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Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific

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ABSTRACT

We studied the foraging behavior and marine habitats used by Laysan (*Phoebastria immutabilis*) and Black-footed (*Phoebastria nigripes*) Albatrosses, during four consecutive breeding seasons to investigate whether these marine predators changed habitat preferences, foraging distributions, or both, in accordance with natural interannual variability in the marine environment. We used satellite telemetry to track a total of 37 Laysan and 36 Black-footed Albatrosses during the incubation periods of 2002–2006 at Tern Island, Northwest Hawaiian Islands. First passage time analysis was used to determine search effort of individual albatrosses along their respective tracks, and this metric was then related to oceanographic habitat variables using linear mixed-effects regression. The majority of individuals traveled to pelagic waters of the North Pacific, with Laysan Albatrosses demonstrating a more northwesterly distribution from the breeding colony. Laysan Albatrosses traveled farther, for longer periods, and demonstrated greater interannual variability in trip characteristics than Black-footed Albatrosses. For Laysan Albatrosses, maximum trip distance was negatively correlated with body mass change during foraging and overall breeding success. There was considerable interspecific segregation of foraging habitats, and low overlap of foraging distributions between years. For all years, and both species, sea surface temperature was consistently the most important environmental variable predicting search effort of albatrosses, suggesting that both species use similar environmental cues when searching for prey. In the context of climate variability, our results suggest that Hawaiian albatrosses demonstrate flexibility in foraging strategies and track preferred marine habitats. However, adjusting foraging behavior to climatic variability may have energetic, and subsequent reproductive consequences.

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1. Introduction

Climate variability can have significant impacts on marine ecosystems (McGowan et al., 1998; Walther et al., 2002; Stenseth et al., 2003; Grebmeier et al., 2006; Lehodey et al., 2006), and may present a challenge for marine top predators dependent on patchily distributed prey in the pelagic realm (Schreiber and Schreiber, 1984; Trillmich et al., 1991; Polovina, 1996; Croxall et al., 2002; Crocker et al., 2006; Weise et al., 2006; Costa, 2008). Understanding the mechanisms that link physical forcing to primary production, and, ultimately, to prey abundance and distribution, is critical to predicting how climate variability may impact the physiology, behavior and demography of top predators. As concern increases over the effects of global climate change on species of conservation interest, it is important that we begin to investigate how current patterns of natural climate variability impact such species in order to build predictive models for the future.

For any marine consumer, the search for food occurs within a fluid, dynamic environment where resources are patchily distributed (Mackas and Boyd, 1979; Russell et al., 1992; Fauchald et al., 2000; Weimerskirch, 2007). However, physical features in the ocean environment may stimulate local primary production or serve to aggregate prey resources where they can be efficiently exploited by marine predators (Schneider, 1990; Hunt, 1997; Hunt et al., 1998; Croll et al., 2005; Keiper et al., 2005). By analyzing the movements of top predators, it is possible to learn what environmental features are important in resource acquisition (Kareiva and Odell, 1987; Weimerskirch et al., 1994; Turchin, 1998). Because marine predators forage on patchy prey resources, it is expected that they will modify their behavior to search for food at an effective scale to exploit high-density prey patches (Curio, 1976; Fauchald and Tveraa, 2003). This behavior, known as area-restricted searching, can be deduced from movement patterns,

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thus providing a methodology for discerning environmental characteristics where search effort is concentrated (Kareiva and Odell, 1987; Fauchald and Tveraa, 2003). As increased search effort can lead to increased prey capture in some marine predators, it can be used as a proxy for foraging effort in animals where visual observation of foraging behavior is not possible (Bailey and Thompson, 2006; but see Weimerskirch et al., 2007).

Within the North Pacific Ocean, the subarctic-subtropical transition zone is a region in which several physical features link prey resources to pelagic predators, including eddies and frontal systems (Polovina et al., 2000, 2004; Palacios et al., 2006). The North Pacific Transition Zone (NPTZ) is bounded by the eastward flowing currents of the subtropical and subarctic gyres (Roden, 1991), and exhibits a sharp transition in surface phytoplankton chlorophyll-*a* concentration, a feature known as the Transition Zone Chlorophyll Front (TZCF). This feature, operationally defined as the 0.2 mg m^{-3} surface chlorophyll isopleth (Polovina et al., 2001), has been demonstrated to be an important foraging habitat for loggerhead turtles (*Caretta caretta*) and albacore tuna (*Thunnus alalunga*). Because zooplankton and other actively swimming or buoyant organisms can maintain their position in the front, the resulting prey aggregation serves to attract these higher trophic level predators (Laurs et al., 1984; Olson et al., 1994; Polovina et al., 2000, 2001). Surface convergence along frontal boundaries may also aggregate neustonic or buoyant prey (Olson and Backus, 1985; Franks, 1992; Govoni and Grimes, 1992; Olson et al., 1994), thereby enhancing foraging opportunities.

Mesoscale features such as eddies and meanders also feature prominently in the oceanography of the North Pacific, especially where the high-energy Kuroshio Extension influences the western portion of the NPTZ (Wyrtki et al., 1976; Qiu, 2002; Palacios et al., 2006). Eddies can stimulate primary productivity through localized upwelling and vertical mixing of nutrients (Strass, 1992; McGillicuddy and Robinson, 1997; Davis et al., 2002), as well as aggregating weakly swimming and buoyant prey (Olson and Backus, 1985), making eddies important foraging areas for marine top predators in many ocean systems (Nel et al., 2001; Davis et al., 2002; Polovina et al., 2004; Weimerskirch et al., 2004; Cotté et al., 2007). Because the physical and biological properties of eddies depend on whether the flow is cyclonic or anticyclonic (Mizobata et al., 2002; Palacios et al., 2006), use of these mesoscale features by marine predators can vary depending on eddy characteristics (Haney, 1986; Davis et al., 2002; Hyrenbach et al., 2006). For instance, in a study by Haney (1986), surface-feeding marine birds were found foraging in the cool center of cyclonic eddies, whereas aerial-feeding seabirds used warm water filaments; other studies have demonstrated associations between seabirds and the edges of both cyclonic and anticyclonic eddies (Nel et al., 2001; Weimerskirch et al., 2004; Yen et al., 2006). The overall intensity of eddy activity in a region can also lead to differences in patterns of local enhancement and productivity (Oschlies and Garçon, 1998).

Albatrosses are far-ranging marine birds that depend on vast oceanic ecosystems, many species of which have experienced significant population declines in the last century (IUCN, 2007). The greatest current threats to global albatross populations include interactions with fisheries, particularly as bycatch in longline fisheries (Brothers, 1991; Tuck et al., 2001), and predation at breeding colonies by introduced mammals (IUCN, 2007; Wanless et al., 2007). With many albatross populations in peril, it is critical to understand how additional stressors, including climatic variation, may contribute to population declines (Croxall, 1992; Pinaud and Weimerskirch, 2002; Inchausti et al., 2003). If there are demographic consequences to global climate change, these should be accounted for when modeling albatross population dynamics. Here, we investigated the foraging behavior and marine habitat use of breeding Laysan (*Phoebastria immutabilis*) and Black-footed (*P. nigripes*) Albatrosses at Tern Island, Northwest Hawaiian Islands, over a period of 4 years. We focused on a single stage of the breeding cycle, the incubation period, so that analysis of foraging behavior would be comparable among years. Our goal was to evaluate how natural climatic variability (on interannual scales) influenced the foraging distribution and habitat use of these top marine predators. As both albatross species have demonstrated dramatic declines in breeding success after major El Niño-Southern Oscillation events (ENSO; Dearborn et al., 2001; Seki et al., 2004), a functional understanding of how variability in the marine environment affects albatross foraging behavior will provide insight into how future environmental perturbations, such as global climate change (Walther et al., 2002; Parmesan and Yohe, 2003; IPCC, 2007), are likely to affect these populations.

Both Laysan and Black-footed Albatrosses are known to extensively use the NPTZ while foraging during the breeding season (Fernández et al., 2001; Hyrenbach et al., 2002). They are surface-feeders, foraging within the top meter of the water column, and as such rely on neustonic or vertically migrating prey, as well as carrion and fishing discards (Harrison et al., 1983; Whittow, 1993a,b; Gould et al., 1997). We expected that Hawaiian albatrosses would increase foraging search effort within the NPTZ in response to oceanographic features likely to aggregate buoyant prey, or environmental parameters that have been shown to correlate strongly with their prey species. While Hawaiian albatrosses consume a diverse array of prey items, Ommastrephid squid and flying fish (Exocoetidae) eggs comprise the largest proportion of the Laysan and Black-footed Albatross diet, respectively (Harrison et al., 1983). Previous studies have demonstrated a relationship between catches of Ommastrephid squid and sea surface temperature (SST; Gong et al., 1993; Yatsu et al., 1993; Pearcy et al., 1996), productivity (Ichii et al., 2004), and position relative to the North Pacific Subarctic Frontal Zone (SAFZ; Pearcy et al., 1996). Areas of surface convergence, such as those found near fronts and eddies, can also aggregate algae or floating material which many species of flying fish use as a substrate to attach their non-buoyant eggs with sticky filaments (Breder and Rosen, 1966; Bakun, 2006). Adult flying fish, also prey of Hawaiian albatrosses (Harrison et al., 1983), can be found at the outer edges of rapidly rotating eddies (Johannes, 1981; Bakun, 2006). The habitat relationships of these prey items informed our selection of environmental parameters with which to investigate albatross habitat use. We used SST and primary productivity (PP) to characterize regional thermal and phytoplankton production patterns; latitudinal gradients in SST, proximity to the TZCF, and wind stress curl to describe large-scale frontal characteristics; and eddy proximity, rotation, and regional mesoscale activity to describe local eddy characteristics.

