Foraging destinations and marine habitat use of short-tailed albatrosses: A multi-scale approach using first-passage time analysis

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Abstract

We used satellite telemetry, remotely sensed data (bathymetry, chlorophyll *a* (chl *a*), sea-surface temperature (SST), wind speed) and first-passage time (FPT) analysis to determine the distribution, movement patterns, and habitat associations of short-tailed albatrosses (*Phoebastria albatrus*) during the non-breeding season, 2002 and 2003. Satellite transmitters were deployed on birds immediately prior to their departure from a breeding colony at Torishima, Japan ($n = 11$), or at-sea in the Aleutian Islands ($n = 3$). Tracking durations ranged from 51 to 138 days for a total of 6709 locations after filtering (131 – 808 per bird). FPT (time required to transit a circle of given radius) revealed the location and spatial scale of area-restricted search (ARS) patterns along flight paths. On average, ARS occurred within 70 km radii. Consequently, the fit of the habitat use models increased at spatial scales beyond a 40 km FPT radius ($R^2 = 0.31$) and stabilized for scales of 70 km and larger ($R^2 = 0.40$– 0.51). At all scales, wind speed, depth or depth gradient, and chl *a* or chl *a* gradient had a significant effect on FPT (i.e., residence time). FPT increased within regions of higher gradients of depth and chl *a*. In contrast, FPT decreased within regions of greater depth and wind speed, with a significant interaction of wind speed and depth at some scales. Sea-surface temperature or its interactions were only significant at large spatial scales ($\geqslant 160$ km FPT radius). Albatrosses engaged in ARS activities primarily over the shelf break and slope, including Kuroshio and Oyashio regions off the western subarctic gyre. Occasionally, birds transited the northern boundary of the Kuroshio Extension while in-route to the Aleutian Islands and Bering Sea, but overall spent little time in the western gyre. In the Aleutian Islands, ARS occurred within straits, particularly along the central and western part of the archipelago. In the Bering Sea, ARS occurred along the northern continental shelf break, the Kamchatka Current region, and east of the Commander Islands. Non-breeding short-tailed albatross concentrate foraging in oceanic areas characterized by gradients in topography and water column productivity. This study provides an understanding of the foraging ecology for a highly migratory, imperiled

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seabird, and confirms the importance of shelf break and slope regions as hot spots for a variety of top marine predators in the North Pacific.

1. Introduction

The distribution of upper trophic-level consumers often reflects the patchy productivity of dynamic marine ecosystems, with the highest densities typically occurring within productive shelf-slope regions, coastal upwelling zones, regions of water mass convergence or divergence, and transition zones between current systems (Shuntov, 1972; Gould and Piatt, 1993; Springer et al., 1996a, 1999). The aggregation and behavior of upper trophic level consumers therefore, has, been proposed as proxies for identifying biological "hot spots"; regions of increased productivity and energy transfer through marine food webs. Apex consumers may be particularly useful bio-indicators because their occurrence reflects an integration of bio-physical processes resulting in the production of prey resources. Furthermore, because consumers require dense prey aggregations for efficient foraging (Piatt and Methven, 1992; Fauchald and Erikstad, 2002), their distributions can identify areas of elevated production and prey concentration (e.g., Ancel et al., 1992; Hunt et al., 1996).

On an ocean-basin scale, this approach can be applied using satellite telemetry to track movements and remote sensing to identify habitat associations of far-ranging species such as albatrosses (Wilson et al., 2002). Albatrosses, like other pelagic predators, frequently seek out locations of physical and biological oceanographic features that enhance the availability of prey. Satellite tracking studies demonstrate that albatrosses will travel thousands of kilometers seeking hydrographic (e.g., polar frontal zone; Rodhouse et al., 1996) and bathymetric (e.g., Patogonian Shelf; Prince et al., 1997) features that characterize foraging hot spots. However, not all species or populations equally utilize similar oceanographic features and these differences are typically associated with the exploitation of distinct prey assemblages (Cherel et al., 2002; Hyrenbach et al., 2002; Waugh et al., 2002). It is, therefore, critical to consider species- or population-specific differences in interpreting the biological importance of a potential hot spot, as identified by apex consumers.

Other important considerations are how an animal is sampling the environment (e.g., actively searching for prey or simply traveling through the area) and the spatial and temporal scales of response (Hunt and Schneider, 1987; Wiens, 1989; Fauchald, 1999; Fauchald et al., 2000). An analytical approach to address both of these concerns for animal tracking data is first-passage time (FPT) analysis (Johnson et al., 1992; Fauchald and Tveraa, 2003). FPT is the time required for an individual to cross a circle of a given radius. When calculated for every location along an animal's path and for radii of varying size, this technique quantifies the spatial scales of area restricted search (ARS) patterns (highly tortuous movements associated with prey searching and foraging). FPT analysis should therefore be a precursor to modeling habitat use (Pinaud and Weimerskirch, 2005). Herein, we apply a novel FPT approach to create habitat use models for a far-ranging marine predator, the short-tailed albatross (*Phoebastria albatrus*).

The short-tailed albatross inhabits the North Pacific Ocean above 20°N (Hasegawa and De-Gange, 1982; McDermond and Morgan, 1993). Little is known about the at-sea distribution and migrations of this once abundant (>1 million), but now rare (~2000) species that breeds on remote islands in Japan (Hasegawa and DeGange, 1982; Sievert and Hasegawa, unpubl. data). Opportunistic sightings from shipboard observers (Hasegawa and DeGange, 1982 and references therein; Piatt et al., 2006) indicate that short-tailed albatrosses primarily range along the continental shelf and slope regions of the North Pacific. Therefore, the main objectives of our study included: (1) to determine post-breeding season migration routes; (2) to identify an optimum spatial scale(s) to analyze short-tailed albatross habitat relationships; and (3) to quantify marine habitat affinities of short-tailed albatrosses. We present a novel technique to investigate resource selection as a multi-scale continuous process along a flight path, and construct the first habitat use models for this rare species.

2. Methods

2.1. Satellite telemetry

All short-tailed albatrosses were tracked during the post-breeding season, 8 May–23 September 2002 and 7 May–30 November 2003. We deployed satellite transmitters (Platform Transmitter Terminal, PTT) on albatrosses at two locations over a 2-yr period. During 6–10 May 2002 and 2003, 16 albatrosses were captured at the Tsubame-zaki breeding colony on Torishima ($30°$ 28.3′ N, $140°$ 18.6′ E; Fig. 1), Izu Islands, Japan. In 2003, we captured four individuals at-sea in Seguam Pass ($52°$ 25.8′ N, $172°$ 46.4′ W; Fig. 1) Aleutian Islands, Alaska, between 12 and 17 August. The reproductive status of tagged birds was unknown; however, no birds returned to the colony during tracking. Fourteen transmitters provided long-term (>15 days) data considered herein. We determined ages of captured albatrosses from banding records (chick banding at Torishima began in 1977; H. Hasegawa, unpublished data) and gender from blood samples (Fridolfsson and Ellegren, 1999).

We attached satellite transmitters to the dorsal feathers of albatrosses with either adhesive tape (#4651, Tesa Tape, Inc.) or Velcro® tape and epoxy. Several models of PTTs were used (Table 1) and all weighed 35–100 g, $<2.5\%$ of the animal's body mass. All PTTs were programmed to operate on a duty cycle (Table 1) and to transmit at 75 or 90 s repetition rate.

Satellite-derived position fixes of PTTs were provided through the Argos system (Service Argos, Inc.). Argos assigns each position a location quality code ranging from level 3, the most accurate (<150 m radius), to level B, in which accuracy is unknown. Therefore, we applied a filtering algorithm (prepared by David Douglas, USGS, Alaska Science Center, Juneau, Alaska, USA) to the data. First, we retained all level three positions. Other locations were evaluated for filtering based on a maximum speed cut-off of 80 km h^{-1} (a prominent break in the frequency distribution of movement rates between consecutive level 3 locations) and a minimum redundant distance of 1 km ($\geqslant 2$ consecutive locations $\leqslant 1$ km apart were retained). These filtering procedures are similar to those previously employed by other investigators (Hyrenbach et al., 2002; Austin et al., 2003) and retained 86% (6709) of all locations obtained. When this filtering algorithm was applied to data from stationary PTTs ($n = 11$), the average accuracy was <1.2 km (SE $= 0.66$) for LQCs3-A and <7.1 km (SE $= 15.3$) for B fixes. Thus, we believe the resolution of our filtered locations were sufficient to analyze movement paths and habitat associations at spatial scales considered herein.

2.2. First-passage time analysis

In calculating FPT, we first linearly interpolated each albatross track at 5-km intervals while retaining original locations. We included the $\leqslant 24$ h PTT off-cycle when interpolating because FPT was often much greater than 8 h (days to weeks in some cases, especially at larger spatial scales). We calculated FPT at every location along the track of each albatross for radii ranging from 5 to 500 km by 5-km increments. Next, we plotted variance in FPT (log transformed) for each individual and a mean across individuals vs. radii to ascertain the peak, or dominant spatial scale of ARS (Fauchald and Tveraa, 2003). The variance peak identifies which spatial scale is best to differentiate high (ARS) vs low (transitory) passage times.

FPT analysis permitted a multi-scale analysis of habitat use, whereby FPT for any given location could be associated with habitat variables at various spatial scales (within radii of varying size). However, because FPT analysis produces results for overlapping radii along a track, we developed a two-stage approach to subsample the FPT data for habitat analysis, and thereby reducing spatial autocorrelation. First, we used only the original (not interpolated) locations to address habitat associations. Second, we selected the location of maximum FPT for a given radius and excluded all other locations with overlapping radii (within $2\times$ the radial distance from that location), and then searched for the maximum FPT (most intense ARS) among the remaining locations. This iterative approach was repeated until the entire track had been subsampled such that none of the radii overlapped (Fig. 2). The outcome of these subsampling iterations was a range of possible FPTs for any given individual, including the less tortuous portions of the flight path (lower FPT). As FPT radius increases, the sample size (n) and range of FPT values decreased with this subsampling procedure. We then analyzed the habitat characteristics within the various radii from the subsampled points, using the FPT metric as a continuous response variable.
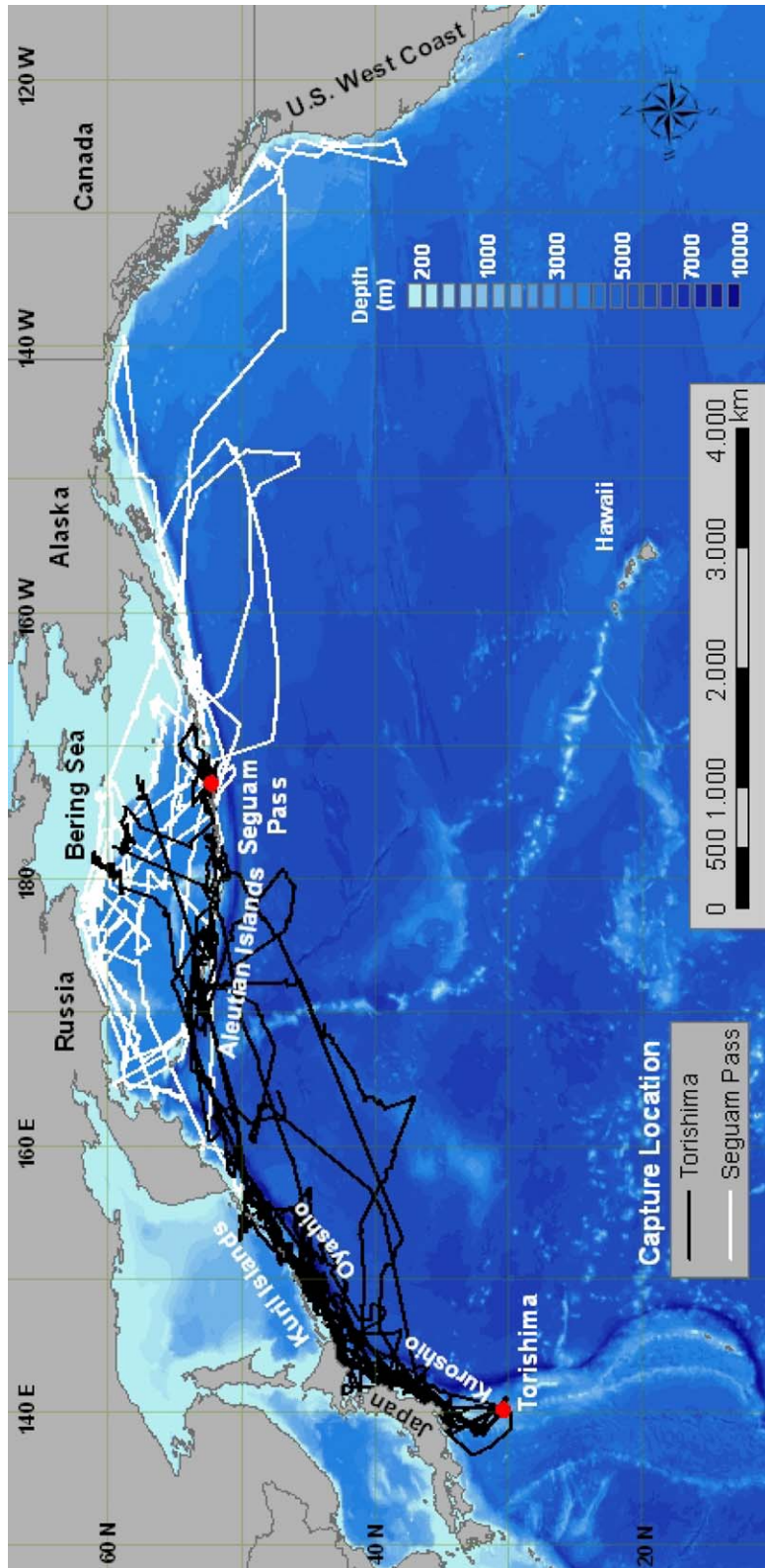
Fig. 1. Flight paths of short-tailed albatrosses satellite tracked from the breeding colony on Torishima, Japan (*n* = 11) and Seguam Pass, Alaska (*n* = 3, captured at-sea). Individuals were tracked May–November 2002 and 2003.

Table 1
Summary of satellite tracking data for 14 short-tailed albatrosses tagged at Torishima, Japan, and Seguam Pass, Alaska, following the breeding seasons in 2002 and 2003

Animal ID[a]	Gender	Age (yrs)	♯ Days tracked	♯ Filtered locations	Minimum distance traveled (km)	Deployment date
Torishima						
B0963[b,c]	F	—[h]	104	664	11,732	10 May 2003
A0837[d,e]	F	9	101	680	9525	6 May 2003
A1034[b,c]	F	6	113	634	13,661	6 May 2003
A1076[d,e]	F	5	138	369	14,303	7 May 2002
B0899[b,c]	M	—[h]	54	400	8454	6 May 2003
B0900[b,c]	M	—[h]	87	483	14,205	10 May 2003
B0962[d,e]	M	18	74	437	9749	10 May 2003
A1181[b,c]	M	4	86	279	15,364	7 May 2002
A1311[b,c]	M	4	51	131	5869	10 May 2003
A1281[d,f]	M	3	81	375	9621	7 May 2002
A1291[b,c]	—	3	120	427	16,863	7 May 2002
Seguam pass						
A7040[b,g]	M	2	81	513	13,264	17 August 2003
B2428[b,c]	M	<1	110	509	27,814	12 August 2003
B2493[b,c]	M	<1	102	808	24,251	12 August 2003

[a]Actual band # is preceded by 13, e.g., 13A0837.
[b]Duty cycle: 8 h on and 24 h off.
[c]Satellite transmitter brand: Sirtrack.
[d]Duty cycle: 6 h on and 18 h off.
[e]Satellite transmitter brand: Toyocom.
[f]Satellite transmitter brand: North Star.
[g]Satellite transmitter brand: Microwave.
[h]Unbanded individuals, but all had adult plumage (⩾8 yr old).

2.3. Marine habitats

We selected seven variables to characterize marine habitats; seafloor depth, chlorophyll a concentration (chl a), sea surface temperature (SST), gradients in these three variables, and wind speed. Depth was obtained from the General Bathymetric Chart of the Oceans (British Oceanographic Data Centre, www.bodc.ac.uk). We used a grid of 5 min latitude and longitude resolution (~8 km). We defined bathymetric domains as: continental shelf (⩽200 m depth), shelf break (>200 m and ⩽1000 m), slope (>1000 m and ⩽3000 m), and oceanic (>3000 m). Chl a concentration (mg m^{-3}) was obtained from Moderate Resolution Imaging Spectroradiometer Terra imagery (level 3 post processing) provided by the Physical Oceanographic Data Archiving and Acquisition Center (NASA Jet Propulsion Laboratory, http://podaac.jpl.nasa.gov). We used a ~4-km spatial resolution for Chl a, and monthly composites to compensate for frequent cloud cover. We obtained SST from the same source as chl a imagery

and of the same spatial resolution. However, we were able to use a finer temporal resolution of 8-day composites. As a proxy for frontal boundaries, we calculated gradients in SST, chl a, and depth over distance (3 × 3 pixel) using the Sobel Gradient Operator (Russ, 1995).

We obtained QuikSCAT ocean wind data for 10 m above the ocean surface from the SeaWinds sensor aboard the QuikBird satellite. These data were obtained from remote sensing systems (www.remss.com; sponsored by the NASA Ocean Vector Winds Science Team) and provided in a global coverage of 0.25° latitude/longitude (~23 km) spatial resolution grids of wind speed (m s^{-1}), direction, and a binary rain flag. We used a temporal resolution of 3-day averages, and removed erroneous data affected by rainfall.

2.4. Albatross habitat associations

In our multi-scale analysis of albatross habitat associations, we used a lower threshold of ~20 km spatial scale (10 km FPT radius); because this was
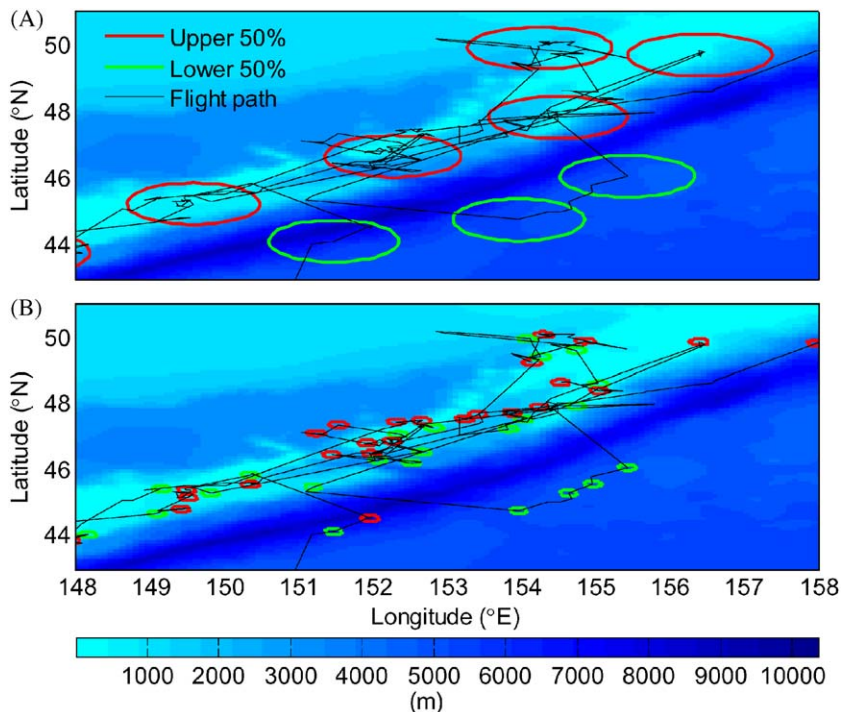
Fig. 2. Locations and first-passage time (FPT) radii for a portion of the flight path of albatross B2493, superimposed over a map of sea floor depth near the Kuril Islands, Russia. Regions of area-restricted search vs. more transitory movements are signified by longer (upper 50%) and shorter (lower 50%) FPT, respectively, for spatial scales of 70 km (A) and 10 km (B) radii.

the coarsest resolution of the habitat data. The upper limit was constrained by sampling limitations: as FPT radius increased, sample size is diminished. For each subsampled FPT location along a track, we extracted median values (to reduce the influence of outliers) of each habitat variable, including gradients, within areas of different radii. When FPT in a given area was greater than ~1.5 times the temporal resolution of a particular environmental coverage, we time-averaged multiple consecutive files within the given FPT radius. For example, if FPT was 16 days at a search radius of 160 km, we extracted the median from a single chl *a* file (monthly composite) within the radius, but extracted the median from two SST files (8-day composite) and five wind speed files (3-day composite).

2.5. Statistical analyses

We used mixed effects linear models (SAS, 1990) with FPT as the response variable to assess habitat affinities. Individual albatross was included as a random effect in all models, whereas habitat variables (chl *a*, SST, depth and their gradients, wind speed, and interactions) were fixed effects and

retained only if they improved model fit. We did not include sex or age variables in the models because of limited sample sizes. We used Akaike's information criteria (AIC) to identify the most parsimonious model (Burnham and Anderson, 1998). For competing models with a $\Delta AIC < 2$, we selected the model with the least number of parameters. All possible combinations of main effects and interactions were considered. All variables were visually tested for normality using normal probability plots; FPT and depth were the only variables requiring transformation $[y = \ln(x + 1)]$. All model residuals were examined for secular (i.e. linear) or periodic (i.e. cyclic) signals and evaluated with autocorrelation metrics (Priestley, 1982). Remote sensing data processing and FPT analyses were conducted with custom programs using Matlab software (The MathWorks, Inc.).

3. Results

3.1. Albatross migration and movements

The ages of 11 of 14 albatrosses (three were unbanded) tracked during this study ranged from

<1 to 18 yr, with an unequal sex ratio of nine males to four females, and one individual of undetermined gender. The three youngest albatrosses ($\leqslant 2$ yr) were males captured in the Aleutian Islands (Table 1). Deployment durations ranged from 51 to 138 days. After filtering, we obtained ∼five locations per individual per day ($\overline{X} = 5.3$, SE $= 0.45$, range $=$ 2.6–8.3, $n = 14$ PTTs).

Albatrosses tracked from Torishima ($n = 11$) initially traveled north within the Kuroshio Current system (Fig. 1). From here, however, two different migration patterns were observed: six individuals remained within the coastal realm, while the five others traveled offshore and northeast to the western Aleutian shelf. There was a notable difference in the at-sea distribution and movement patterns of individuals captured at Seguam Pass and Torishima (Fig. 1). Seguam Pass birds ranged much more widely, venturing into coastal waters of the western Bering Sea and California Current. Indeed, the <1 yr old birds captured in Seguam Pass traveled nearly twice the distance per day ($\overline{X} =$ 245 ± 8 km d^{-1}) than older albatrosses ($\overline{X} = 133\pm$ *Table*1).

The peak in variance of FPT among all individuals occurred at a search radius of 70 km (Fig. 3). However, as evidenced by the dispersion about the mean, there was considerable variability among individuals in scale of interaction with the environment. A comparison of albatrosses B0899 and A1181 illustrates these differences. Upon leaving Torishima, albatross B0899 took a direct route to the western Aleutian Islands, where his flight path became highly tortuous within a consistent spatial scale (Fig. 4A), thus producing a narrow peak in FPT variance at 70 km (Fig. 4B). In contrast, albatross A1181 exhibited ARS patterns within two different regions and at greater spatial scales (Fig. 4A), producing a broader peak in FPT variance and at a much larger radius (230 km) than albatross B0899 (Fig. 4B). The radius of maximum FPT variance was not related to the total number of PTT locations ($R^2 < 0.12$, $P < 1.59$, $n = 14$, $P = 0.23$) or to the mean number of locations per day ($R^2 < 0.07$, $n = 14$, $P = 0.35$). Therefore, differences in the spatial scale of ARS among individuals were not merely artifacts of variability in PTT performance and deployment lengths.

Variability in the scale of ARS was also evident within a given movement path, as exemplified by albatross A0837. For this individual, small-scale and large-scale ARS occurred in different regions, although large-scale ARS sometimes encompassed regions of small-scale ARS (Fig. 5). To assess the
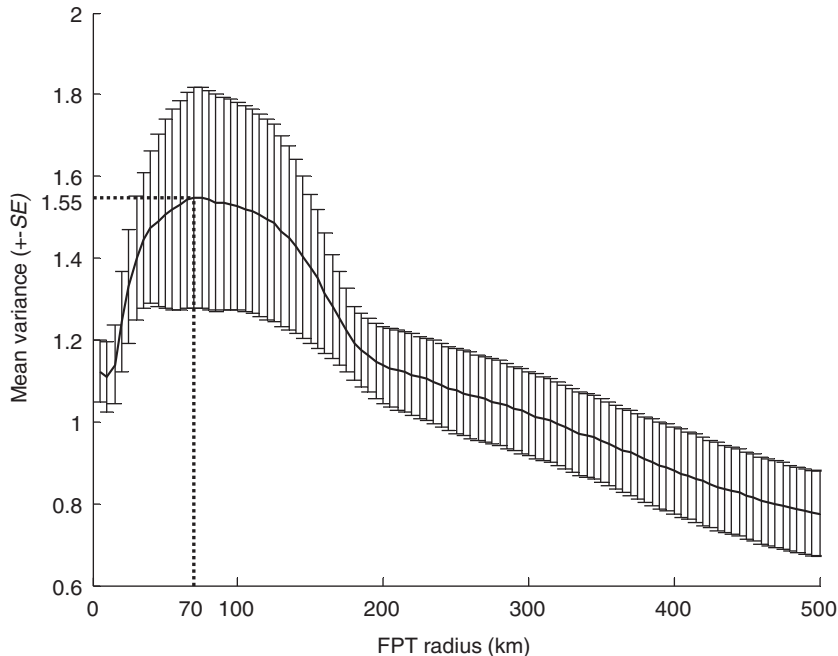

Fig. 3. Mean variance ($\pm$ SE) in log-transformed first-passage time (FPT) vs. FPT radius for 14 satellite-tracked short-tailed albatrosses. The peak in variance occurred at a search radius of 70 km.
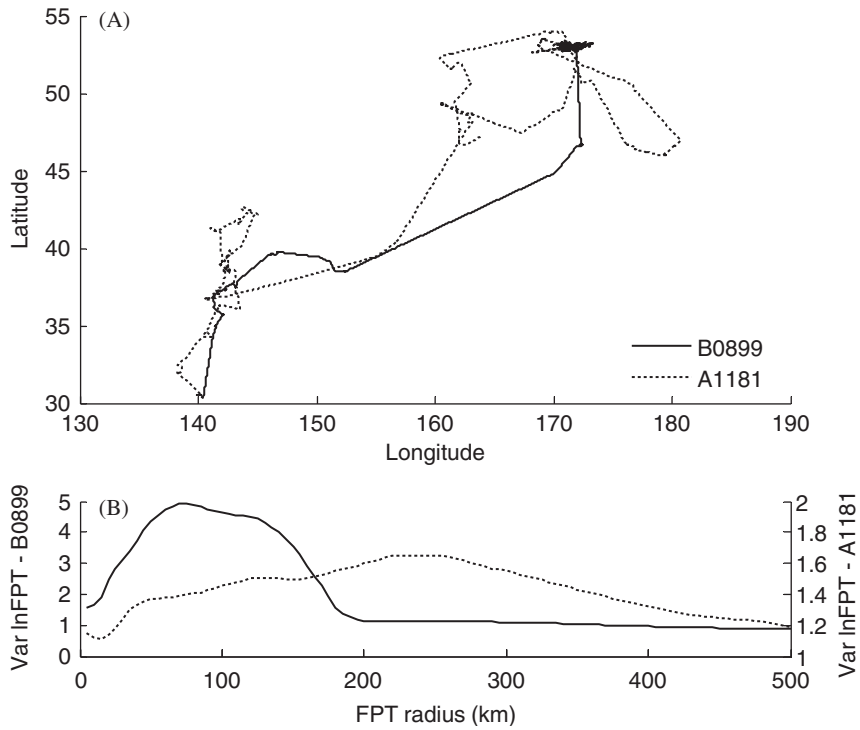
Fig. 4. Flight paths of albatrosses B0899 and A1181 showing differing spatial scales of area-restricted search (A) and corresponding differences in peaks in variance of the of first-passage time (FPT, log transformed) among various search radii (B). The single, well defined region of area-restricted search of albatross B0899 produced a well-defined peak in variance of FPT that occurred at a smaller spatial scale than A1181.
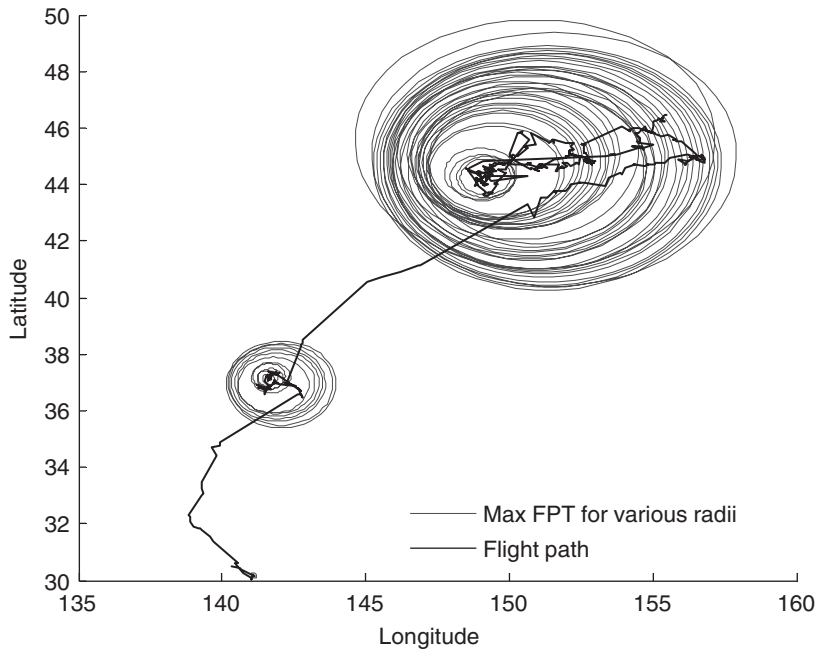

Fig. 5. Locations of maximum first-passage time (FPT) for search radii from 10 to 500 km, at 10-km increments along the flight path of albatross A0837. The locations of the 50 radii illustrate how various spatial scales of area-restricted search can occur at different locations along flight paths.

Table 2
Mixed effects linear model results modeling the effect of marine habitat variables on first-passage time (FPT) for short-tailed albatrosses

Variable	10 km $R^2 = 0.30$, $n = 775$, ΔAIC = 4.6			70 km $R^2 = 0.40$, $n = 304$, ΔAIC = 2.0			160 km $R^2 = 0.51$, $n = 140$, ΔAIC = 7.7			220 km $R^2 = 0.49$, $n = 104$, ΔAIC = 3.5		
	β	t	P	β	t	P	β	t	P	β	t	P
wspd	−0.088	−6.78	<0.001	−0.660	−4.94	<0.001	−0.758	−2.98	0.004	−0.162	−3.89	<0.001
depth	−0.152	−4.84	<0.001	−0.907	−6.27	<0.001	−0.931	−3.23	0.002	−0.373	−3.63	<0.001
depthg	16.195	2.12	0.035	11.210	4.11	<0.001	27.846	5.04	<0.001	29.916	3.69	<0.001
chl	0.138	2.58	0.010				−1.557	−2.57	0.011	−2.131	−2.30	0.024
chlg				3.731	1.62	0.107	50.973	4.90	<0.001	50.877	3.02	0.003
SST							0.001	0.04	0.966	−0.008	−0.20	0.841
wspd*depth				0.066	3.88	<0.001	0.076	2.36	0.020			
depth*depthg	−1.666	−1.66	0.098									
chl*SST							0.217	3.28	0.001	0.238	2.38	0.020
chlg*SST							−5.984	−3.66	<0.001	−4.842	−1.76	0.082

Analyses were conducted for eight spatial scales (FPT radii) of 10–220 km, in 30 km increments, and results of four final models are presented (10, 70, 160, and 220 km radii). Individual was included in all models as a random effect. Environmental variables of seafloor depth (log transformed), wind speed (wspd), chlorophyll *a* (chl), sea surface temperature (SST), plus gradients (g) of each (except wspd) and selected interactions (interactions tested: wspd*depth, wspd*chl, wspd*SST, SST*chl, SSTgrad*chl, SSTgrad*depth, chlgrad*depth, depthgrad*chl, depthgrad*SST, depthgrad*depth) were evaluated as fixed effects. ΔAIC is the change in Akaike's information criterion between the final and next best models. R^2 was calculated from log-likelihood ratios following Magee (1990).

effect of variation in ARS scales on habitat associations, we constructed models of habitat use for 8 FPT radii (10–220 km, at 30-km increments). Mean (range, *n*) FPT varied from 0.30 day (0.01–3.1, 931) for 10 km to 7.3 days (0.44–56.6, 113) for 220 km radius.

3.2. Albatross habitat associations

Our most parsimonious models included wind speed, depth (median or gradient), and chl *a* (median or gradient) as highly significant variables at all spatial scales (Table 2). There was a positive relationship between FPT and depth gradient and chl *a* gradient. The relationship between FPT and chl *a* was positive at the smallest spatial scales (10 km), but negative at larger scales ($\geqslant 160$ km;

Table 2). FPT was inversely related to water depth and wind speed. SST was only a significant model component at two of the larger spatial scales (Table 2). Interactive effects of habitat variables on FPT included depth*depth gradient at 10 km, wind speed*depth at 70 and 160 km, and chl *a**SST and chl *a* gradient*SST at the 160 km and 220 km search radii.

Model fit was lowest at 10 km and 40 km FPT radii ($R^2 = 0.30$ and 0.31, respectively), improved for 70 km ($R^2 = 0.40$), and stabilized at $R^2 \leqslant 0.51$ for larger FPT radii (Table 2). Because of changes in FPT variance, number of model parameters, and *n*, R^2 values are not directly comparable. However, this trend was consistent when holding the number of parameters constant and despite decreases in sample size at larger scales. The improvement in
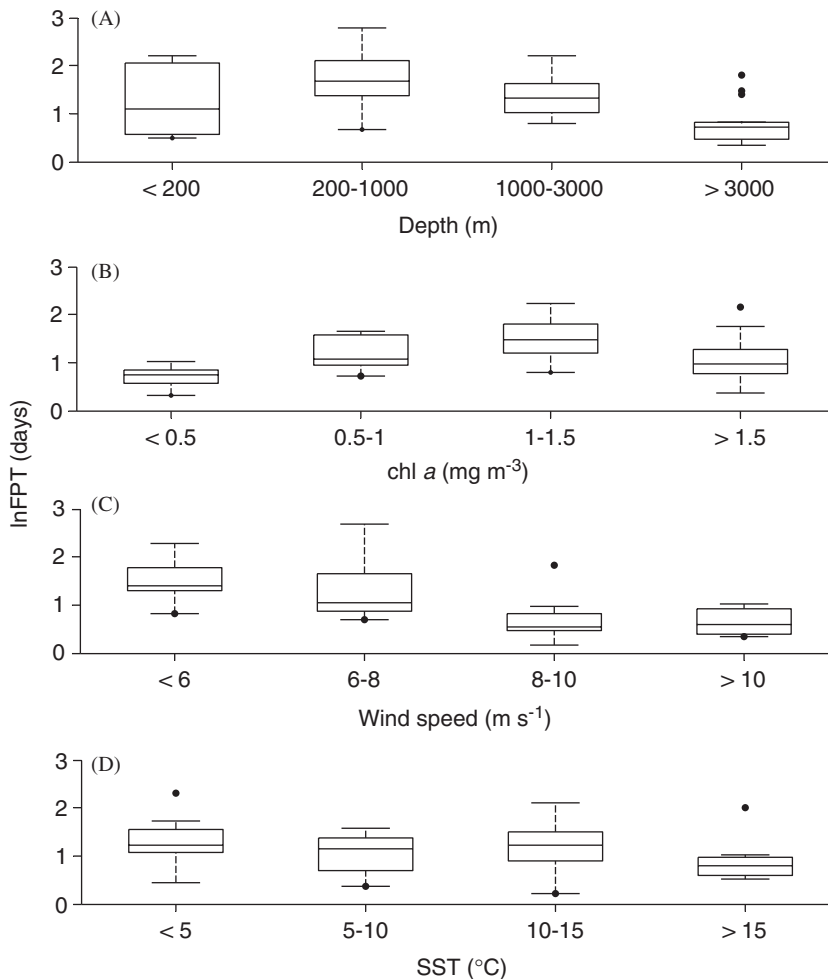

Fig. 6. First-passage time of short-tailed albatrosses at a 70 km search radius in relation to marine habitat variables. Bin sizes represent specific depth domains (A) and equal sample sizes of chl *a* (B), wind speed (C), and sea-surface temperature (D) among bins. Box plots depict median (horizontal line), interquartile range (box), 1.5*interquartile range (error bars), and outlying data (dots).

model fit for the 70 km FPT radii coincides with the peak variance in FPT (Fig. 3), indicating that habitats measured at this spatial scale explained more variance in FPT. Graphically, the improved fit of a 70 km FPT radius model over a 10 km model is exemplified by the ARS behavior for albatross B2493 (Fig. 2). Therefore, the remaining results focus on the 70 km FPT spatial scale.

Among the bathymetric domains, FPT was greatest within continental shelf break and slope regions, compared to shelf and oceanic waters (Fig. 6A) and generally increased within regions of greater bathymetric gradients (Fig. 7A). FPT was higher in waters of greater chl *a* concentrations (Fig. 6B) and chl *a* gradients (Fig. 7B), suggesting the birds followed a more contorted path within elevated productivity regions. In contrast, we detected a negative effect of wind speed on FPT, with the greatest values at the lowest wind speeds $<5\,\mathrm{m\,s^{-1}}$ (Fig. 6C). FPT showed no consistent

trend with respect to SST (Fig. 6D) or gradient (Fig. 7C), except that FPT was shorter and less variable within the higher SST bin ($>15\,°C$). These results are supported by variables retained and their coefficients from the statistical modeling (Table 2). Our search-radius dependent subsampling procedure for FPT locations was successful in reducing autocorrelation in the response variable. Autocorrelation was low ($r<0.20$) and attempts to model it (using harmonic terms) offered little improvement in overall fit, likely because periodicity was highly irregular within and among individuals at the various FPT radii (e.g., