



Relative influence of static and dynamic features on black-footed albatross (*Phoebastria nigripes*) habitat use in central California Sanctuaries

P. E. MICHAEL,^{1,*} J. JAHNCKE² AND
K. D. HYRENBACH¹

¹Hawai'i Pacific University, Marine Science Program at Oceanic Institute, Kalamianaole Hwy, Waimanalo, HI 96795, USA

²Point Blue Conservation Science, Petaluma, CA 94954, USA

ABSTRACT

Effective conservation of highly mobile species requires an understanding of the factors that influence their habitat use patterns, locally and within a large-scale oceanographic context. We characterized the seasonal (chick-rearing, post-breeding) and inter-annual (2004–2008) distribution and abundance of black-footed albatross (*Phoebastria nigripes*; BFAL) along the central California continental shelf/slope using standardized vessel-based surveys. We used a hypothesis-based information-theoretic approach to quantify the relative influence of environmental conditions on BFAL occurrence and abundance by assessing their association with: (i) local static bathymetric features, (ii) local and regional dynamic oceanographic processes, and (iii) seasonal and inter-annual basin-wide variability. While the presence/absence models yielded stronger results than the abundance models, both revealed that static and dynamic features influence BFAL habitat use. Specifically, occurrence was greatest near the shelf-break, particularly in months with strong upwelling. High BFAL densities were associated with Rittenburg Bank, especially during the chick-rearing season, periods of positive North Pacific Gyre Oscillation index and large northern monthly upwelling, evidenced by cool, salty waters in the study area. BFAL aggregation intensity was greatest onshore of the shelf-break (200 m isobath). Behavioral observations reinforced the notion that transiting BFAL are widely dispersed near the shelf-break and concentrate in large flocks of birds sitting on the water farther onshore. These results underscore the need to

consider oceanographic processes at multiple spatial scales when interpreting changes in BFAL dispersion within marine sanctuaries, and highlight the feasibility of implementing bathymetrically defined protected areas targeting predictable BFAL aggregations within these larger management jurisdictions.

Key words: black-footed albatross, Cordell Bank, Gulf of the Farallones, habitat use, information-theoretic approach, National Marine Sanctuaries, *Phoebastria nigripes*, shelf-break

INTRODUCTION

In 2001 the U.S. National Oceanic and Atmospheric Administration (NOAA) initiated a process to review and formulate an updated management plan for three of the current 13 National Marine Sanctuaries (NMS) based on an ecosystem-level approach. As part of this mandate, NOAA aimed to promote a thorough assessment of the habitats and biota present in these sanctuaries and adjacent areas (NCCOS, 2003). A shared objective of the management plans for Cordell Bank and the Gulf of the Farallones National Marine Sanctuaries (CBNMS and GFNMS, respectively) is to 'maintain the natural biological communities, protecting and (where appropriate) restoring and enhancing natural habitats, populations, and ecological processes' (NOAA-CBNMS, 2008; NOAA-GFNMS, 2008). Implementation of this broader ecosystem-based mandate calls for the assessment of the status of protected marine resources within the sanctuaries and in adjacent shelf/slope habitat.

Monitoring data suggest that Cordell Bank is an area of aggregation for three North Pacific albatrosses and occasional southern hemisphere visitors (Stallcup and Terrill, 1996). The black-footed albatross (*Phoebastria nigripes*; BFAL) is the most common albatross species in the region, with the highest densities and a year-round presence (NOAA-CBNMS, 2008; NOAA-GFNMS, 2008).

Despite breeding on islands in the central and western North Pacific, BFAL forage on the central

*Correspondence. e-mail: pmichael@my.hpu.edu

Received 22 September 2012

Revised version accepted 24 May 2013

California shelf during the chick-rearing (April–June) and the post-breeding (July–October) seasons (Hyrenbach *et al.*, 2002; Kappes *et al.*, 2010). As tubenose seabirds (Procellariiformes), a highly specialized order of oceanic birds with far-ranging habits, BFAL use the power of the wind to travel extensive distances while expending relatively little energy through the use of ‘dynamic soaring’ (e.g., Weimerskirch *et al.*, 2000; Shaffer *et al.*, 2004; Suryan *et al.*, 2008; Adams and Flora, 2009). Currently, the BFAL is listed as vulnerable by the International Union for the Conservation of Nature (IUCN), with the major at-sea threats involving ongoing impacts from longline fisheries by-catch, plastic ingestion, and the accumulation of organochlorinated pollutants (Naughton *et al.*, 2007; Arata *et al.*, 2009; BirdLife International, 2012).

Effective protection of albatrosses and other highly migratory species within CBNMS and GFNMS requires adaptive management (e.g., Hyrenbach *et al.*, 2000; Hooker *et al.*, 2011), which includes monitoring the abundance and habitat use patterns of such species during periods of changing oceanographic conditions (e.g., Hyrenbach *et al.*, 2006; Benson *et al.*, 2007). Although vessel-based surveys and satellite tracking have provided a wealth of information on BFAL distributions off California (e.g., Hyrenbach *et al.*, 2002, 2006; Kappes *et al.*, 2010; NCCOS, 2007), important aspects of BFAL habitat use remain poorly understood, including the degree to which the larger-scale physical forcing influences their association with local static and dynamic features and their aggregation. Our analysis aims to facilitate the spatial management of this highly mobile species within existing management jurisdictions by enhancing the understanding of its local dispersion, using information on environmental drivers operating at local, regional and basin-wide spatial scales.

MATERIALS AND METHODS

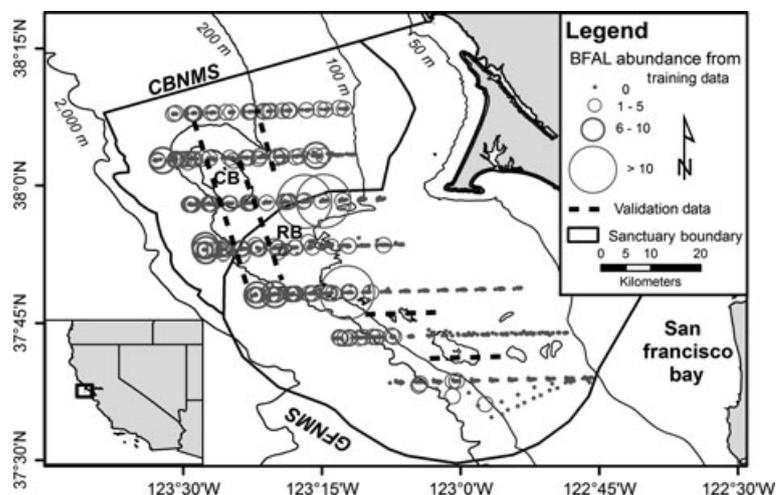
Study region

We modeled the seasonal (chick-rearing, post-breeding) and inter-annual (2004–2008) variation in BFAL distribution and abundance within the productive continental shelf/slope system of central California using vessel-based observations. Surveys were conducted as a part of the ACCESS (Applied California Current Ecosystem Studies) Partnership, and sampled seven east–west parallel lines, from north of Cordell Bank (38°8′N) to south of the Farallon Islands (37°34′N) CA, extending from the upper continental slope (1084 m depth) to coastal waters (50 m depth) within 15 km from the shore. These surveys cover the majority of CBNMS and GFNMS and repeatedly cross the shelf-break (200-m isobath). Three survey lines also cross shallow (<100 m) bathymetric features within the study site: two over Cordell Bank (shallowest depth = 37 m) and one over Rittenburg Bank (shallowest depth = 79 m) (Fig. 1).

This region includes complex physiographic (shelf-break, banks, canyons) and hydrographic features (upwelling plumes, fronts) associated with highly productive habitats (Huyer *et al.*, 1991; Palacios *et al.*, 2006; Jahncke *et al.*, 2008), which are exploited by locally breeding and migratory upper-trophic marine predators (Keiper *et al.*, 2005; Hyrenbach *et al.*, 2006; Yen *et al.*, 2006). A steep shelf-break/slope (200–2000 m depth) region, which delineates the transition between coastal and oceanic waters, is broader to the south (~80 km) and narrower to the north (~45 km).