While oceanographic features in the North Pacific demonstrate considerable variability at seasonal, interannual, and decadal time scales (Chai et al., 2003; Bograd et al., 2004), we expected that Hawaiian albatrosses would have the capacity to track dynamic habitats given their wide-ranging foraging movements (Fernández et al., 2001; Hyrenbach et al., 2002). We hypothesized that Laysan and Black-footed Albatrosses would respond consistently to environmental cues in each year of study, even if foraging locations changed. We also hypothesized that in years when birds traveled farther to reach prey resources, there would be associated costs to adult condition and overall breeding success.

2. Study area and methods

2.1. Study area and albatross tracking

We studied the foraging behavior of breeding Laysan and Black-footed Albatrosses during the incubation period at Tern Island (23.87°N, 166.28°W), French Frigate Shoals, Northwest Hawaiian

Islands. Seventy-three adult albatrosses (37 Laysan and 36 Black-footed) were equipped with satellite platform terminal transmitters (30 g Pico-100, Microwave Telemetry, Columbia, MD; and 35 g SPOT4, Wildlife Computers, Redmond, WA) to determine at-sea locations during a single foraging trip (Table 1). Tracking activities were conducted during four consecutive breeding seasons, from 2002–2003 to 2005–2006, between mid-December and the end of January, except in 2003–2004 when tracking was conducted from the end of November until mid-January.

Satellite tags were attached to dorsal feathers with adhesive tape (Tesa®, Hamburg, Germany), and satellite transmissions were downloaded via the ARGOS satellite system (Service ARGOS, Inc., Largo, MD). During all field seasons except 2003–2004, individuals were also equipped with temperature recorders (10 g Lotek LTD 2400, Lotek Wireless, St. John's, Newfoundland) attached to a plastic leg band for use in another study. The combined mass of these devices was less than 2% of total bird's body mass in all cases, well below the recommended limit for studies involving albatrosses (Phillips et al., 2003). Body mass was measured to the nearest 50 g at deployment and retrieval, using a spring-loaded Pesola scale (Pesola AG, Baar, Switzerland). Satellite tags were programmed to transmit continuously every 90 s, with the exception of 19 of the 73 foraging trips, when tags were programmed to use a 6:18 h on:off duty-cycle (11 trips), a 20:4 h on:off duty-cycle (6 trips), or a 9:15 h on:off duty-cycle (2 trips) to conserve battery life on anticipated longer trips. In three instances, the battery on the satellite transmitter failed or the satellite transmitter fell off the bird before completion of the foraging trip. In these cases, only the portion of the trip with satellite coverage was included in subsequent analyses.

Gender was determined from blood samples for 67 of 73 individuals tracked (Fridolfsson and Ellegren, 1999), and from comparison of culmen lengths (Fernández et al., 2001) in the six individuals from which we did not collect blood samples. Age was determined from banding records (Hawaiian Islands National Wildlife Refuge, US Fish and Wildlife Service, Department of the Interior) for 48 of 73 individuals tracked. Reproductive success of Laysan and Black-footed Albatrosses breeding at the Tern Island colony was determined by estimating the total number of chicks fledged and dividing by the total number of eggs laid (data provided by the Hawaiian Islands National Wildlife Refuge, US Fish and Wildlife Service, Department of the Interior) for all 4 years of the study.

2.2. Track analysis

Albatross foraging locations were first delimited by visual observations of departure and arrival times for individuals in the study, or by the first and last satellite-derived locations away from the colony, so that satellite fixes at the breeding colony were not included in the analysis. When exact departure times were unknown, we defined the first satellite-derived location away from the colony as the first position at least 10 km away from the colony site, followed by at least four more positions of this distance or greater. A similar rule was applied to the end of each track.

To remove unlikely locations from the dataset, each track was then filtered using the Iknos Toolkit (Y. Tremblay, *unpubl. program*) for Matlab (The MathWorks, Natick, MA). This toolbox includes several approaches for removing unrealistic locations and was applied as follows: (1) a speed filter was used by calculating transit rates between successive locations and applying a maximum speed limit of 80 km h^{-1} (following Hyrenbach et al., 2002; Suryan et al., 2006) to remove unrealistic flight speeds (Spear and Ainley, 1997); (2) the maximum change in azimuth between successive locations was set to 170° to remove track spikes (Freitas et al., 2008), as large departures from a point of origin close in space to a point of return are likely to be erroneous (Keating, 1994); and (3) the time elapsed between successive fixes was set at a minimum of 10 min to avoid inclusion of location fixes determined from overlapping sets of satellite transmissions, and to avoid inflation of errors in transit rate determination (Hays et al., 2001). This filtering algorithm was applied to all ARGOS locations, regardless of location quality, and resulted in the retention of 80.1% (n = 16,472) of all satellite locations. Tracks were then interpolated to every 10 min using a Bézier curve with $\mu = 0.3$ (following Tremblay et al. (2006)) so that points were equally spaced in time.

Descriptive characteristics of each track were calculated to compare overall behavior of each species in each year. Maximum distance traveled from the colony was calculated using great-circle distances to all ARGOS locations to account for the earth's curvature. Total distance traveled was calculated using interpolated tracks (Tremblay et al., 2006) with a start and end point on the colony, and was considered the sum of the great-circle distances between each interpolated point. As these two parameters were highly correlated in both species (Laysan: $r_s = 0.84$, $p < 0.0001$; Black-footed: $r_s = 0.88$, $p < 0.0001$), only maximum distance was

Table 1
Summary characteristics (mean ± SD) of foraging trips of Laysan and Black-footed Albatrosses tracked during the incubation period at Tern Island, Northwest Hawaiian Islands. Average annual reproductive success (% chicks fledged/eggs laid) at the Tern Island colony is also included for comparison (provided by the Hawaiian Islands National Wildlife Refuge, US Fish and Wildlife Service, Department of the Interior).

Species		2002–2003	2003–2004	2004–2005	2005–2006	ALL years
Laysan Albatross	Number of individuals tracked	10	7	10	10	37
	Maximum distance from colony (km)	2430 ± 977	2969 ± 653	2437 ± 1121	1772 ± 413	2356 ± 915
	Total distance traveled (km)	10,888 ± 5908	12,750 ± 2962	8860 ± 4150	6712 ± 2033	9564 ± 4515
	Mean track transit rate (km/h)	27.5 ± 4.1	25.7 ± 1.8	28.8 ± 3.9	22.2 ± 4.5	26.1 ± 4.5
	Trip duration (days)	19.1 ± 9.2	24.1 ± 5.3	14.9 ± 7.6	14.3 ± 3.5	17.6 ± 7.6
	ARS spatial scale (km)	50.5 ± 41.8	58.6 ± 57.5	55.5 ± 48.4	64.0 ± 68.5	57.0 ± 52.7
	Distance to most intensively searched area (km)	2010 ± 810	2353 ± 754	1915 ± 620	1529 ± 328	1919 ± 680
	Change in mass (g)	270 ± 184	120 ± 362[a]	295 ± 148	543 ± 464	334 ± 332
	Reproductive success (%)	66.6	65.0	67.4	73.4	68.1
Black-footed Albatross	Number of individuals tracked	10	7	9	10	36
	Maximum distance from colony (km)	1502 ± 500	2127 ± 1114	1564 ± 471	2016 ± 1328	1782 ± 925
	Total distance traveled (km)	5761 ± 2192	8405 ± 2553	6178 ± 2253	6519 ± 3614	6590 ± 2788
	Mean track transit rate (km/h)[b]	28.8 ± 4.7	22.3 ± 1.9	24.6 ± 4.9	25.0 ± 5.6	24.8 ± 4.7
	Trip duration (days)	11.3 ± 4.2	17.3 ± 1.8	12.3 ± 5.5	11.8 ± 5.2	12.9 ± 4.9
	ARS spatial scale (km)	60.5 ± 60.6	57.9 ± 24.6	95.6 ± 87.7	39.5 ± 39.3	62.9 ± 60.3
	Distance to most intensively searched area (km)	1239 ± 640	1927 ± 1115	1372 ± 557	1905 ± 1333	1591 ± 972
	Change in mass (g)	275 ± 228	140 ± 445[a]	228 ± 217	385 ± 281	270 ± 282
	Reproductive success (%)	72.9	86.2	74.8	85.7	79.9

[a] Mass data collected at departure and return from only five tracked Laysan Albatrosses and five tracked Black-footed Albatrosses.
[b] Transit rates calculated only from individuals tracked with continuously transmitting satellite tags (see Section 2.5).

used in statistical analyses. Average transit rate was calculated by dividing the great-circle distances between each off-colony ARGOS location by the time between successive locations (always 10 min due to the interpolation scheme described above). Trip duration was defined as either the time elapsed between the observed departure and arrival of the bird, or the time elapsed between the last satellite location on the colony before departure (as defined above) and the first satellite location on the colony at arrival.

