attached radiotransmitters (PD-2G, Holohil Systems, Carp, Ontario; and model 386, Advanced Telemetry Systems, Isanti, Minnesota) to the skin and feathers between the scapulae with subcutaneous anchors, sutures, and epoxy (Newman et al. 1999). Transmitters weighed 3 g (<2% auklet mass). Immediately after transmitter attachment, we returned birds to their nest sites. In total, we radiomarked 105 adults at 99 nest sites (in 6 nest sites, both members of a pair were radiomarked). Among 28 of 99 sites where we marked parents during the incubation stage, 12 hatched (3 of the other 16 relaid), and 9 of 28 fledged chicks. Of the remaining 71 sites marked during the chick-rearing stage, 41 fledged at least 1 chick (3 sites fledged 2 chicks). Seven radiotransmitters were never detected at sea. Although a separate study indicated that auklet chicks in the present study reared by non-radiomarked pairs had faster growth rates, greater prefledging mass, and greater chick survival (Ackerman et al. 2004), we assumed that distributions at sea were unbiased by radiomarking (Phillips et al. 2003). This assumption (representative foraging areas at sea among radiomarked individuals) was supported by independent data from comparisons between telemetry-derived locations and distribution of auklets at sea during concurrent aerial surveys in 1999, 2000, and 2001 (Ackerman et al. 2004, Mason et al. 2007) and ship surveys in May 2000, which revealed that radiomarked individuals were located where unmarked auklets were found at the highest densities (J. Adams unpubl. data). We restricted the analyses presented here to a subset of 80 chick-provisioning auklets (36 males, 39 females, and 5 of unknown sex) with confirmed nightly attendance patterns (Adams et al. 2004a).

During three consecutive nesting seasons (7 March–24 June 1999, 12 April–20 June 2000, and 6 April–27 June 2001), we conducted aerial telemetry surveys every 2 days, on average (range: 1–8 days), with fixed-wing, twin-engine Cessna Skymaster 337 and Partenavia P-68 aircraft equipped with a receiver (ATS R-4000) connected through a switch box to two wing-mounted three- or four-element Yagi antennae (Adams et al. 2004a). Survey coverage was concentrated over SBCH, with wide-ranging surveys flown from San Nicolas Island (33°30′N, 119°30′W) to Point Reyes (38°00′N, 123°00′W) to search for missing individuals in areas previously documented as offshore auklet habitat during breeding and postbreeding dispersal (Santa Rosa Ridge, Point Buchon; K. Briggs et al. unpubl. report, Institute of Marine Sciences, University of California, Santa Cruz, 1981; Adams et al. 2004a; Fig. 1).

We used a set of 930 auklet locations to establish a minimum convex polygon (MCP) area using ARCVIEW (ESRI, Redlands, California) with the Animal Movement Extension (Hooge and Eichenlaub 1997). Serial locations among individuals were separated by a minimum of ~24 h, and we assumed that each daily location was independent because auklets returned to their colony

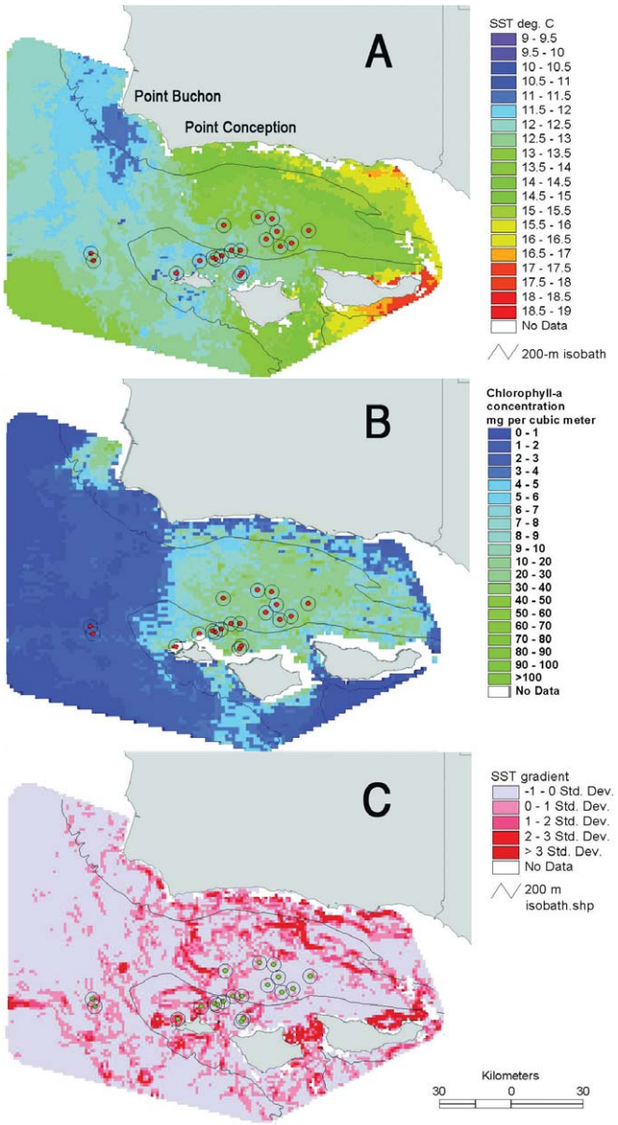

FIG. 2. Ocean habitat within the foraging area of Cassin's Auklets. (A) Advanced Very High Resolution Radiometry sea surface temperature (SST) data from the National Oceanic and Atmospheric Administration (°C; 5-day composite average, 30 April–4 May 2000), showing the infusion of cool, nutrient-rich water (green-blue) upwelled north of Point Conception. Cool waters generally flow toward the southeast through the southern Santa Barbara Channel (SBCH) adjacent to the four main Channel Islands. Warmer, less nutrient-rich waters (yellow-orange) enter the northern SBCH from the southeast. (B) SeaWiFS-derived surface chlorophyll-*a* concentration (mg m^{-3}; 8-day composite average, 27 April–4 May 2000), showing a region of elevated concentration (green) within the central SBCH. (C) GIS-derived SST gradients (depicted as SD of the mean foraging area value) from data in A; strong gradients demarcate the boundary where cool upwelled waters from the north meet warm, stratified waters from the south. (A–C) Dots represent auklet locations detected on 4 May 2000, and circles around dots are 4-km buffers used to select environmental variables for auklets in our analyses.

each night (see White and Garrott 1990). The polygon perimeter was increased by adding a 9-km buffer to account for habitats associated with boundary locations. The polygon represented the total area (12,025 km^2) available to auklets provisioning chicks on Prince Island (hereafter "foraging area"; Fig. 1). We consider the MCP geometry the best representation of available foraging area because previous analyses showed that a relatively stable foraging area persisted throughout the three seasons (Adams et al. 2004b). The MCP is not intended to reflect individual or population-level space-use patterns, but only the ocean habitat available to auklets that provisioned chicks at Prince Island.

Ocean habitat parameters.—We used the image-compositing software programs CWCOMPOSITE and CWFTOARC (CoastWatch 2005) to create 5-day, pixel-averaged composite rasters (1.1 km^2 pixel resolution) from Advanced Very High Resolution Radiometry (AVHRR) to measure SST (°C; National Oceanic and Atmospheric Administration–National Environmental Satellite, Data, and Information Service 2005). We used nighttime satellite overpasses to maximize cloud-free imagery and to minimize variability in SST caused by surface warming during the day.

We also obtained level-2 chl-*a* concentrations (mg m^{-3}) derived from daily Sea-viewing Wide Field-of-view Sensor (SeaWiFS) images (Institute for Computational Earth System Science, University of California, Santa Barbara). We used SEADAS, version 4.0 (NASA Goddard Space Flight Center 2001), to create pixel-averaged composite rasters (1.1 km^2 pixel resolution, isotropic cylindrical equidistant projection) of surface chl-*a* concentration. We used 8-day composite periods to maximize cloud-free coverage while maintaining synoptic coverage with AVHRR satellites, which had more frequent overpasses.

We extracted location-based habitat variables using geographic information systems (ARCVIEW, version 3.2, and ARCINFO; ESRI). First, we generated 4-km-radius circles centered on auklet and random point locations (Fig. 2). The 4-km radius corresponded to the nominal accuracy of our locations (Adams et al. 2004a). Second, we generated two rasters each from 5-day composites of SST and 8-day composites of chl-*a*: mean temperature anomaly (SST_{anom}), maximum temperature gradient (SST_{grad}), mean chl-*a* concentration anomaly (mg m^{-3}; CHL_{anom}), and maximum chlorophyll gradient (CHL_{grad}). To maximize available (i.e., cloud-free) satellite data for SST and chl-*a*, we created composite rasters by averaging SST pixel values during the 4 days (7 days for chl-*a*) preceding and including the telemetry survey day. We considered this appropriate because foraging auklets likely experienced preceding oceanographic conditions before they were located on the date equal to the final composite-day. For each composite raster, we calculated SST_{anom} and CHL_{anom} by subtracting the mean SST and chl-*a* values for the foraging area from each individual pixel value. To calculate SST_{grad} and CHL_{grad}, we generated gradient rasters using the "derive slope" function (ARCVIEW Spatial Analyst Extension). This function calculated the percent slope of a least-squares-plane fit through a roving 3 × 3 pixel-window (i.e., 10.9 km^2) that moved pixel-by-pixel across each SST and chl-*a* composite raster. The corresponding value for the window, representing the gradient, was ascribed to the center pixel, resulting in composite rasters of SST and chl-*a* gradients (1.1 km^2 pixel resolution; Burrough 1986). For each circle (auklet and random), we extracted two variables: the mean SST_{anom} value

and the maximum SST_{grad} value. Depending on cloud cover, the maximum number of pixel values per circle was 25.

Bathymetric data (R. G. Ford Consulting unpubl. data; 100 m^2 pixel resolution, depth ± 10 m) included mean water depth (Z; m) and linear distances (km) from each point (auklet and random) to two static geographic features, the colony ($DIST_{colony}$) and the 200-m isobath ($DIST_{200}$). The latter demarcates the contour where bathymetry falls off rapidly (i.e., the outer edge of the insular and continental shelves).

Statistical analyses.—We examined effects of habitat variables on auklet habitat use within the foraging area by modeling differences between auklet presence (auklet location) and pseudo-absence (random locations) in relation to the suite of environmental variables described above using matched-pairs logistic regression (Hershey et al. 1998, Ormsbee and McComb 1998, Compton et al. 2002). Matched-pairs regression can account for changing environmental conditions and therefore is well suited for studies in which habitat use is expected to vary according to daily changes within the available habitat (Compton et al. 2002). The response variable for each pair was coded as 1 for the auklet location and 0 for the random location. The probability of locating an auklet (p) associated with k location environmental variables ($X_1, \ldots, X_k$) was modeled as the log-transformed odds ($\log[p/1 - p]$) set equal to a linear function of the environmental variables as follows: $\log(p/1 - p) = \beta_0 + \beta_1 X_1 + \cdots + \beta_k X_k$. However, the pairing of random locations with auklet locations precludes unbiased estimates of the log odds. When variables at random locations are subtracted from matching variables at auklet locations, the model for this difference is the log odds ratio,

$$\log\left(\frac{p_A/1-p_A}{p_R/1-p_R}\right)=\beta_1 X_1^* + \cdots + \beta_k X_k^*$$

where p_A and p_R are the respective probabilities of presence at auklet and random locations, and X_i^*, $i = 1, \ldots, k$, is the paired difference between auklet and random location covariates (Agresti 2002). Thus, we analyzed these matched-pairs data using logistic regression with no intercept (β_0) to obtain unbiased estimates of $\beta_1 \ldots \beta_k$. By exponentiation of both sides of the model equation, the odds of an auklet location occurring in a particular location changes by a factor of $\exp(\beta_i)$ for each unit increase in the covariate X_i^*. We exponentiated the 95% Wald-based confidence intervals (CI) for β_i to calculate CI for $\exp(\beta_i)$. The matched-pairs logistic regression analyses can identify important environmental habitat variables and their effects on the odds of use, but not the statistical odds themselves (Keating and Cherry 2004).

Of 930 total auklet locations obtained during tracking, 487 (52%) were associated with a complete suite of habitat measurements available for modeling. After excluding 100 randomly selected auklet–random location pairs included in preliminary exploratory analyses, we used the remaining 387 (42%) location pairs for our final modeling. Because overfitting is a major concern when applying logistic regression models to data containing rare events, Hosmer and Lemeshow (2000) suggested that there should be a minimum of 10 events per model parameter (in the present study, an event is an auklet–random location pair). Our final data set exceeded the recommended minimum ($10 \times k$) number of observations for logistic regression models. For example, a model with five parameters (maximum in our study) would require at least 50 observations; therefore, we considered 387 paired locations to be sufficient.

We used Akaike's information criterion (AIC; Akaike 1973) and Akaike weights (w) to compare models (Burnham and Anderson 2002). We ranked the model with the lowest AIC as best, and we used differences in AIC between that model and every other model (ΔAIC) to identify competing models (Burnham and Anderson 2002).

We developed three *a priori* candidate model sets (Burnham and Anderson 2002) to evaluate effects of SST, chl-*a*, their gradients, bathymetry, and Julian day period (JDP) interactions on the at-sea distribution of auklets. Auklets nesting at colonies are restricted to foraging from a well-defined central place. Therefore, habitat-use models should account for habitat availability, defined in part by foraging range, by including distance from the colony to the foraging site as a covariate (Rosenberg and McKelvey 1999). To control for distance from the colony, all candidate models included $DIST_{colony}$. Because foraging ranges among auklets have been shown to be variable (Obst et al. 1985, Adams et al. 2004a, Boyd et al. 2008), we assumed *a priori* that distance to colony would be an important constraint that affected habitat selection. By including $DIST_{colony}$ and assuming that we used a robust measure of available area, we could examine $DIST_{colony}$ in relation to the other variables. In all three sets of analysis, the univariate model ($DIST_{colony}$) served as a reference for AIC ranking; high ranking of $DIST_{colony}$ alone would indicate little support for the remaining variables when predicting auklet occurrence. Although SST and chl-*a* within the foraging area are variable, chl-*a* maxima generally occur during early spring and are followed by minima later in summer (Kahru and Mitchell 2001). Furthermore, taxonomic composition of food delivered to chicks also differed between early and late chick rearing (Adams et al. 2004b). We constructed a categorical variable to indicate early and late JDP defined by the midpoint of the colony chick-rearing period in each year (Adams et al. 2004b) to examine potential intra-seasonal differences in conditions within the foraging area. We examined intra-seasonal effects by including JDP interaction terms. Models in candidate set 1 included SST_{anom} or CHL_{anom} or both, and additional models included JDP interaction effects with these anomalies. Candidate set 2 was similarly constructed, except that it included gradients instead of anomalies. Candidate set 2 also included a model containing both CHL_{anom} and CHL_{grad}. Candidate set 3 included a series of nested models starting with $DIST_{colony}$ only, then increased in complexity to successively include $DIST_{200}$, depth (Z), CHL_{anom}, and finally JDP interaction with Z. CHL_{anom} was the only biotic variable examined and, therefore, was retained in each of the three sets, assuming that primary auklet prey (krill) availability might be most influenced by near-surface chl-*a* concentrations (Ressler et al. 2005). We calculated Nagelkerke's generalized R^2 to assess the goodness-of-fit for all models (Nagelkerke 1991, SAS Institute 2004). All values are expressed as means ± SE, unless indicated otherwise.

RESULTS

Auklet telemetry and ocean environment within the foraging area.—We recorded 346 locations (30 auklets) in 1999, 435 locations (26 auklets) in 2000, and 149 locations (24 auklets) in 2001.

Auklets foraged within 12,025 km^2 over the continental shelf-slope domains, primarily within the western SBCH between Santa Cruz Island and Point Conception (Fig. 1). Mean SST during the chick-provisioning period and throughout the foraging area differed among years (analysis of variance [ANOVA]: $F = 40.6$, df = 2 and 58, $P < 0.001$) and between early and late chick-provisioning periods (ANOVA: $F = 15.5$, df = 1 and 58, $P < 0.001$, nonsignificant interaction). Sea surface temperature increased by about 1°C year^{-1} (11.8 ± 0.1°C in 1999, 13.1 ± 0.1°C in 2000, and 13.8 ± 0.2°C in 2001), and the late period in each year was about 0.5°C warmer than SST in the early period. Within 5-day SST composite periods during both early and late periods in all years, auklet locations consistently occurred in water that was cooler than the mean SST of the entire foraging area (auklet location values are anomalies from the 5-day foraging area mean; early 1999: −0.2 ± 0.02°C, late 1999: −0.4 ± 0.04°C; early 2000: −0.6 ± 0.04°C, late 2000: −0.2 ± 0.03°C; early 2001: −0.3 ± 0.1°C, late 2001: −0.4 ± 0.1°C).

Mean chl-*a* concentration throughout the foraging area during chick provisioning varied among years (ANOVA: $F = 15.8$, df = 2 and 80, $P < 0.001$; significant year * period interaction, $P < 0.001$). Chlorophyll-*a* concentrations were greater in early 2001 (7.2 ± 0.9 mg m^{-3}) than in late 2001 (2.6 ± 0.3 mg m^{-3}). Chlorophyll-*a* concentrations were least in 1999 (2.4 ± 0.2 mg m^{-3}), greater in 2000 (4.5 ± 0.4 mg m^{-3}), and greatest, but more variable, in 2001 (5.1 ± 0.7 mg m^{-3}). With the exception of late 1999, auklet locations within 8-day chl-*a* composite periods occurred in waters that were more chlorophyll-rich than the foraging-area mean (auklet location values are anomalies from the 8-day foraging area mean; early 1999: 0.2 ± 0.3 mg m^{-3}, late 1999: −0.8 ± 0.1 mg m^{-3}; early 2000: 5.4 ± 1.1 mg m^{-3}, late 2000: 4.5 ± 0.3 mg m^{-3}; early 2001: 10.9 ± 2.1 mg m^{-3}, late 2001: 0.01 ± 0.27 mg m^{-3}.