This region is characterized by strong seasonality in atmospheric and oceanographic conditions, which define three distinct oceanographic seasons: upwelling, oceanic, and Davidson (Hickey, 1979; Largier *et al.*,

Figure 1. Study area showing BFAL abundance from vessel-based surveys during the chick-rearing and post-breeding season, 2004–2008: training data set (circles, birds per 3 km bin) and validation dataset (dashed lines, showing survey effort) are plotted separately. Important bathymetric features include Cordell Bank (CB) and Rittenburg Bank (RB), defined by their 100-m isobath, and the shelf-break (200-m isobath). CBNMS (Cordell Bank National Marine Sanctuary) and GFNMS (Gulf of the Farallones National Marine Sanctuary) boundaries are shown.



1993). The upwelling season spans from early spring (mid-March) to late summer (mid-August), with the strongest upwelling occurring in May and June (NCCOS, 2007; Schwing *et al.*, 1991). Its onset, associated with the strengthening of upwelling-favorable winds, is marked by an abrupt decrease in sea surface temperature (SST; Breaker and Mooers, 1986; Schwing *et al.*, 1991). Episodic, upwelling-favorable winds persist for 3–10 days separated by 3–10-day periods of relaxation or wind direction reversal (Schwing *et al.*, 1991). The oceanic season (mid-August to mid-November) is characterized by relatively extensive periods of calm due to weak, variable winds (NOAA National Centers for Coastal Ocean Science (NCCOS), 2007).

At-sea surveys and BFAL distribution

Trained observers collected BFAL distribution and abundance data using standardized strip transect methods as the vessel cruised at a speed of 18–22 km h⁻¹ (Tasker *et al.*, 1984; Jahncke *et al.*, 2008). One to two observers continuously counted BFAL during daylight hours from the flying bridge of one of three vessels (17.1 m R/V *John H. Martin*, 20.4 m R/V *Fulmar*, 68.3 m NOAA Ship *McArthur II*), with observer eye-heights of 5.3, 5.5, and 14.4 m, respectively, above the surface of the water. Observers recorded the number and behavior (flying, milling, ship-following, sitting/eating) of every BFAL sighted within a 100–300-m strip transect (depending upon the height of the survey platform and the visibility) extending abeam to 90° off of the side of the vessel with the best visibility (i.e., lowest glare) in a field computer with a temporal resolution of 0.1 min. These methods have been used to survey BFAL off California previously (Hyrenbach *et al.*, 2006; Yen *et al.*, 2006).

We did not develop density correction factors using flight direction data because the non-directional flight patterns of ship-following BFAL (circling the vessel) inhibit such an approach. Instead, ship-following birds were recorded the first time they were seen, and ignored thereafter (Hyrenbach, 2001). Furthermore, we identified BFAL transit areas by integrating information on their behavior and spatial aggregation (described below). This approach accounted for potential inflated BFAL densities from ship-following and flying birds.

Point Blue Conservation Science Geographic Information System (GIS) technicians binned the survey data into ~3 km sections. Because shorter survey sections occasionally arose upon arrival at a station, some bins were <3 km. To avoid inflated BFAL densities, we discarded bins <1 km from the analysis.

Accordingly, the minimum (maximum) area surveyed per bin ranged from 0.10 km² (0.90 km²) or 0.10 (0.30) km wide, 1.0 (3.0) km long, with the mean bin area 0.30 km².

Habitat variables

We used 23 variables to characterize temporal variability and environmental conditions: breeding season (Julian day), year (cumulative Julian day), distance to three bathymetric features (shelf-break, Cordell Bank, Rittenburg Bank), mean depth, coefficient of variation (CV) of depth, latitude, mean SST, CV of SST, mean sea-surface salinity (SSS), CV of SSS, zonal (E-W) wind, meridional (N-S) wind, wind modulus, (change in) atmospheric pressure, 6 h and monthly upwelling indices north (39°N) and south (36°N) of the study area, the Pacific Decadal Oscillation (PDO) index, and the North Pacific Gyre Oscillation (NPGO) index (Table S1).

Static habitats. Point Blue GIS technicians derived depth data from California Department of Fish and Game, Marine Region GIS lab 200-m Exclusive Economic Zone (EEZ) bathymetry grids (ftp://ftp.dfg.ca.gov/R7_MR/BATHYMETRY/). We calculated the association of BFAL with the shelf-break (200-m isobath), Cordell and Rittenburg Banks (100-m isobaths) using a macro provided by Point Blue (designed by Michael Fitzgibbon), embedded in ARCVIEW 9.3 GIS software (ESRI, 2009 Redlands, CA, USA). The latitude at the middle of each bin was identified using shipboard GPS units, with an accuracy of 3–10 m.

Dynamic habitats. We included local and regional dynamic habitats in our analysis. For the local features, we calculated the mean and CV of SST and SSS from the vessel's underway data-logging system, with a spatial resolution from 3–10 m (Jahncke *et al.*, 2008).

For the regional environmental variables, we retrieved publicly available wind and upwelling data compiled by the Pacific Fisheries Environmental Laboratory (PFEL, 2009). Wind-scape data included zonal (E-W) and meridional (N-S) wind speed (m s⁻¹) at a 0.25° latitude/longitude spatial resolution and 6-h temporal resolution, derived from blended satellite and buoy data. We calculated the absolute speed (modulus) of the wind from these two components using trigonometry. In addition, we included atmospheric pressure (millibars), derived from a spatial scale larger than the wind data (1° latitude/longitude spatial resolution and 6-h temporal resolution) to represent the regional weather systems during the cruises. Because the movement of weather systems has been

demonstrated to influence seabird distribution (Garthe *et al.*, 2009), we also calculated the change in atmospheric pressure (pressure during survey minus pressure 24 h before survey) to identify bird flux in response to weather systems. Due to the spatial mismatch of the atmospheric data and the vessel-based survey bins, the larger-scale wind and pressure data reflected broader atmospheric mechanisms potentially affecting albatross movement in and out of the smaller study area.

We used upwelling data including 6-h and monthly upwelling index values ($\text{m}^3 \text{s}^{-1} 100 \text{ m coastline}^{-1}$; 1° latitude/longitude resolution) calculated at locations north (39°N , 125°W) and south (36°N , 122°W) of the study area, to identify the phasing and intensity of upwelling during cruises (Keiper *et al.*, 2005; Thayer and Sydeman, 2007). This approach provided complete spatial coverage of the study area and enabled the evaluation of BFAL association with short-term (6-h) and long-term (monthly) upwelling.

We calculated these 23 environmental variables for every 3-km survey bin. Whenever a bin overlapped with multiple time (e.g., 6-h data) and/or space (e.g., 0.25° data) units, we weighted the variable values by the proportion of time the vessel spent within each period and area, assuming a constant cruising speed.

Basin-wide indices. To investigate BFAL association with basin-wide variation, we retrieved monthly PDO (<http://jisao.washington.edu/pdo/PDO.latest>) and NPGO (<http://npggo.o3d.org/data/NPGO.txt>) index values from publicly available online repositories. The PDO (NPGO) is the first (second) empirical orthogonal function, EOF1 (EOF2), of the analysis of the detrended sea surface temperature anomalies (SST height anomalies) north of 20° (25°) latitude north (Mantua *et al.*, 1997; Di Lorenzo *et al.*, 2008). A positive PDO index relates to anomalously warm SST in the California Current System, whereas a positive NPGO index relates to anomalously high salinity, nutrients, and chlorophyll-*a* concentration. The PDO is the dominant influence north of 38° and the NPGO the dominates influence south of 38° . Although a correlative relationship between BFAL dispersion and short-term variation in these basin-wide ocean-atmosphere patterns would not establish a causal link, these indices facilitate the investigation of potential remote forcing of local BFAL dispersion patterns off central California.

Data analysis

Habitat modeling. We modeled BFAL habitat in association with multiple variable classes (temporal, static

and dynamic). To facilitate the application of these results to BFAL spatial management, we adopted a hierarchical approach, whereby we first evaluated BFAL occurrence (presence/absence) and then abundance using only those records where BFAL were present (e.g., Louzao *et al.*, 2006). Both analyses were performed using the 3-km bin data for the same seasons and years but the sample sizes varied (1353 bins for occurrence, 184 bins for abundance).

We followed an information-theoretic approach and chose to model specific hypotheses instead of testing all possible combinations of available variables. We modeled the relative influence of each predictor variable on BFAL occurrence and abundance using generalized linear models with a 'logit' link function for the binomial data (occurrence) and with a 'log' link function for the Poisson data (abundance) (Crawley, 2007). We used this approach to identify which models were the most likely to accurately identify BFAL occurrence/abundance using custom scripts and the MASS package (Venables and Ripley, 2002) for R (R Development Core Team, 2009).

We developed four model sets based on our understanding of the system, to describe BFAL association with static and dynamic habitats, response to temporal variation, and the influence of basin-wide indices. By only evaluating those models with a theoretical link to the specific study objectives, we were able to systematically test hypotheses regarding the influence of the environmental variables on BFAL dispersion. For a complete list of the 160 models compared under this approach and the specific questions they addressed, see Table S2.

In short, we addressed the following four objectives:

Objective 1: BFAL response to temporal variation (45 models). We modeled the influence of year (cumulative Julian day since the beginning of the study) and breeding season (Julian day; to account for variation in survey date) on BFAL occurrence/abundance individually, as their distribution varies on both seasonal and inter-annual temporal scales (Ainley *et al.*, 2005; Ainley and Hyrenbach, 2010; Kappes *et al.*, 2010). To determine if BFAL association with a given feature changed in relation to temporal variation, we also evaluated the interaction between year (and breeding season in separate models) and all other individual habitat variables. For example, the BFAL range may expand during years of varying foraging conditions. Documenting such temporal trends would clarify habitat use patterns and could facilitate the design of seasonal or inter-annual management actions (e.g., time-area closures).

Objective 2: BFAL response to static features (94 models). We modeled static features (distance to three specific bathymetric features, mean and CV of depth) individually and according to their uniqueness; we considered three ‘common features’ (distance to the shelf-break, mean and CV of depth), and two ‘unique features’ (distance to Cordell and distance to Rittenburg Banks). Furthermore, to compare the relative association of BFAL with static versus dynamic features, we evaluated each static variable in combination with hydrographic variables, mean and CV of SST, mean and CV of SSS, and with the interaction of the mean and CV of SST with the mean and CV of SSS, where a high CV of both SST and SSS indicates hydrographic fronts (Smith *et al.*, 1986).

To explore the influence of zonal wind on BFAL association with the shelf-break, we modeled the interaction of the distance to the shelf-break and zonal wind. The potential influence of latitude was modeled individually only. Although different sample sizes prevented a direct comparison with the suite of 160 models, we further explored the relationship of BFAL occurrence and abundance with the shelf-break relative to their onshore–offshore position graphically. This yielded four models of onshore/offshore occurrence/abundance.

Objective 3: BFAL response to dynamic features (19 models). We modeled 13 dynamic features (mean SST and CV of SST, mean SSS, and CV of SSS, 6-h upwelling at 39 and 36°N, monthly upwelling at 39 and 36°N, atmospheric pressure, change in atmospheric pressure, zonal wind, meridional wind, and wind modulus) individually and in ecologically meaningful combinations. We evaluated the interaction of SST (the mean and CV) and SSS (the mean and CV), with individual variables to explore the cumulative influence of variation in these hydrographic parameters. We also modeled the influence of zonal wind and 6-h local upwelling (at 39° and 36°N) on BFAL occurrence/abundance to assess the relationship of wind and instantaneous upwelling with BFAL dispersion. A strong association of BFAL with dynamic features would suggest the utility of integrating dynamic components to current management strategies.

Objective 4: BFAL response to basin-wide fluctuation (2 models). We evaluated the influence of the PDO and NPGO, two basin-wide indices indicative of low frequency signals, on BFAL occurrence and abundance. Identification of BFAL association with either index would suggest that spatial management, even at a local scale, would benefit by considering large-scale

variability beyond the physical extent of the study area. To identify those model(s) or variable(s) with the greatest explanatory power across objectives, we ranked the models using the Akaike information criterion (AIC). In short:

$$\text{AIC} = -2 * \ln(\text{likelihood}) + 2 * K \quad (1)$$

where K is the number of parameters. We also calculated the relative likelihood of all models within an objective using the Akaike weight (w_i ; Burnham and Anderson, 2002) with the following equation:

$$w_i = (\exp(-0.5 * \Delta_i)) \left(\sum_{r=1}^R \exp(-0.5 * \Delta_r) \right)^{-1} \quad (2)$$

where the numerator is the likelihood of a given model (Δ_i is the change in AIC of the given model from the model with the lowest AIC; Δ_r is the change in AIC of each model from the model with the lowest AIC) and the denominator is the sum of all of the relative weights for all models. The sum of the weights of the models being compared = 1, with the most likely model(s) having a weight of ≥ 0.90 .

If > 2 models were needed to achieve this weight (thus complicating the interpretation), the most important variables were identified. This was achieved by summing the weights of all models that included each variable (e.g., the importance of SST = sum of the weights of all models including SST; Burnham and Anderson, 2002). Because each variable was not necessarily used in the same number of models, the sum of the model weights including each variable was first divided by the number of models it was included in (i.e., average weight of all models with a given variable), and then by the average weight of all models across objectives. The resulting ‘scaled average weight’ values indicate the influence each variable had on the average weight of the models it was included in. Using this metric, we identified important variables as having a scaled average weight > 1 , suggesting that the models including that particular variable had a greater weight than the average model (where average Akaike weight of the models compared had a scaled average weight of 1).

When ≤ 2 models were selected, we calculated the linear predictor (LP) using the appropriate constant (intercept) and coefficients from the most likely model, and calculated the probability (Pr) of BFAL occurrence using the inverse of the ‘logit’ link function, so that $\text{Pr}_{\text{occurrence}} = e^{LP} / (1 + e^{LP})$ (Crawley, 1993). To more thoroughly explore our BFAL habitat use models onshore and offshore of the shelf-break, we calculated the Pr of BFAL abundance

using the inverse of the ‘log’ link function, with $\text{Pr}_{\text{occurrence}} = e^{LP}$.

We also evaluated the intensity of BFAL aggregation as a function of the distance from the shelf-break using Green’s index of dispersion (hereafter Gx):

$$Gx = (S^2 * X^{-1}) * \left(\sum x - 1 \right)^{-1} \quad (3)$$

where S^2 is the variance of densities within the line, X is the mean bird density for the line and $\sum x$ represents the sum of bird densities across all bins within the line. Values range from 1 (maximum aggregation: all birds in a single survey bin) to a small negative number equal to $-1 * (\sum x - 1)^{-1}$ (uniform distribution: same density of birds in each bin and variance of 0), with a value of 0 indicating a random distribution (variance equal to the mean) (Green, 1966; Andrew and Mapstone, 1987; Hyrenbach *et al.*, 2006).

Albatross behavior. Following previous studies of BFAL distributions, we considered three behaviors: (i) ship-following, (ii) flying and (iii) sitting on the water/feeding (Hyrenbach, 2001; Spear *et al.*, 2004). We used Gx to assess the degree of aggregation of BFALs engaged in each behavior separately. For this analysis, we used the maximum offshore distance surveyed from the shelf-break (4.32 km) to define five onshore–offshore distance intervals, and compared the distribution of BFAL behaviors across these five regions using G tests.

Model validation. We used a receiver operating characteristic (ROC) curve to evaluate the predictive power of the most likely model(s) selected for BFAL occurrence. ROC curves graphically display the compromise between sensitivity (accurate prediction of presence rate) and false positive (incorrect prediction of a presence rate) as the threshold for defining a presence (Swets, 1988; Pearce and Ferrier, 2000). If the discriminatory power of a model is perfect, its ROC curve will follow the left hand and top axis: sensitivity = 1; false positive rate [or $1 - \text{true negative rate (specificity)}$] = 0, whereas a model completely lacking discriminatory power will display a 45° line (sensitivity = false positive rate) (van Erkel and Pattynama, 1998; Pearce and Ferrier, 2000; Boyce *et al.*, 2002).