We used first passage time analysis, a scale-dependent metric of time spent in a given area by an animal (Fauchald and Tveraa, 2003), to discern locations where area-restricted search (ARS) effort was concentrated (Kareiva and Odell, 1987; Fauchald and Tveraa, 2003; Pinaud, 2008). Thus, first passage time was used as an index of foraging importance within each individual's track in order to discern relative use of habitats (Pinaud and Weimerskirch, 2005; Suryan et al., 2006). We calculated first passage time at every location along each track for radii ranging from 5 to 500 km, at 5-km increments, using a custom-built program in Matlab (Robinson et al., 2007). The circle radius associated with the peak log(variance) in first passage time, hereafter called "ARS spatial scale," was determined for each track separately to account for individual differences in movement patterns (Robinson et al., 2007). First passage time for every point along the track was calculated using the ARS spatial scale, as this is the best spatial scale to differentiate high (area-restricted searching) versus low (transitory) passage times (Fauchald and Tveraa, 2003; Suryan et al., 2006). The maximum first passage time, at the appropriate ARS spatial scale, was then identified as the most intensively searched foraging area for each individual. For each track, first passage time was scaled by ARS spatial scale (first passage time/area of circle) so that this track metric could be compared between individuals. This continuous measure of search effort, hereafter referred to as "scaled first passage time," was used as a dependent variable to investigate marine habitat parameters.

2.3. Foraging distribution

To determine overall patterns of spatial foraging distribution, we employed a kernel density analysis (Worton, 1989) to investigate overlap of foraging distributions between species and between each year of study. Geographic coordinates of interpolated albatross locations were transformed to Cartesian coordinates using a Lambert Cylindrical Equal Area projection (Wood et al., 2000), and 2D Gaussian kernel densities were computed on a 50-km grid. The smoothing parameter (h) was estimated using an adaptive method (Worton, 1989) to estimate an optimal local value, following Sheather and Jones (1991). The density surface was then divided into concentric polygons to calculate utilization distribution (UD) contours of 25% (core area), 50% (focal region), and 95% (foraging range; following Hyrenbach et al. (2002)). For each UD contour, coordinates were transformed back to geographic coordinates and their area computed on the Earth spheroid. We then calculated percent overlap between species, and between years for each species, based on these area estimates. Because area of overlap can be divided by the area of each polygon that was being compared (González-Solís et al., 2000; Wood et al., 2000), we present mean overlap estimates for each UD contour.

2.4. Habitat use

We extracted remotely sensed oceanographic data associated with satellite tracking data through a Thematic Real-time Environmental Distributed Data Service (THREDDS) system housed by NOAA's Environmental Research Division (http://oceanwatch.pfeg.noaa.gov/thredds/catalog.html). We used a blended product of SST derived from both microwave and infrared sensors carried on multiple platforms at a spatial resolution of 0.1° and as a 5-day temporal composite (Powell et al., 2008). Measurements were gathered by Japan's Advanced Microwave Scanning Radiometer (AMSR-E) instrument, a passive radiance sensor carried aboard NASA's Aqua spacecraft, NOAA's Advanced Very High Resolution Radiometer (AVHRR), NOAA's GOES Imager, and NASA's Moderate Resolution Imaging Spectrometer (MODIS). As SSTs in the central North Pacific are distributed in broad latitudinal bands, latitudinal gradients in SST (dySST) were used to describe frontal structure (Ullman et al., 2007), by computing the local derivative of adjacent 0.1-degree pixels in the north–south direction.

Monthly PP estimates (Behrenfeld and Falkowski, 1997) were derived at a spatial resolution of 0.1° from monthly chlorophyll-*a* values and photosynthetically available radiation obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) on the Orbview-2 satellite, and SST values from the AVHRR Pathfinder Oceans Project. Monthly chlorophyll-*a* values obtained from SeaWiFS were also used to calculate distance to the TZCF. Following Polovina et al. (2001) and Bograd et al. (2004), the TZCF was defined as the 0.2 mg m^{-3} chlorophyll-*a* contour.

Daily composites of wind speed and direction were gathered by the SeaWinds scatterometer aboard NASA's QuikSCAT satellite at a resolution of 0.25° and a reference height of 10 m. The NOAA CoastWatch West Coast Node processes wind vector fields to calculate wind stress curl from these data. We used wind stress curl as a metric of surface convergence/divergence (Bograd et al., 2004), and therefore a proxy for local aggregation of neustonic or buoyant prey. For each location of interest, we calculated a mean wind stress curl from the previous 30 days to get a representation of past physical forcing in the area of interest.

We also used 1-day composites of wind speed to exclude data points where wind speeds fell below 3 m s^{-1}, the speed at which albatrosses must switch to energetically costly flapping flight (Pennycuick, 1982). At such low wind speeds, albatrosses may be forced to remain in an area even when not engaging in foraging activities; this could artificially inflate the first passage time value for these locations. These considerations resulted in the exclusion of 0.83% of data points used in the marine habitat analysis.

Individual eddies were identified using the Okubo–Weiss parameter, W (Okubo, 1970; Weiss, 1991), which measures the balance between strain and enstrophy in surface currents. W is expressed in terms of the shear strain, s_s, the normal strain, s_n, and the vorticity, ω:

$$W = s_n^2 + s_s^2 - \omega^2. \tag{1}$$

The strain components and vorticity are in turn calculated using geostrophic current components u and v derived from AVISO (Archiving Validation and Interpretation of Satellite Data in Oceanography) sea level anomaly, h, and the Coriolis parameter, f, (e.g., Isern-Fontanet et al., 2004; Henson and Thomas, 2008),

$$s_s = \frac{\partial u}{\partial y} + \frac{dv}{dx}, \quad s_n = \frac{\partial u}{\partial x} - \frac{\partial v}{\partial y}, \quad \omega = \frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}, \tag{2}$$

$$u = \frac{-g}{f}\frac{\partial h}{\partial y}, \quad v = \frac{g}{f}\frac{\partial h}{\partial x}. \tag{3}$$

Large negative values of W typify the eddy core, with smaller, positive W in the strain-dominated margins of the eddy. Once identified, these eddies were then tracked through the successive weekly images using custom-built image recognition routines (Henson and Thomas, 2008).

Eddy kinetic energy (EKE) was used to quantify mesoscale variability (Stammer, 1998; Waugh et al., 2006), in terms of regions where eddies and meanders are particularly energetic. EKE was calculated from surface ocean currents derived from four satellite altimeters (Jason-1, ENVISAT, ERS-1 and 2, and TOPEX/Poseidon) provided by the AVISO program at a resolution of 0.25°. For each

location of interest, a 10 × 10-degree spatial mean was removed from each weekly composite of zonal and meridional surface ocean currents to generate zonal and meridional velocity anomalies (u' and v'). The EKE (per unit mass) was then calculated as

$$\mathrm{EKE} = \frac{1}{2}(u'^2 + v'^2). \quad (4)$$

In general, oceanographic data were extracted along the birds' satellite tracks, so that extracted values fell within the ARS spatial scale as determined by first passage time analysis, from composite data that matched closest in time to satellite locations. The median value in each oceanographic variable was calculated for each non-overlapping ARS zone to relate to the scaled first passage time. If the size of the first passage time circle was the same size or smaller than the pixel size of oceanographic data, the surrounding pixels were also included in the median (so that each oceanographic data value was derived from the median of at least nine adjacent pixels) to reduce the effect of spurious values, and to decrease the number of missing values due to cloud cover in some of the datasets.

2.5. Statistical analysis

After visual inspection of these data, parametric two-sample *t*-tests and one-way ANOVAs were used to compare summary trip characteristics between species and among years, and age distribution among years. Non-parametric Wilcoxon Rank-sum and Kruskal–Wallis tests were used to compare ARS spatial scale between species and among years due to non-normality of this parameter. Chi-squared tests were used to compare proportions of males and females tracked during each year of study. All tests were conducted using S-Plus (Insightful Corporation, Seattle, WA); reported *p*-values are two-tailed, and the significance level was set as $p = 0.05$. All averages are reported as mean ± SD in the text.

We compared trip characteristics of albatrosses equipped with duty-cycled satellite tags to those equipped with continuously transmitting satellite tags, to examine potential effects of duty-cycling. We found no significant effect of duty-cycling on estimates of maximum trip distance (Laysan: $t_{35} = 1.60$, $p = 0.12$; Black-footed: $t_{34} = -0.06$, $p = 0.96$), trip duration (Laysan: $t_{35} = 0.35$, $p = 0.73$; Black-footed: $t_{34} = -0.47$, $p = 0.64$), or transit rates in Laysan Albatrosses ($t_{35} = 0.11$, $p = 0.91$); however, duty-cycling had a significant effect on Black-footed Albatross transit rates ($t_{34} = 2.72$, $p = 0.01$). We, therefore, present transit rates for this species only from individuals tracked with continuously transmitting satellite tags.

We tracked 14 female and 23 male Laysan Albatrosses and 21 female and 15 male Black-footed Albatrosses. Gender did not differ proportionally by year for either species (Laysan: $\chi^2_3 = 2.03$, $p = 0.57$; Black-footed: $\chi^2_3 = 2.81$, $p = 0.42$). Average known age of albatrosses in the study was 13.3 ± 3.60 years for Laysan Albatrosses and 10.7 ± 2.70 years for Black-footed Albatrosses, and did not differ among years for either species (Laysan: $F_{3,23} = 0.98$, $p = 0.42$; Black-footed: $F_{3,17} = 0.26$, $p = 0.85$). Because the sex ratio and age structure did not differ among years, we did not include these factors as covariates in our habitat analysis.

We examined the relationship between scaled first passage time and SST (°C), dySST (°C km^{-1}), modeled PP (mg C m^{-2} day^{-1}), distance to the TZCF (distTZCF; km), wind stress curl (CURL; Pa m^{-1}), distance to the nearest eddy (distEDDY; km), whether the nearest eddy was cyclonic or anticyclonic (EDDYtype), and EKE (cm^2 s^{-2}). We used linear mixed-effects regression (*lme* in the program R; R Foundation for Statistical Computing, Vienna, Austria) to relate scaled first passage time to oceanographic variables, while accounting for non-independence of points within each individual's track (Pinheiro and Bates, 2000).

Scaled first passage time was log-transformed to meet the normality assumption for linear models, and to achieve an even spread of covariate values, thus avoiding undue leverage of a few high values (Sokal and Rohlf, 1995), main effects were also transformed as follows: EKE and distEDDY were log-transformed, and dySST, PP, and distTZCF were square-root transformed. To investigate the potential effect of transmitter duty-cycle in habitat analyses, we used a linear mixed-effects model to regress a categorical duty-cycle variable on scaled first passage time. The effect of duty-cycle setting on scaled first passage time was not significant ($\beta = -0.047$, $t_{71} = -0.31$, $p = 0.76$). In addition, there was no difference in the radius associated with the peak log(variance) in first passage time among the four transmission settings (Kruskal–Wallis test $\chi^2_3 = 6.56$, $p = 0.09$) or between groups designated as duty-cycled or continuously-transmitting (Rank-sum test $Z = -1.04$, $p = 0.30$). We, therefore, included all 73 foraging trips in habitat analyses.

Mixed-effect models were fit using maximum likelihood to allow comparison of models with different fixed-effect structures (Crawley, 2002). Tolerance values of predictor variables were checked to ensure that there was not strong collinearity among parameters; all tolerance values were greater than 0.1, the approximate guide suggested by Quinn and Keough (2002). Each model included a continuous first-order autocorrelation term to model the within-group correlation structure in the dataset. Model adequacy was checked with residual plots, autocorrelation function plots, and normal probability plots, which confirmed that the modeling of correlation structure was adequate and that linear modeling assumptions were met. We also examined spatial semivariograms to check for spatial correlation in model structure, and found that residuals were uncorrelated as a function of distance (following Pinheiro and Bates (2000)).

For each species and year of study, a suite of 12 candidate mixed-effect models were selected *a priori* relating to specific hypotheses regarding albatross foraging habitat use (Table 2), and ranked using adjusted Akaike's Information Criterion (AICc; Burnham and Anderson, 2002). We randomly selected 80% of the

Table 2
Candidate models and corresponding hypotheses developed *a priori* to relate scaled first passage time to environmental variables for Laysan and Black-footed Albatrosses during the 2002–2006 breeding seasons on Tern Island, Northwest Hawaiian Islands.

Model	Variables	Hypothesized mechanistic link
1	SST	Temperature of water mass → descriptive of regional thermal regime
2	dySST	Frontal activity → local convergence and prey aggregation
3	PP	Primary production → descriptive of regional biochemical regime
4	distTZCF	Dominant frontal feature of NPTZ → large-scale convergence and prey aggregation
5	CURL	Index of large-scale convergence (divergence) → regional aggregation of prey
6	distEDDY	Proximity to eddy → local enhancement of productivity or prey aggregation
7	EDDYtype	Eddy type → cyclonic (increased productivity) or anticyclonic (convergence)
8	EKE	Mesoscale variability → increased local productivity and prey aggregation
9	EKE + distEDDY + EDDYtype	All eddy-related variables → eddies linked to prey
10	dySST + distTZCF + CURL	All frontal-related variables → frontal characteristics linked to prey
11	SST + PP	All large-scale production-related variables → regional production linked to prey
12	EKE + SST + dySST + PP + distTZCF + CURL + distEDDY + EDDYtype	All factors equally important → all cues used by albatrosses to find prey

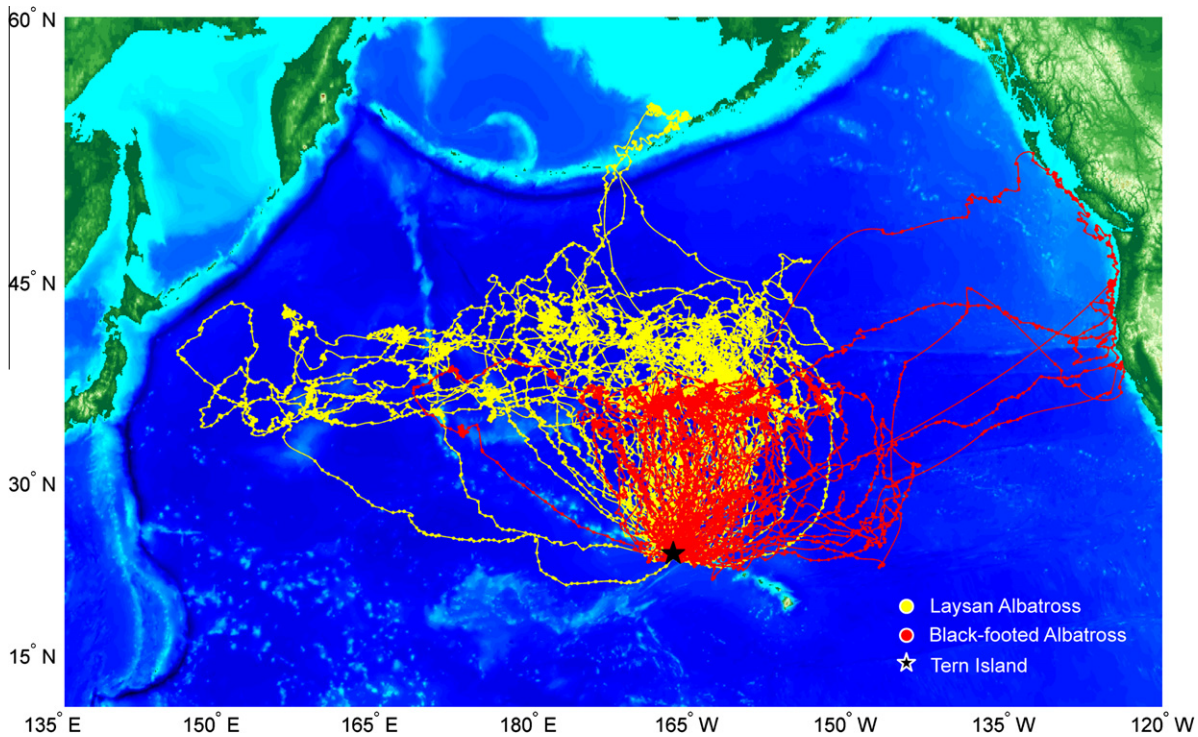

Fig. 1. Foraging trips of 37 Laysan and 36 Black-footed Albatrosses breeding at Tern Island, Northwest Hawaiian Islands during the incubation period, as determined by satellite telemetry. Data encompass a period of four breeding seasons, from 2002–2003 to 2005–2006. ARGOS satellite locations are denoted by marker points along the interpolated tracks, overlaid on ocean bathymetry.

data points from each individual trip to use for model building, and reserved the remaining 20% of the dataset for model validation. We present the percent prediction error for each of top candidate models based on root mean-squared error of prediction (Rawlings et al., 1998). Competing models (ΔAICc < 2) are presented, as well as their model-averaged coefficients and unconditional standard errors (Burnham and Anderson, 2002). For those variables appearing in only one model, we used the original coefficient and standard error from the appropriate model. For each species and year of study, we also ranked each variable according to its relative importance weight (the sum of the Akaike weight over the subset of models that include the variable; Burnham and Anderson (2002)).