Auklets were located 17 ± 10 [SD] km from their colony in early 1999 (n = 166 locations), 13 ± 7 [SD] km in late 1999 (n = 180 locations), 20 ± 11 [SD] km in early 2000 (n = 148 locations), 19 ± 11 [SD] km in late 2000 (n = 287 locations), 16 ± 9 [SD] km in early 2001 (n = 92 locations), and 24 ± 23 [SD] km in late 2001 (n = 57 locations). The proportions of auklet locations on either side of the 200-m isobath that separates insular and mainland shelf areas (<200 m depth) from deeper offshore and basin areas were similar; 63% of auklet locations were in water <200 m deep in 1999 (202 ± 180 [SD] m, n = 346 locations), 52% in 2000 (261 ± 202 [SD] m, n = 435 locations), and 56% in 2001 (272 ± 285 [SD] m, n = 149 locations).

*Influences of sea surface temperature and chlorophyll-*a *on auklet locations at sea.*—The distribution of auklet locations was nonrandom and was influenced by several environmental parameters. Ranked candidate models that included SST_{anom}, CHL_{anom}, $DIST_{colony}$, and JDP interactions (set 1) indicated that the best model (lowest AIC value) for discriminating between auklet locations and random locations included SST_{anom} (parameter estimate, β = 0.79 ± 0.30) and CHL_{anom} (β = 0.11 ± 0.04). Two competing models ($\Delta AIC_i \leq 2$) both included CHL_{anom} and SST_{anom} interaction terms with JDP, but the top-ranked multivariate model without interactions was more than twice as likely, on the basis of AIC weights, to rank as the best model (Table 1). Using this model, the odds ratio for SST_{anom} (2.21, 95% CI: 1.24–3.95) indicated that the odds of a telemetry-derived auklet location occurring in a particular location increased by 121% for each 1°C increase in SST_{anom} (i.e., auklets were more likely to be located in warmer surface waters after accounting for CHL_{anom} and, especially, $DIST_{colony}$). The odds ratio for CHL_{anom} (1.12, 95% CI: 1.04–1.20) indicated that the odds of a telemetry-derived auklet location occurring in a particular location increased by 12% for each increase of 1 mg m^{-3} in CHL_{anom} (i.e., auklets were more likely to be located in water with greater chl-*a* concentration). The univariate null model $DIST_{colony}$ ranked last.

*Association of temperature and chlorophyll-*a *gradient with auklet locations at sea.*—Ranked candidate models that included SST_{grad} and CHL_{grad}, CHL_{anom}, $DIST_{colony}$, and JDP interactions (set 2) indicated that the best model (lowest AIC value) for discriminating between auklet locations and random locations included CHL_{anom} (parameter estimate, β = 0.25 ± 0.06) and CHL_{grad} (β = −3.17 ± 0.94; Table 2). The top-ranking multivariate model was 17× as likely as the next-highest model to rank as the best model on

Table 1. Habitat models used to explain differences between Prince Island Cassin's Auklet locations (n = 387) and paired random locations (n = 387) in relation to anomalies in sea surface temperature (SST) or chlorophyll-*a* concentration, 1999–2001. See text for definitions of environmental parameters. All models contain $DIST_{colony}$, and "*JDP" indicates an interaction with Julian day period (JDP). The null model is $DIST_{colony}$ alone. The generalized R^2, Akaike's information criterion (AIC) values, the difference in AIC values between the *i*th model and the model with the lowest AIC value (ΔAIC), and the percentage Akaike weights (Percent) are presented for each model.

Model effects	R^2	K	AIC	ΔAIC	Percent
SST_{anom}, CHL_{anom}	0.86	3	145.72	0.00	50.65
SST_{anom}, CHL_{ANOM}, CHL_{ANOM}*JDP	0.86	4	147.32	1.60	22.73
SST_{anom}, CHL_{anom}, SST_{anom}*JDP	0.86	4	147.70	1.98	18.83
CHL_{anom}	0.85	2	150.76	5.04	4.07
CHL_{anom}, CHLANOM*JDP	0.85	3	152.60	6.88	1.62
SST_{anom}	0.84	2	152.90	7.18	1.40
SST_{anom}, SST_{anom}*JDP	0.84	3	154.75	9.03	0.55
No anomaly variables (null model)	0.84	1	157.32	11.60	0.15

Table 2. Habitat models used to explain differences between Prince Island Cassin's Auklet locations (n = 387) and paired random locations (n = 387) in relation to sea surface temperature (SST) and chlorophyll-*a* (CHL) concentration gradients, 1999–2001. See text for definitions of environmental parameters. All models contain $DIST_{colony}$, and "*JDP" indicates an interaction with Julian day period (JDP). See Table 1 for further details.

Model effects	R^2	K	AIC	ΔAIC	Percent
CHL_{anom}, CHL_{grad}	0.86	3	139.73	0.00	99.97
No gradient variables (null model)	0.84	1	157.32	17.58	0.01
SST_{grad}	0.84	2	159.15	19.42	0.01
CHL_{grad}	0.84	2	159.29	19.56	0.01
SST_{grad}, SST_{grad}*JDP	0.84	3	160.96	21.23	0.00
SST_{grad}, CHL_{grad}	0.84	3	161.12	21.39	0.00
CHL_{grad}, CHL_{grad}*JDP	0.84	3	161.29	21.56	0.00
SST_{grad}, CHL_{grad}, SST_{grad}*JDP	0.84	4	162.95	23.22	0.00
SST_{grad}, CHL_{grad}, CHL_{grad}*JDP	0.84	4	163.12	23.39	0.00

Table 3. Habitat models used to explain differences between Prince Island Cassin's Auklet locations (n = 387) and paired random locations (n = 387) in relation to bathymetric variables $DIST_{200}$, Z, and CHL_{anom}, 1999–2001. See text for definitions of environmental parameters. All models contain $DIST_{colony}$, and "*JDP" indicates an interaction with Julian day period (JDP). See Table 1 for further details.

Model effects	R^2	K	AIC	ΔAIC	Percent
CHL_{anom}	0.64	2	150.76	0.00	71.14
$DIST_{colony}$*JDP, CHL_{anom}	0.64	3	152.76	2.00	26.17
No bathymetric variables (null model)	0.63	1	157.32	6.56	2.68
CHL_{anom}, Z	0.25	2	430.14	279.37	0.00
Z, Z*JDP, CHL_{anom}	0.25	3	432.08	281.32	0.00
CHL_{anom}, DIST200	0.21	2	449.14	298.38	0.00
CHL_{anom}	0.17	1	468.52	317.75	0.00

the basis of AIC weights. Within model set 2, AIC did not identify any competing models (i.e., no models with ΔAIC ≤ 2). Using the top-ranked model, the odds ratio for CHL_{anom} (1.28, 95% CI: 1.14–1.44) indicated that the odds of an auklet location occurring in a particular location increased by 28% for each increase of 1 mg m^{-3} in CHL_{anom}. The odds ratio for CHL_{grad} (0.04, 95% CI: 0.01–0.26) indicated that the odds of an auklet location occurring within the colony-based foraging area decreased by 96% for each percent-unit increase in CHL_{grad} (i.e., auklets tended to occur in regions with greater surface chl-*a* concentrations and were not associated with strong chl-*a* gradients). The univariate null model $DIST_{colony}$ ranked second, and there was little support for any models that included interactions with JDP (Table 2).

*Association of water depth, underwater topography, and chlorophyll-*a *with auklet locations at sea*.—Ranked candidate models that included Z, $DIST_{200}$, CHL_{anom}, $DIST_{colony}$, and JDP interactions indicated that the best model (lowest AIC value) for discriminating between auklet and random locations included CHL_{anom} (parameter estimate, β = 0.09 ± 0.03; Table 3). A second competitive model (ΔAIC_i = 2.0) included $DIST_{colony}$*JDP and CHL_{anom}. The univariate null model $DIST_{colony}$ ranked third (ΔAIC_i = 6.56). The top-ranked multivariate model was more than 2× as likely as the next-highest model to be the best model on the basis of Akaike weights (Table 3). Using the top model, the odds ratio for CHL_{anom} (1.10, 95% CI: 1.03–1.17) indicated that the odds of an auklet location occurring in a particular location increased by 10% for each increase of 1 mg m^{-3} in CHL_{anom} (i.e., auklets tended to occur in regions with greater surface chl-*a* concentrations).

Discussion

We found that habitat use by radiomarked auklets was influenced by both dynamic (satellite-sensed oceanography) and static (bathymetry) habitat variables within their foraging area. After controlling for distance to the colony, the logistic models predicted that occurrences of auklets were improved by including five environmental variables: SST, chl-*a* concentration, chl-*a* gradient, distance to the 200-m isobath (shelfbreak), and depth. The SST gradient was the only factor that did not improve model ranking. Although distance to the colony alone never ranked as competitive with the top model selections, this factor likely was important for explaining variability, as evidenced by appreciably high generalized R^2 values in the logistic response of auklet presence. This was expected, because auklets were constrained to return to their colony to feed chicks. Hence, provisioning adults should minimize their energy expenditure by traveling shorter distances, provided that enough prey were available close to their colony (Obst et al. 1985, Adams et al. 2004b, Boyd et al. 2008).

The locations of provisioning auklets were related to habitat variables, including SST and chl-*a* concentration, which have been shown by others to correlate with prey availability (i.e., chlorophyll concentration and zooplankton density; Ressler et al. 2005). Auklets from Prince Island were consistently located in cooler waters compared with the mean available, in part because SST also tended to be cooler closer to their colony during the spring–summer upwelling period (Pearson's r = 0.382, P < 0.0001; Fig. 2A; see also Harms and Winant 1998). After controlling for distance to colony, however, auklets were more likely to occur in relatively warmer, more chlorophyll-rich waters. Most auklets occurred in warmer waters when near their colony (i.e., not the coldest, most recently upwelled waters), yet auklets were more likely to occur in cooler waters when located farther from their colony (i.e., where temperatures generally are warmer). Briggs et al. (1988) also found that auklets located downstream from the upwelling area off Point Conception avoided the coldest, most recently upwelled waters in favor of slightly warmer waters with greater surface chlorophyll concentrations.

Although densities of surface feeders are expected to be greater in areas with increased frontal densities, presumably because physical processes associated with fronts concentrated suitable prey near the surface (Spear et al. 2001, Ballance et al. 2006), auklets (which feed near, but not at the surface) in our study did not appear to be associated with, nor did they seem to avoid, SST fronts. Given the relatively small scale of the foraging area (i.e., thousands of square kilometers) used by auklets in our study, we likely could not effectively resolve fine-scale frontal associations using radiotelemetry and satellite remote sensing. Circulation patterns in the SBCH are dynamic, and 5-day composite satellite images would tend to "smear" gradients and thereby prevent detection of auklet associations with these features (Breaker et al. 2010, J. Adams and L. Breaker unpubl. data). Furthermore, in high-productivity regions, diving seabird associations with temperature fronts may be less obvious, seasonal, or nonexistent (Hoefer 2000). For example, off the central California coast during the spring–summer upwelling season, Briggs et al. (1987, 1988) found auklets in greater densities in waters with moderate temperature gradients (0.01–0.10°C km^{-1}). Hoefer (2000), however, found that auklet density during the fall oceanic season (nonbreeding period) off California, Oregon, and Washington was not significantly related to distance from strong thermal fronts (≥0.51°C km^{-1}). Briggs et al. (1988) described auklets aggregated along the edges of cool filaments of water with salinity and temperature characteristics consistent with "relict upwelling" near (<20 km) the South Farallon Islands, California, colony. Off the central California and Oregon coast, greater auklet densities were typically associated with the shelfbreak in cooler, but not necessarily the coldest, waters (Ainley et al. 2005).

Large-scale frontal zones (e.g., current boundaries) delineated by ocean color often are recognized as areas of greater biological productivity with increased densities of upper-trophic-level marine predators (Polovina et al. 2000, Hyrenbach et al. 2002, Ream et al. 2005), but few studies have related the distribution of seabirds and other predators directly to small-scale features (e.g., upwelling filament fronts). In our study, auklets were negatively associated with chlorophyll gradients (i.e., fronts). This may have resulted from the birds' nonrandom occurrence in anomalously more chlorophyll-rich areas within their foraging area, rather than avoidance of fronts per se. Briggs et al. (1988) also found that auklets were associated with areas characterized by "moderate" water clarity, but no data exist for evaluating the degree to which auklets in their study were associated with gradients in water clarity or surface chlorophyll concentrations. Because spatial patterns in the location and strength of these fronts is difficult to resolve using 8-day composite SeaWiFS imagery, associations between seabirds and small-scale chlorophyll fronts will remain difficult to measure using remote-sensing data alone.

In two instances, models were selected as competitive when they included the interaction terms with Julian day period (SST_{anom}*JDP and CHL_{anom}*JDP; candidate set 1) and the interaction term between distance to colony and JDP ($DIST_{colony}$*JDP; candidate set 3). In both sets, however, models without JDP interactions were more than twice as likely as those with JDP interactions to be selected as leading models. Model ranking revealed only marginal support for differences among auklet responses to chl-*a*, SST, and $DIST_{colony}$ between early and late chick rearing, which reflected the variable conditions within the western SBCH. Indeed, currents, SST, and chl-*a* concentrations changed rapidly with relaxation in upwelling in this region. Northward dispersal of auklets from the SBCH in 2000 and, especially, in 2001 coincided with the cessation of breeding after relaxation of upwelling off Point Conception, surface heating and stratification, and intrusion of warmer, less chlorophyll-rich waters from the south (Adams et al. 2004a). Auklets in 1999 and 2000 appeared to have experienced more stable foraging conditions throughout the breeding period, which were reflected in longer breeding seasons, greater reproductive success (i.e., proportion of pairs raising two young), and prolonged access to euphausiids (Adams et al. 2004b). By contrast, during 2001, when SST was warmest and chlorophyll concentrations were most variable within the foraging area, their diet contained substantially more fish and auklets also moved farther offshore to utilize deeper waters during late chick rearing (Adams et al. 2004b). Off the Oregon coast, Julian date failed to explain appreciable variability in auklet density between chick rearing (May to early June) and the postbreeding period (late July to early August) (Ainley et al. 2005). Ainley et al. (2005) suggested that variation in auklet densities was most affected by environmental features rather than by variation associated with breeding phenology, migration, or postbreeding dispersal.

Vermeer (1981) recognized that the auklet's range coincides with the distribution of the euphausiid *Thysanoessa spinifera*. Off central and southern California during chick rearing, *T. spinifera* is the most important prey item (Ainley et al. 1990, 1996; Manuwal and Thoresen 1993; Adams et al. 2004b). Abundance of *T. spinifera* in near-surface waters off the California coast increases during cool-ocean periods associated with enhanced upwelling (e.g., La Niña years and negative phases of the Pacific Decadal Oscillation; Smith and Adams 1988, Marinovic et al. 2002). At Prince Island, auklets provisioned chicks predominantly with juvenile *T. spinifera* in all three study years, especially during the late chick-rearing period (Adams et al. 2004b).

Auklets in our study aggregated along the shelfbreak during both early and late chick-rearing periods. Although auklets generally remained closely associated with the shelfbreak, during the late periods in 2000 and 2001, chick provisioning auklets moved slightly (~10 km) offshore into deeper waters with greater chl-*a* concentrations. We suggest that spatial and interannual persistence of radiomarked auklets near the shelfbreak northeast of Prince Island resulted from seasonally predictable prey that were aggregated and made available to auklets foraging in the upper 30 m of the SBCH. For example, cyclonic eddies in the western SBCH concentrate pelagic larval and juvenile fishes (Nishimoto and Washburn 2002) and likely also euphausiids (Fiedler et al. 1998, J. Adams et al. unpubl. data). Off central California, Oedekoven et al. (2001) found that auklets shifted offshore and occurred in lower densities during years with higher SSTs, apparently in response to interannual variation in offshore displacement of the shelfbreak front and associated distribution of euphausiid prey. Radiotelemetry and simultaneous shipboard acoustic zooplankton surveys off Prince Island in late May 2000 revealed that auklet radiolocations and large aggregations of auklets at sea (>50 birds km^{-1}) were associated with near-surface (5–15 m deep) concentrations of juvenile euphausiids (probably *T. spinifera*, based on preliminary examination of net samples and concurrent diet collections at the colony; Adams et al. 2004b) over the Santa Barbara Basin (>200 m deep). Auklets were absent from waters closer to Prince Island (<200 m deep), where acoustic data revealed that the greatest concentrations of zooplankton were concentrated at greater depths (15–45 m) and perhaps were less accessible to foraging auklets from Prince Island, which appear to concentrate diving effort within the upper 15 m (J. Adams et al. unpubl. data). Off the Oregon coast, Ainley et al. (2005) found that auklets were associated with abundant larval and subadult *T. spinifera* and subsurface chlorophyll maxima (Ainley et al. 2005). Ressler et al. (2005; same ship-based transects as Ainley et al. 2005) found that euphausiid aggregations were positively correlated with maximum near-surface (i.e., 5 m deep) chlorophyll concentrations.

Traditionally, studies of habitat associations of seabirds have quantified density distributions of seabirds and their habitats using vessel-based surveys (Briggs et al. 1987; Oedekoven et al. 2001; Ainley et al. 2005, 2009). Although such static "snapshots" provide unique insights into predator aggregation at specific habitat features encountered during surveys, they yield little information about how individuals associate with environmental features over longer periods. In the future, similar approaches to measuring habitat associations over greater time and spatial scales for animals tracked as they move through dynamic oceanographic habitats might provide further insight during other periods in the annual cycle and among a variety of marine species. Such efforts would increase our ability to predict species distributions at sea on the basis of remotely sensed environmental data and enable better identification of important coastal marine habitats (Sydeman et al. 2006). Unraveling the finer-scale patterns according to regional and intraseasonal relationships between physical forcing,

phytoplankton dynamics, euphausiid aggregations, and auklet distributions remains complex.

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