The area under the ROC curve (AUC) can be used to quantify a model’s predictive power, where an AUC of 0.5 indicates no predictive power and an AUC of 1 indicates perfect discrimination (Bradley, 1997; Jiménez-Valverde *et al.*, 2009; but see Lobo *et al.*, 2008; Peterson *et al.*, 2008). In cases where the relative cost of an incorrect identification of a presence is

not equal to an incorrect identification of absence, the threshold used to define ‘presence’ can be shifted to balance these costs/benefits (van Erkel and Pattynama, 1998). Here, as with most ecological literature, we assumed an equal ‘cost’ to an erroneous identification of a presence/absence (Pearce and Ferrier, 2000). The value which maximized the sensitivity and specificity for the model predictions was identified by the threshold value at their point of intersection (Louzao *et al.*, 2006, 2009; Jiménez-Valverde *et al.*, 2009).

We used a distinct data set in the ROC curve and AUC analyses (hereafter ‘validation’ data) which was not included in the original analyses (‘training’ data) from which the LP and models were derived. The validation data were collected using identical techniques to the training data (see ‘At-sea surveys and BFAL distribution’ in Materials and methods). The calibration data originated from survey lines which occurred between the replicated training data survey lines or crossed them (Fig. 1). Validation data were collected during the same study period, the same region (latitude, longitude), and depth ranges of the training data. See Table S3 for a comparison of the spatial and temporal coverage of the test and validation data. Because we did not compare classification schemes of our data, standard errors were not presented (Bradley, 1997). All validation computations were run in R (R Development Core Team, 2009) using custom scripts and the ROCR package (Sing *et al.*, 2005).

Predicted habitat. We mapped the predicted BFAL occurrence in ARCGIS 9.3 and calculated BFAL occurrence from the most likely occurrence models using the threshold identified by the ROC curves. We used high resolution bathymetry data provided by the NOAA Centers for Coastal Monitoring and Assessment (<http://ccma.nos.noaa.gov>) and measured distances using the macro described in the ‘Habitat Variables, Static Habitats’ section and created the contours using the Spatial Analyst extension of ARCGIS 9.3. In the predicted occurrence map, we only evaluated areas (longitude and latitude), depths and months included in the training data. For any given cell, the months where BFAL occurrence was predicted by both models were only tallied once.

RESULTS

At-sea surveys and BFAL distribution

Replicate surveys of the study area during the chick-rearing period (April–June) and the post-breeding period (July, September–October) of 5 y (2004–2008) yielded 115 individual survey lines for the training

data and 20 for the validation data (Table S3). Of the 1353 survey bins in the training data, BFAL occurred in 184, with a total of 368 individuals. For the validation data, a total of 83 BFAL occurred in 38 of the 168 surveyed bins. When present, the number of BFAL per survey bin ranged from 1 to 18 (mean = 2.0, SD = 1.03, $n = 184$) in the training data and from 1 to 22 (mean = 2.0, SD = 1.90, $n = 38$) in the validation data. For a description of the cross-correlations between habitat variables, see Table S4.

Habitat modeling: occurrence

The two most likely models relating BFAL presence/absence to habitat characteristics identified high occurrence near the shelf-break, especially during periods of strong upwelling. Specifically, both models included the distance to the shelf-break and either northern (39°N; hereafter ‘primary occurrence model’) or southern (36°N; hereafter ‘secondary occurrence model’) monthly upwelling. The primary and secondary occurrence models accounted for 0.808 and 0.192 of the total likelihood across all models, respectively (Table 1). BFAL occurrence decreased with increasing shoreward distance from the shelf-break (slope = -0.185 ± 0.0240 SE, $P < 0.001$, $df = 1072$) but it did not significantly change offshore of the shelf-break (slope = -0.0116 ± 0.106 SE, $P > 0.9$, $df = 277$; Fig. 2a).

Habitat modeling: abundance and behavior

The ‘most important variable’ was the NPGO index, with the average weight of models including NPGO index being ~ 114 times greater, therefore more likely,

Figure 2. BFAL (a) occurrence and (b) abundance relative to the distance onshore (positive)/offshore (negative) of the shelf-break. Absence depicted with empty circles and presence depicted with filled circles. Solid lines represent occurrence and abundance trends identified by generalized linear models for onshore and offshore data (see ‘Habitat Modeling’ in Materials and Methods). Distances from shelf-break in onshore and offshore habitats were restricted to distances observed in the training data.

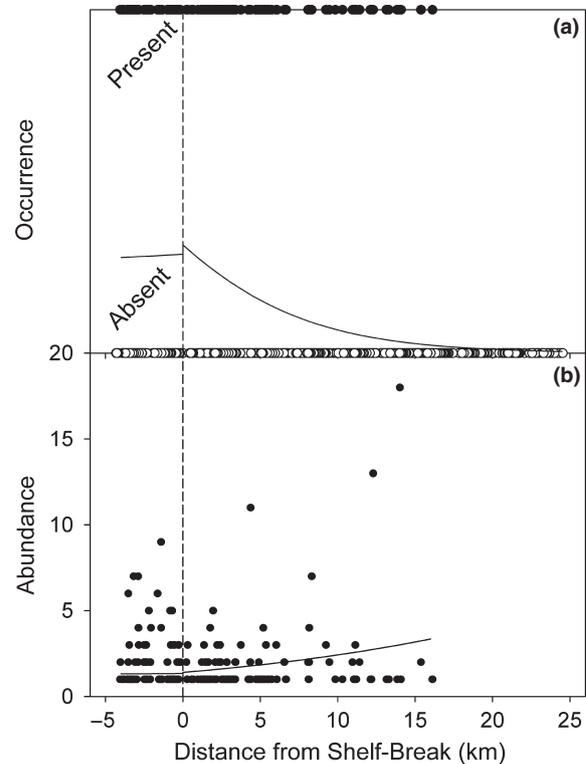


Table 1. Results of the information-theoretic approach to model selection using multimodel inference to identify habitat characteristics relating to BFAL occurrence (presence/absence) and abundance across objectives. The relative likelihood of all models within an objective was calculated using the Akaike weight (Akaike wt.). If more than two models were selected to reach a summed Akaike weight of ≥ 0.9 , the scaled average weight (Scaled avg. wt., > 1) was used to identify important variables (see ‘Habitat Modeling’ in Materials and Methods).

Occurrence		Abundance	
Models	Akaike wt.	Important variables	Scaled avg. wt.
<i>Distance to shelf-break + Monthly upwelling at 39N</i>	0.808	NPGO index	114.3
<i>Distance to shelf-break + Monthly upwelling at 36N</i>	0.192	Monthly upwelling at 39N	3.2
		Year	2.1
		<i>Breeding season</i>	1.9
		<i>SST*</i>	1.5
		<i>Distance to Rittenburg Bank</i>	1.4
		SSS	1.1

Italic (bold) text indicates a negative (positive) relationship with the dependent variable. NPGO, North Pacific Gyre Oscillation; SST (SSS), sea surface temperature (salinity).

*Positive when modeled with the interaction of SST and SSS.

than the average model weight. Positive NPGO index values, indicative of high regional ocean productivity, were associated with high BFAL abundance. Additionally, high BFAL abundance was also associated with strong monthly northern upwelling (39°N), low SST, and high SSS, especially during the chick-rearing season and in the vicinity to Rittenburg Bank. In contrast to the occurrence patterns, BFAL abundance increased with distance from the shelf-break in shoreward habitats (slope = $+0.0543 \pm 0.3410$ SE, $P < 0.001$, $df = 103$), whereas there was no significant relationship with abundance in the offshore habitat (slope = $+0.0034 \pm 0.0649$ SE, $P > 0.9$, $df = 77$; Fig. 2b). Furthermore, BFAL abundance increased with year (i.e., over the course of the study; Table 2).

BFAL aggregation (when present) was most intense onshore (Table 3), where the highest percentage of

Table 2. BFAL abundance models identified by Akaike weight sum ≥ 0.900 .

Model	Akaike weight
<i>Season * NPGO index</i>	0.267
NPGO index	0.183
Year * NPGO index	0.122
Year * Monthly upwelling at 39°N	0.114
<i>Distance to Rittenburg Bank + Mean SST</i>	0.059
<i>Distance to Rittenburg Bank + (Mean SST * Mean SSS) + Mean SSS + Mean SST</i>	0.052
<i>Distance to Rittenburg Bank + Monthly upwelling at 39°N</i>	0.036
<i>Distance to Rittenburg Bank + (Mean SST * Mean SSS)</i>	0.035
Year * Monthly upwelling at 36°N	0.023
Distance to shelf-break + Mean SST	0.008

Italic (bold) text indicates a negative (positive) relationship with the dependent variable or of the interaction (symbolized with *).

Table 3. BFAL offshore and onshore aggregation intensity relative to the distance from the shelf-break (SB).

Habitat	Distance (km) from SB	Gx	No. Bins	Proportion (% presence)	Max. density (birds km ⁻²)	Avg. density \pm SD (birds km ⁻²)
Offshore	0.001–4.32	0.02	279	39.50	30.00	1.49 \pm 3.35
Onshore	0.001–4.32	0.02	238	21.85	13.33	0.78 \pm 1.88
Onshore	4.33–8.64	0.07	246	12.60	36.67	0.70 \pm 3.07
Onshore	8.65–12.97	0.22	182	6.67	43.33	0.53 \pm 3.43
Onshore	12.98–17.29	0.50	246	3.25	60.00	0.35 \pm 3.90
Onshore	17.30–21.61	n.a.	97	0	0	0
Onshore	21.62–24.54	n.a.	65	0	0	0

Gx, Green's index of dispersion. n.a., indicates that the value could not be calculated as no BFAL were observed. SD, standard deviation.

BFAL was observed sitting or feeding on the water (Fig. 3). The opposite pattern was observed for ship-following and flying BFALs (G -test = 26.255, $df = 8$, $P > 0.001$).

Model validation

Validation of the primary and secondary occurrence models indicated a very good (AUC = 0.811) and good (AUC = 0.759; Fig. 4a) model performance, respectively (Swets, 1988). The threshold achieving the best compromise (least difference) between sensitivity and specificity for the primary and secondary occurrence models, assuming an equal weight of these measures, yielded intersection points with a $Pr_{\geq 0.357}$ (primary occurrence model) and 0.326 (secondary occurrence model; Fig. 4b). The primary occurrence model successfully predicted 78.9% (30/38) of

Figure 3. Percent of all BFAL observed in each distance interval onshore (positive) and offshore (negative) of the shelf-break (dashed line), that were engaged in three behaviors: following the ship (dense grids), flying (white) or sitting on the water (fine grids). The total number of BFAL observed is shown in parentheses above distance intervals.

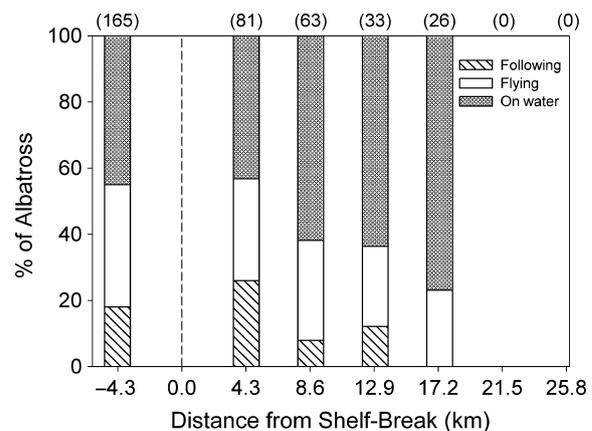
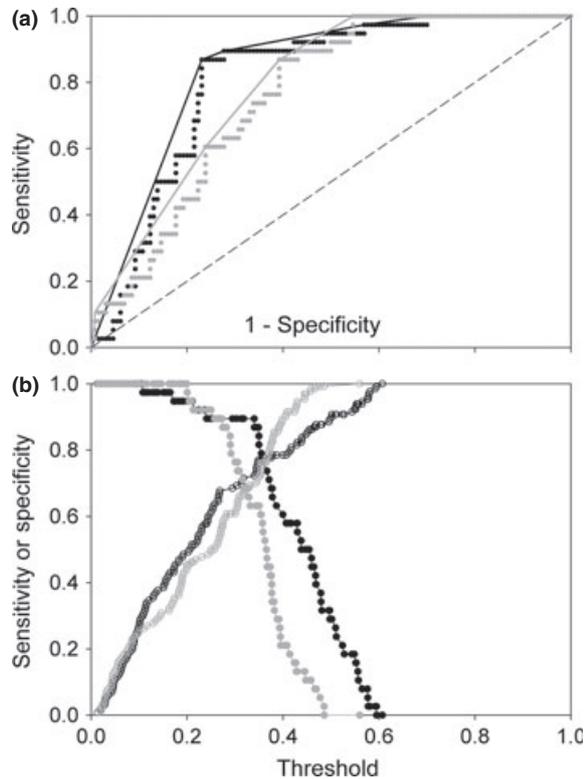


Figure 4. Receiver operating characteristic (ROC) curves showing (a) tradeoff between sensitivity and 1 – specificity, with the dashed 1:1 line indicating a null model with random BFAL distribution, and (b) threshold (point of intersection) at which there is the least difference between sensitivity (empty circles) and specificity (filled circles), identifying a presence using the primary (black) and secondary (gray) BFAL occurrence models. In (a) the points represent the actual data, while the smoothed curve represents the convex hull of those data.



occurrences and 76.9% (100/130) of absences, and the secondary occurrence model correctly predicted 68.4% (26/38) and 67.7% (88/130), respectively. Together, the models correctly defined 94.7% (36/38) of the occurrences and 86.1% (112/130) of the absences from the validation dataset.

Predicted habitat

We developed a total of 38 habitat use predictions using 19 monthly surveys, from which we predicted BFAL occurrence using the primary and secondary models. The two model predictions agreed to a great extent: predicting 7 of the 11 months expected to contain BFAL within the study area, and the 8 months with BFAL absences (Fig. 5).

DISCUSSION

Our models of BFAL dispersion revealed predictable associations with a variety of environmental parameters. While the presence/absence models yielded stronger results than the abundance models, both revealed that static and dynamic features influence BFAL habitat use.

BFAL occurrence

Our finding of BFAL association with the shelf-break, especially during months of strong regional upwelling, reinforces the notion that seabird habitat use results from the interplay between static and dynamic features (e.g., Hunt *et al.*, 1998; Louzao *et al.*, 2006). In particular, we attribute the importance of the shelf-break to enhanced prey aggregation due to local oceanographic processes and the concentration of fishery activities. Shelf-breaks are characterized by water flow conducive

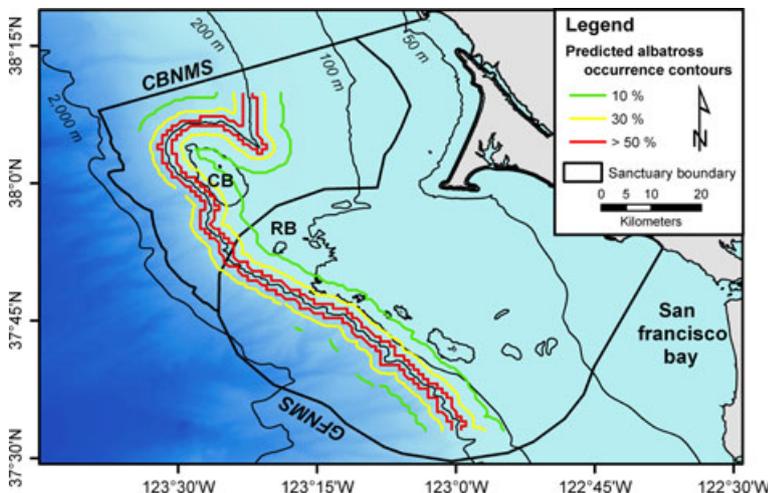


Figure 5. Predicted occurrence contours for BFAL in Cordell Bank and Gulf of the Farallones National Marine Sanctuaries (CBNMS and GFNMS, respectively) during the chick-rearing and post-breeding season, 2004–2008. Important bathymetric features include the shelf-break, defined by the 200-m isobaths, and two shallow banks, Cordell Bank (CB) and Rittenburg Bank (RB), defined by the 100-m isobaths. Of 19 months modeled, 11 predicted BFAL occurrences. The percent occurrence contours indicate two (10%), six (30%) and 10 (>50%) months predicting occurrence.

to the aggregation of zooplankton and larval fish (Simard *et al.*, 1986; Larson *et al.*, 1994). Furthermore, the shelf and shelf-break off central California are important fishing grounds for a variety of species, including ground fish and albacore (Scholz *et al.*, 2006), whose discards could provide food for BFAL. The strong association of BFAL with northern monthly upwelling is likely due to the equator-ward surface flow of the California Current during the study period, which advects water (and weakly swimming plankton and neuston) through the study area (Hickey, 1979; Lynn and Simpson, 1987; Largier *et al.*, 1993). Thus we speculate that, provided there are appropriate conditions of elevated northern upwelling, the shelf-break along the study provides enhanced foraging opportunities for BFAL through physical aggregation of prey at convergence zones at the edge of the upwelling plumes (Briggs *et al.*, 1984; Hyrenbach *et al.*, 2006; Yen *et al.*, 2006).

Our validation indicated good performance by the primary and secondary occurrence models and confirmed the relative likelihood of each model, since the AUC was larger for the primary than for the secondary model. Together, the models created with the validation data accurately identified 94.7% (36/38) of occurrences and 86.1% (112/130) of absences. Although ROC curves tend to overestimate the distributions of rare species by inaccurately predicting their occurrence (e.g., Manel *et al.*, 2001), the 22% occurrence of BFAL in the validation data set does not appear to have impaired the predictive power of the ROC curve.

These findings are unique in their quantification and differentiation of the relative importance of relationships noted or suggested in more qualitative studies (e.g., Briggs *et al.*, 1987). By evaluating a broad suite of habitat characteristics and with the support of our ROC analysis, we validated the importance of upwelling and the shelf-break across the study period.

BFAL abundance

Seasonal and inter-annual shifts in albatross distribution are well noted in the literature (Hyrenbach *et al.*, 2002; Kappes *et al.*, 2010; NOAA National Centers for Coastal Ocean Science (NCCOS), 2007). While the abundance models identified many important habitat variables, BFAL abundance was related to both static and dynamic features. Specifically, seven explanatory variables were related to high BFAL abundance: a large NPGO index (the strongest variable), elevated monthly northern upwelling, the chick-rearing season, low mean SST, high mean SSS, proximity to Rittenburg Bank, and the latter part of the study period, as suggested by the positive relationship with cumulative

Julian day. Although lacking explicit mechanistic links, the significant relationships with many of these variables suggest that high BFAL abundances occur during periods of strong upwelling conditions (Table 1).

The increasing BFAL abundance over the study period and the chick-rearing season reinforces the importance of the existing sanctuaries to foraging BFAL (Hyrenbach *et al.*, 2006; NOAA-CBNMS, 2008; NOAA-GFNMS, 2008). Although we were unable to discern breeders from non-breeders, previous studies have shown that breeding birds from Tern Island (French Frigate Shoals) commuted to the West Coast of the U.S. and foraged within the study area (Hyrenbach *et al.*, 2006). During the post-breeding season, BFAL are known to disperse broadly across the north Pacific, when they range from the Gulf of Alaska to Japan (Springer *et al.*, 1999; Hunt *et al.*, 2005; Hyrenbach, 2008).

High BFAL abundance near Rittenburg Bank may be associated with the enhanced foraging opportunities that steep, submarine features provide, by trapping vertically migrating prey and concentrating weakly swimming planktonic and neustonic organisms in secondary flows associated with turbulent mixing and fronts (Simard *et al.*, 1986; Haney *et al.*, 1995).

BFAL aggregation and behavior

Our analyses of aggregation intensity and behavior suggest that BFAL use shelf-break and onshore habitats differently. Specifically, the high overall occurrence and disproportionate amount of flying/ship-following BFAL near the shelf-break suggests that the birds search for prey (including fisheries discards) through this area as they transit between the breeding colonies and West Coast sanctuaries. The highest BFAL aggregation intensity in onshore waters is in agreement with previous observations of BFAL aggregations during the chick-rearing season, north of the Monterey Bay canyon, and south of our study area (Hyrenbach *et al.*, 2006). The overall low occurrence, but occasionally high abundances, of sitting/feeding BFAL onshore of the shelf-break may represent aggregations of becalmed birds during low wind conditions, or the signature of an earlier feeding event caused by an ephemeral prey patch or attraction to a fishing vessel. Upon the dispersal or vertical emigration of the prey beyond the birds' reach, BFAL may remain in the area digesting or awaiting for favorable wind conditions to resume their search for food. Although vessel survey observations do not enable the tracking of individual bird behavior, previous satellite-tracking studies have documented that BFAL movement rates slow

down (or altogether stop) during periods of low wind (Adams and Flora, 2009).

Following Burnham and Anderson (2002), we developed the scaled average weight to facilitate the comparison between individual variables used in a different number of models, when the model-based approach does not yield clear results. The resulting weights, though un-bounded (< 0 to infinity), are easy to interpret, as the scaled average weight is the proportional increase in likelihood for models containing the variable in question. We hope that other researchers will continue to develop, refine, and standardize techniques addressing the challenges of abundance data for individual species and communities (McGill *et al.*, 2007).

Management applications. Our findings suggest that BFAL dispersion within CBNMS and GFNMS is influenced by features at multiple spatial and temporal scales. Thus, the assessment of BFAL distribution and abundance within sanctuary waters should consider both local and larger-scale environmental drivers.

We developed separate model predictions for the BFAL range (occurrence data) and the areas of aggregation (abundance data, when present). The occurrence data can be used to implement certain diffuse management and monitoring actions, such as fishery observers and vessel-based survey, during the time periods and areas in which the species is expected to occur. While seabird abundance data are highly variable and problematic to model, they augment the inferences from the occurrence models. The abundance models identify areas of aggregation, which can be targeted with special management actions, such as time–area closures (Hyrenbach *et al.*, 2006; Louzao *et al.*, 2006).

Our results will enable NMS managers to refine their definition of the BFAL range and aggregation areas off central California. Additionally, our analysis of BFAL behavior highlights the unique importance of habitats encompassed within this region. Monitoring could be extended to include important features (e.g., the shelf-break) adjacent to sanctuary boundaries, helping managers to identify if BFAL habitat use and aggregation are focused within the sanctuaries or extend past the current boundaries.

Despite the broad range of processes influencing BFAL habitat use and the limited spatial scale of our surveys, the existing CBNMS and GFNMS management framework encompasses important features of BFAL aggregation. Furthermore, it appears that chick-rearing birds commute to these bathymetric features from distant breeding areas (Hyrenbach *et al.*, 2006),

further underscoring the ecological significance of these sanctuary waters. However, because dynamic oceanographic processes also play a role, sanctuary management could be enhanced by developing dynamic approaches, like those used to mitigate loggerhead turtle (*Caretta caretta*) bycatch in driftnet fisheries off California (NMFS, 2002) and in the Hawaii-based longline fishery (Howell *et al.*, 2008).

In particular, the predicted BFAL habitat use patterns can provide a dynamic layer for inclusion in the NOAA coastal and marine spatial planning (CMSP) framework; the sectioning of the marine environment into spatially/temporally explicit areas of compatible and future uses (IOPTF, 2009; Young *et al.*, 2007). To this end, this study has begun to address some of the specific CMSP needs, such as the identification of important static features (Rittenburg Bank) and dynamic processes (upwelling) influencing BFAL dispersion, and the description of the ‘relative ecological importance’ of different habitat features (shelf-break and continental shelf) within CBNMS and GFNMS. The next step of this process would entail overlaying information on the distribution of potential threats over the current understanding of BFAL spatial/temporal dispersion.

Fisheries represent an ongoing threat to BFAL, as bycatch is known to occur in demersal longlines in the Bering Sea, the Gulf of Alaska, and the West Coast of North America (Dietrich and Fitzgerald, 2010; Jannot *et al.*, 2011). In particular, bycatch has been reported by limited-entry sablefish-endorsed vessels operating in the CCS, primarily north of our study area (Jannot *et al.*, 2011). The precautionary management of BFAL interactions with fisheries can afford managers several bycatch reduction options. Managers could empower fishers to reduce their own bycatch by informing them of the location of bycatch-prone areas (Howell *et al.*, 2008) or require the use of bycatch mitigation techniques, including the use of tori-lines or night-setting at times/areas of high BFAL abundance (see Bull, 2007 for more examples). Such condition-specific time–area closures have already been implemented in southern California, where drift gillnet fisheries are temporarily closed during El Niño conditions to reduce the bycatch of loggerhead turtles (first implementation; National Marine Fisheries Service (NMFS), 2002). Similarly, protective measures could be expanded to important shelf-break and shoreward habitats during those seasons (chick-rearing period) and years (elevated localized upwelling) of high BFAL abundance. Furthermore, the consideration of additional regional and basin-wide indices could provide a powerful tool for the spatial management of highly

mobile mega-fauna and ocean productivity related to atmospheric/oceanographic forcing (e.g., Mantua *et al.*, 1997; Benson *et al.*, 2007).

ACKNOWLEDGEMENTS

This work was supported in part by the Applied California Current Ecosystem Studies (ACCESS, www.accessoceans.org) Partnership, an ongoing collaboration between Point Blue, Cordell Bank, and Gulf of the Farallones National Marine Sanctuaries, to support marine wildlife conservation and healthy ecosystems in northern and central California. Funding for ACCESS was provided by Resources Legacy Fund, California Sea Grant, National Fish and Wildlife Foundation, and contributions from a very much appreciated anonymous donor. We thank J. Howar for her assistance and sharing the macro created by M. Fitzgibbon as well as L. Etherington, V. Grundmanis, C. Carstenn, P. J. and J. H. Michael and other reviewers for their constructive comments and feedback on this manuscript. P. E. Michael received a Nancy Foster award for this research, as a part of her master's thesis. We would also like to thank the birds. This is Point Blue contribution number 1937.

REFERENCES

- Adams, J. and Flora, S. (2009) Correlating seabird movements with ocean winds: linking satellite telemetry with ocean scatterometry. *Mar. Biol.* **157**:915–929.
- Ainley, D.G. and Hyrenbach, K.D. (2010) Top-down and bottom-up factors affecting seabird populations in the California current system (1985–2006). *Prog. Oceanogr.* **84**:242–254.
- Ainley, D.G., Spear, L.B., Tynan, C.T. *et al.* (2005) Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep-Sea Res. II* **52**:123–143.
- Andrew, N.L. and Mapstone, B.D. (1987) Sampling and the description of spatial pattern in marine ecology. *Oceanogr. Mar. Biol. Ann. Rev.* **25**:39–90.
- Arata, J.A., Sievert, P.R. and Naughton, M.B. (2009) Status assessment of Laysan and Black-footed Albatrosses, North Pacific Ocean, 1923–2005. *US Geol Surv Scient Investig Rep* 2009-5131, 80 pp.
- Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J.V. and Dutton, P.H. (2007) Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. *Fish. Bull.* **105**:337–347.
- BirdLife International. (2012) *Phoebastria nigripes*. In: IUCN 2012. IUCN Red List of Threatened Species, Version 2012.1 www.iucnredlist.org [accessed 12 March 2013].
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. and Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecol. Model.* **157**:281–300.
- Bradley, A.P. (1997) The use of the area under the ROC curve in the evaluation of machine learning algorithms. *Pattern Recogn.* **30**:1145–1159.
- Breaker, L.C. and Mooers, C.N.K. (1986) Oceanic variability off the central California coast. *Prog. Oceanogr.* **17**:61–135.
- Briggs, K.T., Dettman, K.F., Lewis, D.B. and Tyler, W.B. (1984) Phalarope feeding in relation to autumn upwelling off California. In: *Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships*. D.N. Nettleship, G.A. Sanger & P.F. Springer (eds) Ottawa: Canadian Wildlife Service, pp. 51–58, 61–62.
- Briggs, K.T., Tyler, W. B., Lewis, D.B. and Carlson, D.R. (1987) Bird communities at sea off California: 1975 to 1983. *Stud. Avian Biol.* **11**:1–74.
- Bull, L.S. (2007) Reducing seabird bycatch in longline, trawl and gillnet fisheries. *Fish Fish.* **8**:31–56.
- Burnham, K.P. and Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer Verlag, 488 pp.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Oxford: Blackwell Scientific Publications, 392 pp.
- Crawley, M.J. (2007) *The R Book*. Chichester: John Wiley & Sons Ltd., 942 pp.
- Di Lorenzo, E., Schneider, N., Cobb, K.M. *et al.* (2008) North Pacific gyre oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.* **35**:L08607. doi:10.1029/2007GL032838.
- Dietrich, K.S. and Fitzgerald, S.M. (2010) Analysis of 2004–2007 Vessel-specific Seabird Bycatch in Alaska Demersal Longline Fisheries. Seattle, WA: Alaska Fisheries Science Center, Processed Report 2010-04, 52 pp.
- van Erkel, A.R. and Pattynama, P.M.T. (1998) Receiver operating characteristic (ROC) analysis: basic principles and applications in radiology. *Eur. J. Radiol.* **27**:88–94.
- Garth, S., Markones, N., Hüppop, O. and Adler, S. (2009) Effects of hydrographic and meteorological factors on seasonal seabird abundance in the southern North Sea. *Mar. Ecol. Prog. Ser.* **391**:243–255.
- Green, R.H. (1966) Measurement of non-randomness in spatial distributions. *Res. Popul. Ecol.* **8**:1–7.
- Haney, J.C., Haury, L.R., Mullineaux, L.S. and Fey, C.L. (1995) Sea-bird aggregation at a deep North Pacific seamount. *Mar. Biol.* **123**:1–9.
- Hickey, B.M. (1979) The California Current System-hypotheses and facts. *Prog. Oceanogr.* **8**:191–279.
- Hooker, S.K., Cañadas, A., Hyrenbach, D.K., Corrigan, C., Polovina, J.J. and Reeves, R.R. (2011) Making protected area networks effective for marine top predators. *Endang. Species Res.* **13**:203–218.
- Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H. and Polovina, J.J. (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endang. Species Res.* **5**:267–278.
- Hunt, G.L. Jr, Russel, R.W., Coyle, K.O. and Weingartner, T. (1998) Comparative foraging ecology of planktivorous aulets in relation to ocean physics and prey availability. *Mar. Ecol. Prog. Ser.* **167**:241–259.
- Hunt, G.L. Jr, Drew, G.S., Jahncke, J. and Piatt, J.F. (2005) Prey consumption and energy transfer by marine birds in the Gulf of Alaska. *Deep-Sea Res. II* **52**:781–797.

- Huyer, A., Kosro, P.M., Fleischbein, J. *et al.* (1991) Currents and water masses of the coastal transition zone off northern California, June to August 1988. *J. Geophys. Res. C* **96**:14809–14831.
- Hyrenbach, K.D. (2001) Albatross response to survey vessels: implications for studies of the distribution, abundance, and prey consumption of seabird populations. *Mar. Ecol. Prog. Ser.* **212**:283–295.
- Hyrenbach, K.D. (2008) Applying spatially-explicit measures for albatross conservation. In: T. De Roi, M. Jones & J. Fitter (Eds). *Albatross: Their World, Their Ways*. Buffalo: Firefly Books, pp. 118–120.
- Hyrenbach, D.K., Forney, K.A. and Dayton, P.K. (2000) Marine protected areas and ocean basin management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **10**:437–458.
- Hyrenbach, K.D., Fernández, P. and Anderson, D.J. (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar. Ecol. Prog. Ser.* **233**:283–301.
- Hyrenbach, K.D., Keiper, C., Allen, S.G., Ainley, D.G. and Anderson, D.J. (2006) Use of marine sanctuaries by far-ranging predators: commuting flights to the California Current System by breeding Hawaiian albatrosses. *Fish. Oceanogr.* **15**:95–103.
- Interagency Ocean Policy Task Force (IOPTF). (2009) Interim Framework for Effective Coastal and Marine Spatial Planning. Washington, DC: The White House Council on Environmental Quality, 35 pp.
- Jahncke, J., Saenz, B.L., Abraham, C.L., Rintoul, C., Bradley, R.W. and Sydeman, W.J. (2008) Ecosystem responses to short-term climate variability in the Gulf of the Farallones. *California. Prog. Oceanogr.* **77**:182–193.
- Jannot, J., Heery, E., Bellman, M.A. and Majewski, J. (2011) Estimated bycatch of marine mammals, seabirds, and sea turtles in the 2002–2009 U.S. west coast commercial groundfish fishery. West Coast Groundfish Observer Program, National Marine Fisheries Service. Seattle, WA: Northwest Fisheries Science Center, 104 pp.
- Jiménez-Valverde, A., Diniz, F., de Azevedo, E.B. and Borges, P.A.V. (2009) Species distribution models do not account for abundance: the case of arthropods on Terceira Island. *Ann. Zool. Fenn.* **46**:451–464.
- Kappes, M.A., Shaffer, S.A., Tremblay, Y. *et al.* (2010) Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Prog Oceanogr, Climate Impacts on Oceanic Top Predators CLIOTOP International Symposium* **86**: 246–260.
- Keiper, C.A., Ainley, D.G., Allen, S.G. and Harvey, J.T. (2005) Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. *Mar. Ecol. Prog. Ser.* **289**:285–306.
- Largier, J.L., Magnell, B.A. and Winant, C.D. (1993) Subtidal circulation over the northern California shelf. *J. Geophys. Res. C* **98**: (C10) 18147–18179.
- Larson, R.J., Lenarz, W.H. and Ralston, S. (1994) The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off central California. *Calif. Coop. Ocean. Fish. Invest. Rep.* **35**:175–221.
- Lobo, J.M., Jiménez-Valverde, A. and Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecol. Biogeogr.* **17**:145–151.
- Louzao, M., Hyrenbach, D.K., Arcos, J.M., Abelló, P., Gil De Sola, L. and Oro, D. (2006) Oceanographic habitat of an endangered Mediterranean Procellariiform: implications for marine protected areas. *Ecol. Appl.* **16**:1683–1695.
- Louzao, M., Bécas, J., Rodríguez, B., Hyrenbach, D.K., Ruiz, A. and Arcos, J.M. (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Mar. Ecol. Prog. Ser.* **391**:183–197.
- Lynn, R.J. and Simpson, J.J. (1987) The California current system: the seasonal variability in its physical characteristics. *J. Geophys. Res. C* **92**: (C12) 12947–12966.
- Manel, S., Williams, H.C. and Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* **38**:921–931.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**:1069–1079.
- McGill, B.J., Etienne, R.S., Gray, J.S. *et al.* (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* **10**:995–1015.
- National Marine Fisheries Service (NMFS). (2002) Taking of threatened or endangered species incidental to commercial fishing operations. *Federal Register*, 50 CFR Part 223[Docket 020626163-2160-01; I.D. 061902C] RIN 0648-AQ13 67:183 59243.
- Naughton, M.B., Romano, M.D. and Zimmerman, T.S. (2007) A Conservation Action Plan for Black-footed Albatross (*Phoebastria nigripes*) and Laysan Albatross (*P. immutabilis*), Ver. 1.0, Portland, OR: United States Fish and Wildlife Service, 40 pp.
- NOAA National Centers for Coastal Ocean Science (NCCOS). (2003) A biogeographic assessment off north/central California: in support of the National Marine Sanctuaries of Cordell Bank, Gulf of the Farallones ad Monterey Bay. Phase I – marine fishes, birds and mammals. Prepared by NCCOS's Biogeography Team in cooperation with the National Marine Sanctuary Program. 145 pp.
- NOAA National Centers for Coastal Ocean Science (NCCOS). (2007) A biogeographic assessment off north/central California: in support of the National Marine Sanctuaries of Cordell Bank, Gulf of the Farallones ad Monterey Bay. Phase II – environmental setting and update to marine birds and mammals. Prepared by NCCOS's Biogeographic Branch, R. G. Ford Consulting Co. and Oikonos Ecosystem Knowledge, in cooperation with the National Marine Sanctuary Program. NOAA Technical Memorandum NOS NCCOS 40, 302 pp.
- NOAA-Cordell Bank National Marine Sanctuary (NOAA-CBNMS). (2008) Cordell Bank National Marine Sanctuary final management plan. Prepared as a part of the Joint Management Plan Review (JMPR), Vol. I, 55 pp.
- NOAA-Gulf of the Farallones National Marine Sanctuary (NOAA-GFNMS). (2008) Gulf of the Farallones National Marine Sanctuary final management plan. Prepared as a part of the Joint Management Plan Review (JMPR), Vol. II, 80 pp.
- Pacific Fisheries Environmental Laboratory (PFEL). (2009) ERD live access server. <http://las.pfeg.noaa.gov> [Accessed 12 August 2009].
- Palacios, D.M., Bogard, S.J., Foley, D.G. and Schwing, F.B. (2006) Oceanographic characteristics of biological hot spots in the North Pacific: a remote sensing perspective. *Deep-Sea Res. II* **53**:250–269.

- Pearce, J. and Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* **133**:225–245.
- Peterson, T.A., Papeş, S.M. and Soberón, J. (2008) Rethink receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* **213**:63–72.
- R Development Core Team. (2009) R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, ISBN 3-900051-07-0. <http://www.R-project.org> [Accessed 9 March 2009].
- Scholz, A., Steinback, C., Klain, S. and Boone, A. (2006) Socioeconomic Profile of Fishing Activities and Communities Associated with the Gulf of the Farallones and Cordell Bank National Marine Sanctuaries. Portland, OR: Ecotrust, 136 pp.
- Schwing, F.B., Husby, D.M., Garfield, N. and Tracey, D.E. (1991) Mesoscale oceanic response to wind events off central California in Spring 1989: CTD surveys and AVHRR imagery. *Calif. Coop. Ocean. Fish. Invest. Rep.* **32**:47–62.
- Shaffer, S.A., Costa, D.P. and Weimerskirch, H. (2004) Field metabolic rates of black-browed albatrosses *Thalassarche melanophrys* during the incubation stage. *J. Avian Biol.* **35**:551–558.
- Simard, Y., de Ladurantaye, R. and Therriault, J.-C. (1986) Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Mar. Ecol. Prog. Ser.* **32**:203–215.
- Sing, T., Sander, O., Beerenwinkel, N. and Lengauer, T. (2005) ROCR: visualizing classifier performance in R. *Bioinformatics* **21**:3940–3941.
- Smith, R.C., Dustan, P., Au, D., Baker, K.S. and Dunlap, E.A. (1986) Distribution of cetaceans and sea-surface chlorophyll concentrations in the California Current. *Mar. Biol.* **91**:285–402.
- Spear, L.B., Ainley, D.G., Hardesty, B.D., Howell, S.N.G. and Webb, S.W. (2004) Reducing biases affecting at-sea surveys of seabirds: use of multiple observer teams. *Mar. Ornithol.* **32**:147–157.
- Springer, A.M., Paitt, J.F., Shuntov, V.P. *et al.* (1999) Marine birds and mammals of the western and eastern subarctic gyres of the North Pacific. *Prog. Oceanogr.* **43**:443–487.
- Stallcup, R. and Terrill, S. (1996) Albatrosses and Cordell Bank. *Birding* **28**:106–110.
- Suryan, R.M., Anderson, D.J., Shaffer, S.A. *et al.* (2008) Wind, waves and wing loading: morphological specialization may limit range expansion of endangered albatrosses. *PLoS ONE Suppl.* **3**:e4016. doi:10.1371/journal.pone.0004016.
- Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science* **240**:1285–1293.
- Tasker, M.L., Jones, P.H., Dixon, T. and Blake, B.F. (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* **101**:567–577.
- Thayer, J.A. and Sydeman, W.J. (2007) Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. *Mar. Ecol. Prog. Ser.* **329**:253–265.
- Venables, W.N. and Ripley, B.D. (2002) Modern Applied Statistics with S, 4th edn. New York: Springer, 504 pp.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. and Costa, D.P. (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. B* **267**:1869–1874.
- Yen, P.P.W., Sydeman, W.J., Bogard, S.J. and Hyrenbach, K.D. (2006) Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. *Deep-Sea Res. II* **53**:399–418.
- Young, O.R., Osherenko, G., Ekstrom, J. *et al.* (2007) Solving the crisis in ocean governance; place-based management of marine ecosystems. *Environment* **49**:20–32.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of the data sources and ecological interpretation of the habitat variables evaluated.

Table S2. BFAL occurrence/abundance models developed organized by objective and specific questions they address.

Table S3. Survey effort across the study period (2004–2008) for training and validation data (in parentheses).

Table S4. Cross-correlations of habitat variables within (a) 3 km bins and (b) 6 h time periods.