3. Results

3.1. Foraging behavior

The majority of individuals traveled to pelagic waters of the North Pacific, with Laysan Albatrosses demonstrating a more northwesterly distribution (Fig. 1). Both species demonstrated

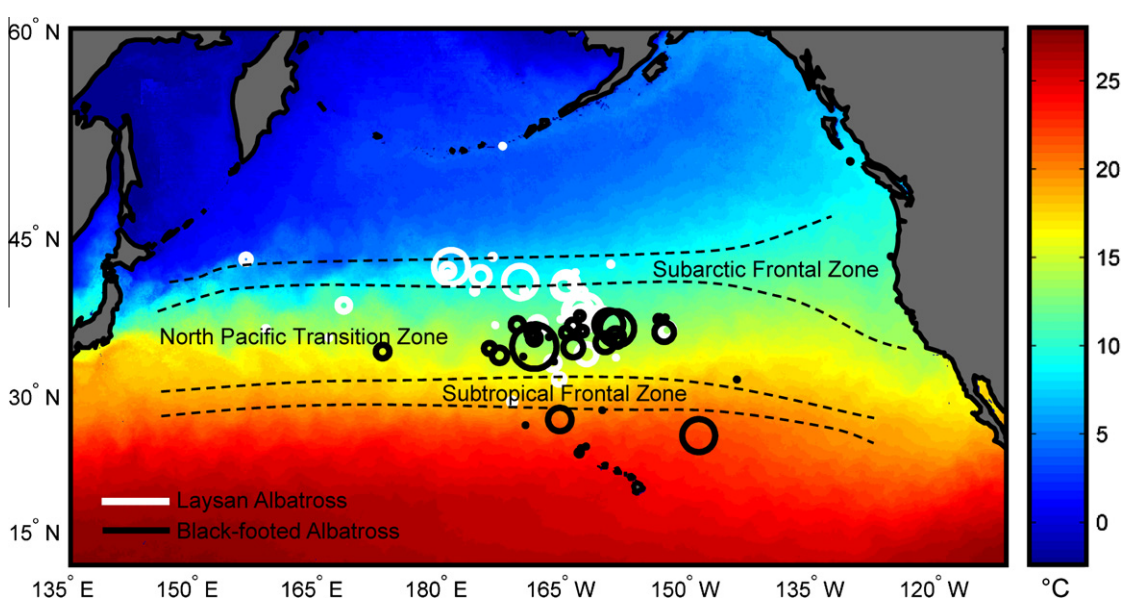

Fig. 2. Intensive search areas visited by Hawaiian albatrosses as determined by first passage time analysis. Each circle represents the area where the individual demonstrated the maximum first passage time, at the appropriate ARS spatial scale determined from the individual's movements. Search areas are superimposed over time-averaged SST (°C) for the study period. Dashed lines indicate the location of the Subarctic Frontal Zone, the North Pacific Transition Zone, and the Subtropical Frontal Zone (after Seki et al. (2004)).

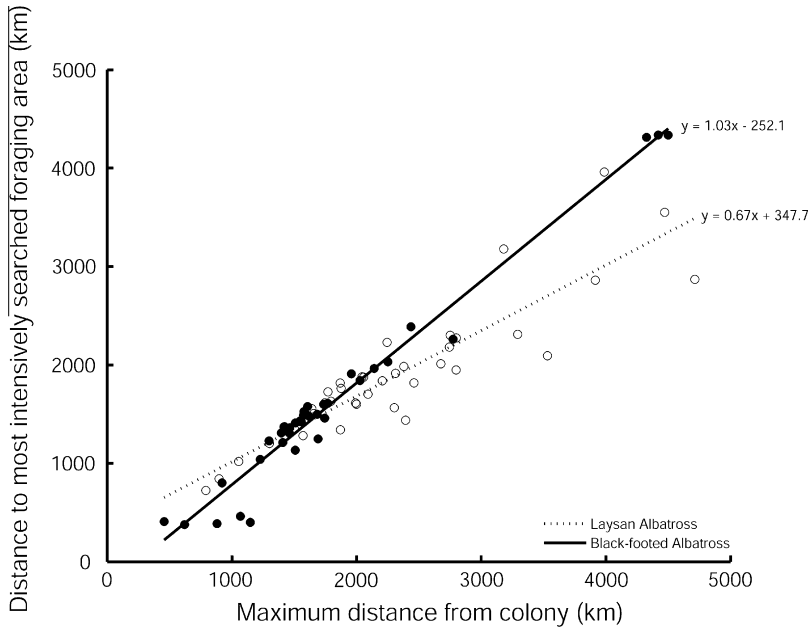

Fig. 3. Maximum distances (km) reached by Hawaiian albatrosses from the Tern Island colony in relation to distances to most intensively searched areas (km), as determined by first passage time analysis.

intensive searching behavior within the NPTZ, however, only Laysan Albatrosses utilized the SAFZ while intensively searching (Fig. 2). Laysan Albatrosses traveled farther ($t_{71} = 2.67$, $p = 0.095$) and for longer periods ($t_{71} = 3.16$, $p = 0.002$) than Black-footed Albatrosses (Table 1); transit rates did not differ between species ($t_{60} = 1.09$, $p = 0.29$). The longest trip recorded was from a Laysan Albatross that traveled a total distance of 20 977 km. The two species did not differ in terms of ARS spatial scale ($Z = 0.089$, $p = 0.93$), or distance to most intensively searched foraging area ($t_{71} = 1.67$, $p = 0.098$), despite greater maximum distances reached by Laysan Albatrosses. This is evident in the differing slopes between maximum distance reached from the colony and distance to intensively searched areas for each species (test for species interaction term: $\beta = -0.18$, $t_{69} = -5.73$, $p < 0.0001$; Fig. 3). Change in body mass during the foraging trip also did not differ between species ($t_{67} = 0.68$, $p = 0.50$), despite slightly larger size of Black-footed Albatrosses (3.15 ± 0.36 kg) compared to Laysan Albatrosses (2.78 ± 0.26 kg; $t_{68} = 3.12$, $p = 0.003$; based on body mass at departure); change in mass adjusted for body weight was also not different between species ($t_{67} = 0.66$, $p = 0.51$).

Laysan Albatrosses demonstrated interannual differences in maximum distance traveled from the colony ($F_{3,33} = 2.82$, $p = 0.05$), trip duration ($F_{3,33} = 3.57$, $p = 0.02$), and transit rates ($F_{3,33} = 5.57$, $p = 0.003$), as well as interannual differences in body mass change during foraging ($F_{3,31} = 3.30$, $p = 0.03$). Average annual body mass changes during foraging were positively correlated with annual reproductive success ($\beta = 0.02$, $t_2 = 7.26$, $p = 0.02$) and negatively related to maximum distance traveled ($\beta = -0.36$, $t_2 = -12.98$, $p = 0.006$) in this species. On average, Laysan Albatrosses reached the greatest maximum distances during the 2003–2004 field season, corresponding with the longest trip durations, lowest mass gains, and the lowest breeding success; the converse was true in 2005–2006 (Table 1).

Black-footed Albatrosses did not demonstrate interannual variation in maximum distance reached ($F_{3,32} = 1.01$, $p = 0.40$), transit rates ($F_{3,21} = 1.78$, $p = 0.18$), trip duration ($F_{3,32} = 2.76$, $p = 0.06$) or change in body mass during foraging ($F_{3,30} = 0.92$, $p = 0.44$). Reproductive success of Black-footed Albatrosses was generally higher compared to Laysan Albatrosses (Table 1), and did not correlate with average annual changes in body mass during foraging ($\beta = 0.18$, $t_2 = 0.02$, $p = 0.99$).

Neither species demonstrated interannual variation in ARS spatial scale (Laysan: $\chi^2_3 = 0.07$, $p = 0.995$; Black-footed: $\chi^2_3 = 2.93$, $p = 0.40$) or distance to the most intensively searched foraging area (Laysan: $F_{3,33} = 2.34$, $p = 0.09$; Black-footed: $F_{3,32} = 1.2$, $p = 0.31$).

3.2. Foraging distribution

Laysan and Black-footed Albatrosses demonstrated interspecific segregation of foraging habitats at sea; only 47.6% of the foraging range (95% UD) overlapped, despite both species making similar, transitory north–south movements between the Tern Island breeding colony and intensive searching areas (Figs. 1 and 2). Thirty-three percent of the 50% UD overlapped, and only 17.6% of the core area (25% UD) overlapped between species (Fig. 4).

There was substantial variation in foraging distributions between years (Fig. 5A and B). On average, the foraging ranges of Laysan Albatrosses overlapped by only 46.9% among years; this was even lower in Black-footed Albatrosses, which demonstrated a 33.5% overlap in foraging range among years. Both species showed a similar overlap of focal areas among years; 17.0% for Laysan Albatrosses and 19.4% for Black-footed Albatrosses. There was very low overlap of core areas for both Laysan Albatrosses (7.61%; Fig. 5A) and Black-footed Albatrosses (7.18%; Fig. 5B) among years.

3.3. Habitat use and oceanography

Laysan and Black-footed Albatrosses increased search effort in relation to similar environmental variables (Table 3). The best-fitting habitat models for both species related SST to scaled first passage time, or the additive effect of SST and PP (Table 3). In all cases, SST was negatively correlated with search effort (Table 4), while PP showed either a positive or a negative relationship with scaled first passage time in both species. During 2004–2005, Black-footed Albatrosses demonstrated a negative relationship between distance to the TZCF and search effort; however, this was the only case where distance to the TZCF was present in one of the top competing models (Tables 3 and 4). Prediction errors for

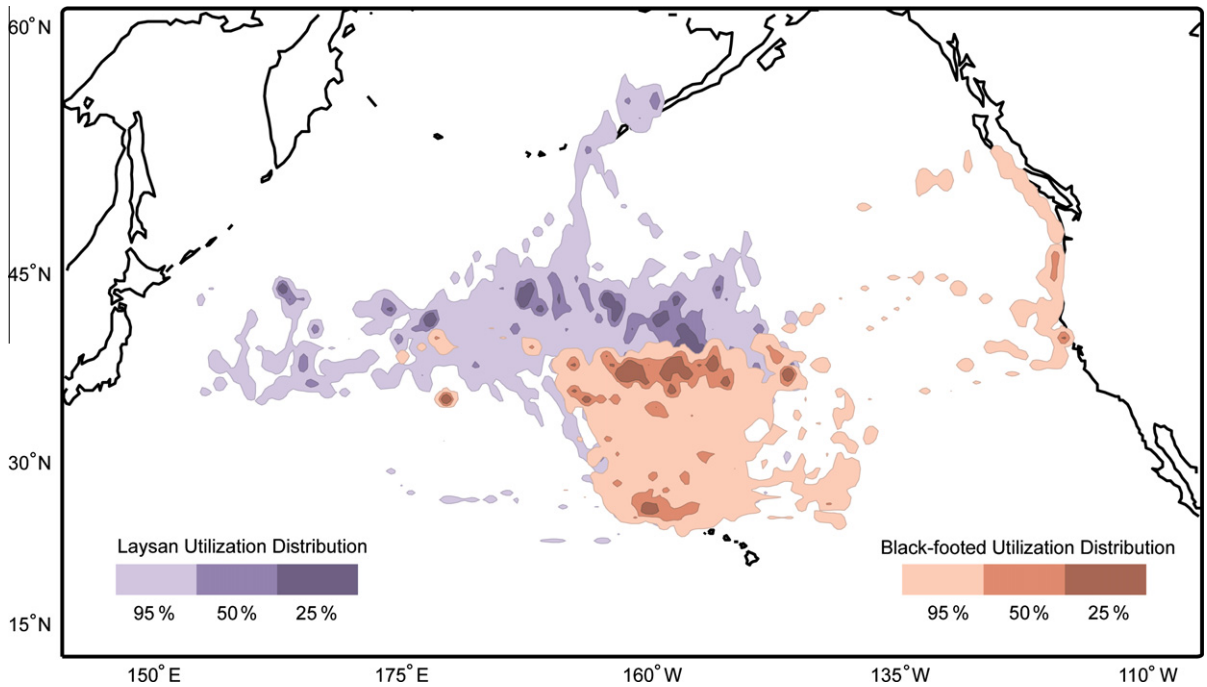

Fig. 4. Foraging distributions of Hawaiian albatrosses as estimated by kernel density analysis. The spatial extent of the foraging range (95% UD), focal areas (50% UD) and core areas (25% UD) are plotted for each species.

the top-ranked habitat use models for both species were between 27.3% and 41.5% (Table 3). In general, prediction errors were lower for Black-footed Albatross habitat models, and highest for both species during the 2005–2006 breeding season (Table 3).

We used Akaike relative importance weights to examine the evidence from all candidate models for the importance of each environmental variable in predicting scaled first passage time. For all years, and both species, SST was consistently the most important environmental variable in predicting search effort (Fig. 6A and B). For Laysan Albatrosses, the next most important variable was PP in all years (Fig. 6A); all other environmental variables that we considered had very low importance weights. For Black-footed Albatrosses, PP was the next most important variable in 2002–2003, 2003–2004, and 2005–2006, however, distance to the TZCF was second most important in 2004–2005 (Fig. 6B). In 2004–2005, PP was the third most important variable; all other environmental variables had very low importance weights in all years.

Laysan Albatrosses spent a greater proportion of time in cooler waters of the NPTZ than did Black-footed Albatrosses (Fig. 2), and the distribution of time spent at sea versus SST differed significantly between species (Kolmogorov–Smirnov $D = 0.17$, $p = 0.0003$; Fig. 7). SSTs in most intensively searched foraging areas were significantly cooler for Laysan Albatrosses (12.4 ± 2.68 °C) than Black-footed Albatrosses (16.3 ± 3.82 °C; $t_{71} = 5.00$, $p < 0.0001$), and there were no interannual differences in SST of most intensively searched foraging areas for either species (Laysan: $F_{3,33} = 1.54$, $p = 0.22$; Black-footed: $F_{3,31} = 1.24$, $p = 0.31$).

4. Discussion

4.1. General patterns in foraging behavior

Laysan and Black-footed Albatrosses demonstrated interspecific segregation at sea during the incubation period, similar to the foraging habitat partitioning seen during the chick-rearing (Fernández et al., 2001; Hyrenbach et al., 2002) and non-breeding periods (Fischer, 2007; Shaffer, *unpubl. data*). While both species traveled to the NPTZ, Laysan Albatrosses traveled farther north to the SAFZ, and Black-footed Albatrosses remained closer to the Subtropical Frontal Zone while intensively searching for food (Fig. 2). This may be attributed to differences in the distribution of preferred prey items; Pearcy et al. (1996) found that Ommastrephid squids, which comprise the largest proportion of the Laysan Albatross diet, demonstrate a more northerly distribution in the North Pacific compared to flying fishes, the eggs of which comprise the largest proportion of the Black-footed Albatross diet (Harrison et al., 1983). Laysan Albatrosses also demonstrated more interannual variability in trip characteristics and mass change during foraging. Ommastrephid squid undergo drastic changes in juvenile recruitment in association with ENSO events (Chen et al., 2007), therefore, it is possible that interannual environmental variability during the study period led to fluctuations in the abundance or distribution of Laysan Albatross prey. The greater consistency in Black-footed Albatross trip characteristics among years may indicate less variability in their prey resources; predictability of preferred prey items could help explain the overall higher reproductive success of Black-footed Albatrosses during the four-year period of study.

The scales at which Laysan and Black-footed Albatrosses directed their search efforts did not differ between species; average ARS spatial scale for Laysan (radius of 57.0 ± 52.7 km) and Black-footed (radius of 62.9 ± 60.3 km) Albatrosses matched the spatial scale of mesoscale features (~100 km diameter). In an analysis of ARS behavior in seven sympatric Indian Ocean Procellariiform species, Pinaud and Weimerskirch (2007) suggest that species relying on neritic habitats, characterized by higher predictability of prey, would have smaller overall ARS spatial scales, as evidenced by the foraging behavior of Black-browed Albatrosses (*Thalassarche melanophrys*). This supposition is supported by our results in that average ARS spatial scale of Hawaiian albatrosses was most similar to those Indian Ocean species that used pelagic habitats (Pinaud and Weimerskirch, 2007), and the ARS spatial scale for those individuals that traveled to coastal, neritic habitats of the Aleutian Islands and California Current was indeed smaller (Fig. 2).

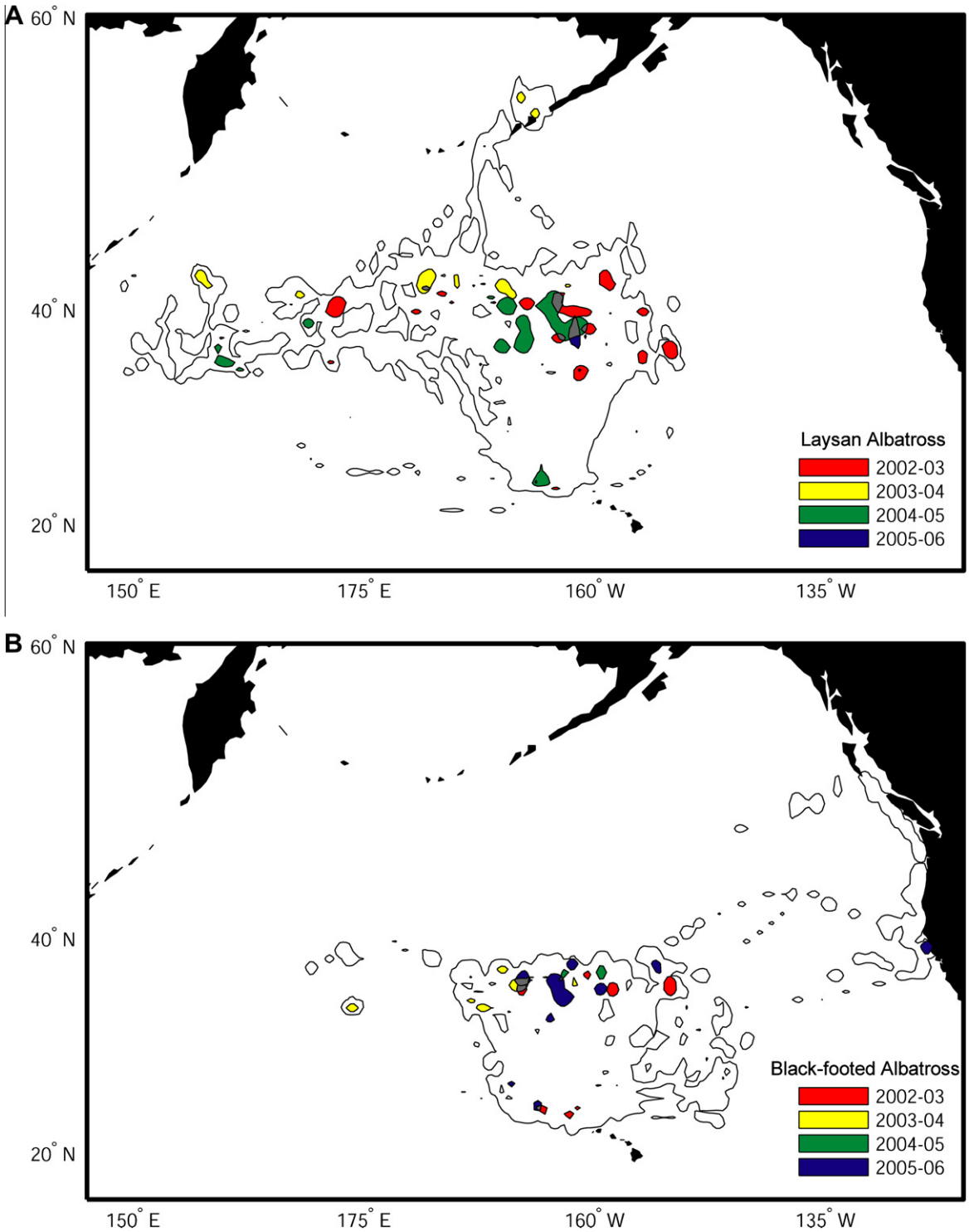

Fig. 5. Interannual overlap of core foraging areas (25% UD) visited by (A) Laysan Albatrosses and (B) Black-footed Albatrosses. Each year is displayed in a uniquely colored polygon, the area of overlap is colored grey, and the foraging range (95% UD) for all years combined is outlined in black.

The relationship between maximum distances reached and distance to most intensively searched foraging areas did, however, differ between species. Laysan Albatrosses reached maximum distances that were farther from the colony than those patches where they engaged in intensive searching behaviors (Fig. 3). Black-footed Albatrosses, on the other hand, did not travel farther from the colony than necessary to reach intensively searched areas (as indicated by the 1:1 relationship between maximum distance reached and distance to intensive search areas; Fig. 3). This may be indicative of more predictable prey resources. If Black-footed Albatrosses can reliably find food within the NPTZ, it is unlikely they would venture farther from the colony than necessary. This hypothesis is supported by the lack of interannual variation in trip characteristics and mass change during foraging, and overall higher reproductive success in this species (Table 1). Alternatively, Black-footed Albatrosses may be more constrained in terms of maximum trip distance due to higher wing loading as compared to Laysan Albatrosses (Suryan et al., 2008). As the relationship between max-

Table 3
Model selection results from linear mixed effects modeling of the effect of marine habitat variables on scaled first passage time for Laysan and Black-footed Albatrosses during 4 years of study. Presented are the habitat variables in the top-ranked models, the number of parameters in each model, including the intercept, residual variance, and random effects (*K*), the difference in adjusted Akaike's information criterion between the top-ranked model and other candidate models (ΔAICc), the AICc weight for each model, and the percent prediction error based on root mean-squared error of prediction. Only competing top-ranked models (ΔAICc < 2) are presented.

	Model	Variables	*K*	ΔAICc	AICc weight	% prediction error
Laysan						
2002–2003	1	SST	7	0	0.557	27.7
	11	SST + PP	8	1.23	0.301	27.8
2003–2004	1	SST	7	0	0.518	35.5
	11	SST + PP	8	1.91	0.199	35.4
2004–2005	1	SST	7	0	0.557	28.1
	11	SST + PP	8	1.64	0.245	28.1
2005–2006	11	SST + PP	8	0	0.513	41.5
	1	SST	7	0.28	0.446	41.4
Black-footed						
2002–2003	11	SST + PP	8	0	0.652	27.3
2003–2004	1	SST	7	0	0.696	28.1
	11	SST + PP	8	1.71	0.297	28.1
2004–2005	1	SST	7	0	0.271	28.2
	4	distTZCF	7	0.08	0.260	28.6
	11	SST + PP	8	0.90	0.173	28.1
2005–2006	1	SST	7	0	0.637	34.7
	11	SST + PP	8	1.65	0.279	34.6

Table 4
Model-averaged coefficients and unconditional standard errors for environmental variables included in top-ranked candidate models of Laysan and Black-footed Albatross habitat use. Note: coefficients are on log-scale because dependent variable (scaled first passage time) was log-transformed to meet requirements of linear models.

	Environmental variable	Model-averaged coefficient	Unconditional standard error
Laysan			
2002–2003	SST	−0.024	0.010
	PP	0.010	0.011
2003–2004	SST	−0.024	0.012
	PP	−0.004	0.010
2004–2005	SST	−0.027	0.012
	PP	0.008	0.012
2005–2006	SST	−0.053	0.015
	PP	−0.021	0.014
Black-footed			
2002–2003	SST	−0.040	0.016
	PP	−0.037	0.016
2003–2004	SST	−0.126	0.026
	PP	0.012	0.018
2004–2005	SST	−0.024	0.017
	distTZCF	−0.019	0.009
	PP	0.031	0.029
2005–2006	SST	−0.063	0.017
	PP	0.006	0.009

imum distance reached and distance to intensive search areas in Laysan Albatrosses (slope = 0.67) was similar to that found in Indian Yellow-nosed Albatrosses (*Thalassarche carteri*; slope = 0.76; Pinaud and Weimerskirch, 2005), the pattern observed for Black-footed Albatrosses may indicate a particularly economical foraging strategy, perhaps necessitated by higher wing loading.

4.2. Marine habitat use

The most important predictor of albatross search effort was SST in both species suggesting that Hawaiian albatrosses use similar environmental cues when searching for prey. Laysan Albatrosses spent more time intensively searching in cooler waters (~12 °C) compared to Black-footed Albatrosses (~16 °C). This may be explained by differences in diets and spatial separation of prey resources along the strong latitudinal gradient in SST in the NPTZ (Harrison et al., 1983; Pearcy et al., 1996).

Core habitats utilized by both Laysan and Black-footed Albatrosses had little overlap among the 4 years of study. While each species generally used the same oceanographic domain in all years (Laysan Albatrosses were distributed predominantly in the northern portion of the NPTZ and the SAFZ, and Black-footed Albatrosses in the southern portion of the NPTZ; Fig. 2); variability in oceanographic features likely influenced the actual locations of core foraging areas. We found that SST was consistently the best predictor of search effort in all 4 years, despite interannual and seasonal variability in SST in the North Pacific (Bograd et al., 2004). Temperature associations did not vary interannually for either species; despite changes in core foraging locations, both species appeared to track specific environmental characteristics. This contrasts with the responses of other albatross species in relation to interannual environmental variability. Yellow-nosed Albatrosses altered both trip characteristics and habitat use during 2 years of study, (Pinaud et al., 2005), and Black-browed Albatrosses consistently visited the same foraging zones at the Kerguelen shelf break despite consequences to body condition and reproductive success in "poor" years (Pinaud and Weimerskirch, 2002).

Both SST and PP were better predictors of search effort than variables characterizing physical features such as fronts or eddies, indicating that Laysan and Black-footed Albatrosses responded to the temperature of water masses or regional production *per se*. Contrary to our expectations, neither Laysan nor Black-footed Albatrosses increased foraging search effort in response to the presence of eddies, the proximity of the TZCF, steep SST gradients, or surface convergence (wind stress curl). Each of these variables characterizes physical features or processes that have been shown to correlate with prey resources of Hawaiian albatrosses (Johannes, 1981; Gong et al., 1993; Yatsu et al., 1993; Pearcy et al., 1996; Ichii et al., 2004; Bakun, 2006). It is, therefore, surprising that we did not see a behavioral response in foraging patterns when albatrosses encountered these oceanographic features. Hyrenbach et al. (2006) found similar results in a multivariate analysis of seabird–eddy associations, where SST, SST gradient, and distance to the breeding colony were more important than sea level anomaly in predicting abundances of three focal seabird species. Indeed, a number of studies of marine top predator habitat associations have also found the greatest behavioral responses to SST compared to other oceanographic variables (Simmons et al., 2007; Teo et al., 2007).

SST is an environmental cue that can be easily sensed by these surface-feeding predators (Wilson et al., 1995; Shaffer et al., 2005);

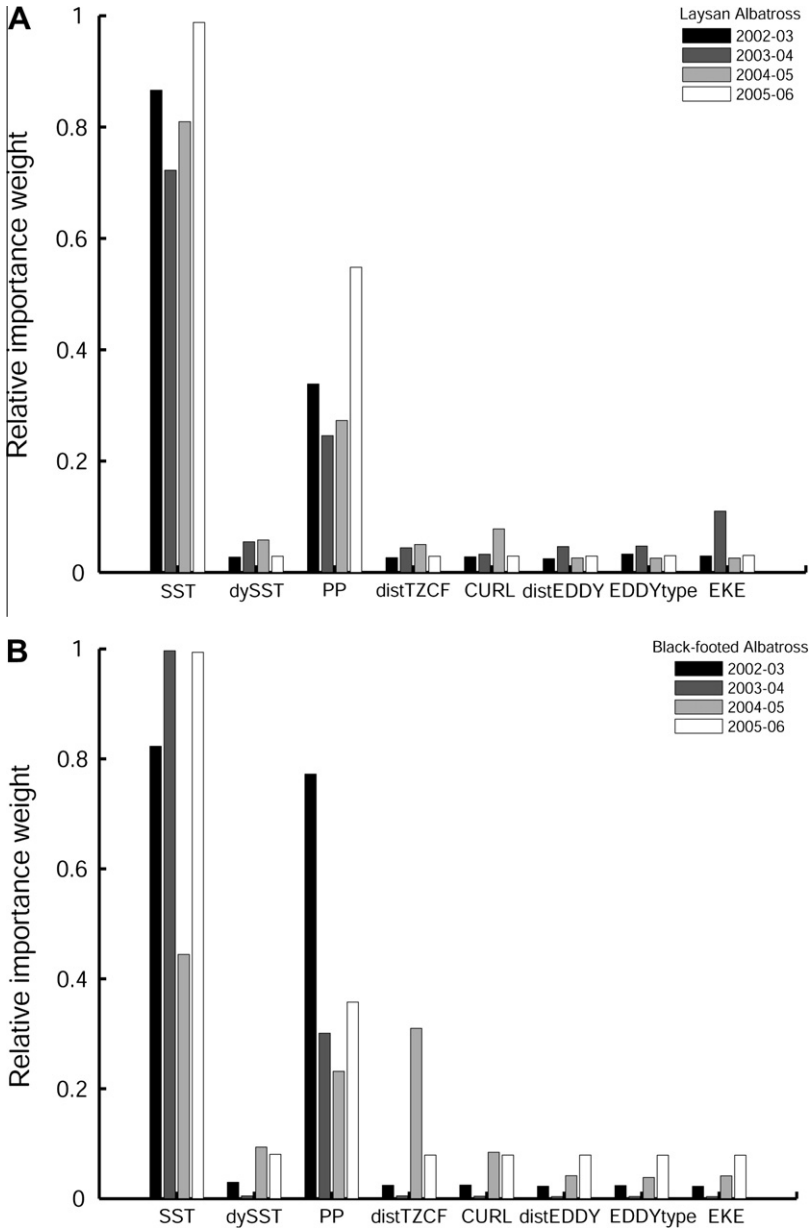

Fig. 6. Relative Akaike importance weights of environmental variables included in (A) Laysan Albatross and (B) Black-footed Albatross habitat use models during 4 years of study.

both Laysan and Black-footed Albatrosses frequently land on the surface of the water during foraging trips (Fernández and Anderson, 2000). Previous success locating prey in cool waters might prompt individual albatrosses to increase search effort in response to particular SSTs, even if prey capture events are not always associated with ARS behavior (Weimerskirch et al., 2007). Therefore, we hypothesize that the mechanism responsible for the relationship between increased search effort and SST is related to previous experience in locating prey resources in cooler water patches, irrespective of visual or olfactory evidence of prey (Nevitt et al., 2008). Similar reasoning was used to explain the association of ARS behavior and shelf edges in the Wandering Albatross (*Diomedea exulans*). Because Wandering Albatrosses demonstrated lower variability in prey capture within ARS zones, Weimerskirch et al. (2007) suggested that the association of particular environments with previous foraging success may induce area-restricted searching (Weimerskirch et al., 2007). In other words, ARS zones may be important as reliable foraging areas, while opportunistic prey captures can occur at any location along the foraging trajectory.

4.3. Implications for climate variability

In the context of environmental variability, our results suggest that Laysan and Black-footed Albatrosses demonstrate flexibility in foraging strategies and appear to track preferred oceanographic habitats. This supports our original hypothesis that Hawaiian albatrosses would respond consistently to environmental cues, even if actual foraging locations changed. While both species appeared to track particular thermal characteristics, changes in SST predicted under global climate change scenarios are likely to alter the distribution of SSTs in the North Pacific (Levitus et al., 2005; IPCC, 2007). In addition, reliable associations between water temperature and prey availability may break down in such an altered ecosystem (Brodeur et al., 2006; Crocker et al., 2006; Grebmeier et al., 2006). Ecosystem

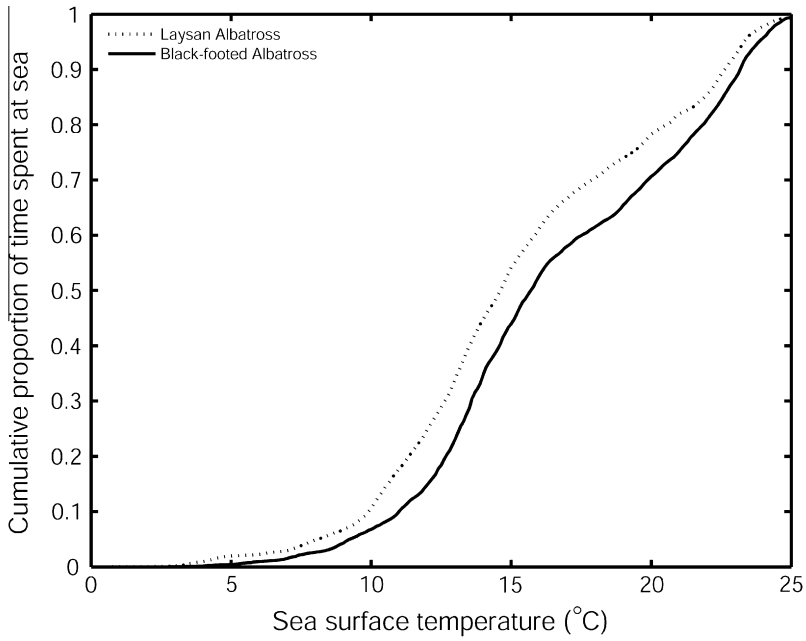

Fig. 7. Cumulative proportion of time spent at sea by Hawaiian albatrosses in relation to SST (°C).

shifts spurred by climatic variability can alter community structure and thus, abundance of prey for top predators. For example, researchers have speculated that a climate-driven shift in food webs has occurred in several marine ecosystems increasingly dominated by gelatinous zooplankton (Brodeur et al., 1999; Attrill et al., 2007; Molinero et al., 2008).

For central place foragers such as Laysan and Black-footed Albatrosses, the proximity of suitable foraging habitats to the breeding colony is also of critical consideration (Orians and Pearson, 1979). Because the frontal features of the North Pacific can migrate dramatically in relation to climatic variability (Bograd et al., 2004), such perturbations may have direct reproductive consequences for these species. In our study, Laysan Albatrosses demonstrated lower breeding success and mass gains when required to range farther and spend longer durations at sea. Previous studies have also documented that after ENSO events, when winter-time position of the TZCF varies significantly from its seasonal norm, both Laysan and Black-footed Albatrosses have experienced dramatic breeding failures (Dearborn et al., 2001; Seki et al., 2004). Therefore, although Hawaiian albatrosses may range across an entire ocean basin in search of prey resources, extreme foraging behaviors likely have energetic consequences that negatively influence demographics of these species. While albatross population dynamics is most sensitive to changes in adult survival (Croxall and Rothery, 1991; Croxall et al., 1998; Russell, 1999), consistent declines in breeding success can also lead to significant population changes (Cuthbert et al., 2004; Weimerskirch, 2004). Many other species of seabirds (Schreiber and Schreiber, 1984; Veit et al., 1996; Montevecchi and Myers, 1997; Inchausti et al., 2003) and top marine predators (Weimerskirch et al., 2003; Forcada et al., 2005; Costa, 2008; Rosa and Seibel, 2008; Saba et al., 2008) have demonstrated behavioral, energetic, and demographic consequences in response to climatic variability or ENSO events. Northern elephant seals (*Mirounga angustirostris*) who similarly forage across the eastern North Pacific, did not change their foraging range during the 1998 El Niño event, however, they exhibited marked reductions in foraging efficiency and mass gain (Crocker et al., 2006). Detailed investigation into the energetic consequences of differing foraging activities in Hawaiian albatrosses would help resolve the mechanistic links between climate variability, foraging behaviors, and demographic effects.

4.4. Relevance to conservation planning

Our study provides a number of results relevant to planning conservation initiatives for Hawaiian albatrosses. Laysan and Black-footed Albatrosses are currently listed by the IUCN as vulnerable and endangered, respectively, and the greatest sources of mortality to both species is bycatch in commercial fisheries (IUCN, 2007; Naughton et al., 2007). Historically, high seas driftnet and pelagic longline fisheries have been the most important sources of mortality, however, after closure of the high seas driftnet fishery, pelagic longline fisheries are currently considered the greatest primary threat to these species (Lewison and Crowder, 2003; Naughton et al., 2007; Véran et al., 2007). In developing a Conservation Action Plan for the Laysan and Black-footed Albatross, the US Fish and Wildlife Service has recommended specific conservation actions for these species, including the need for a clear determination of habitat utilization at sea (Naughton et al., 2007). This study is of particular importance since it adds essential knowledge to several of these specific action items including: (1) the use of empirical data to determine key habitats in core foraging areas, (2) the investigation of colony-based responses to ocean conditions in "high-use" areas, (3) the development of predictive models to forecast at-sea distribution of albatrosses incorporating environmental variables, and (4) the development of a framework for identifying potential pelagic marine protected areas. Our study directly addresses these first two action measures, and contributes to the latter two measures.

We identified SST as a key environmental variable that was related to "high-use" areas over multiple years. This relationship can now be used to inform the development of predictive habitat use models (Guisan and Zimmermann, 2000) as well as to potentially guide the implementation of fisheries closures (Howell et al., 2008). We also documented distributional changes of core foraging areas by both species. Understanding the predictability of marine resource use by Hawaiian albatrosses will be important for planning the formation of open ocean marine protected areas (Mills and Carlton, 1998; Hyrenbach et al., 2000; Gilman, 2001). Data on albatross distributions can be used to identify areas of high overlap with fisheries (Hyrenbach and Dotson, 2003; BirdLife, 2006), thereby identifying high-risk fisheries to target for regula-

tions to reduce bycatch (Naughton et al., 2007). Given future changes to the earth's climate (IPCC, 2007), it is critical that areas considered for fisheries closures or regulations be informed by the dynamic nature of both the marine environment and the behavior of these threatened seabirds.

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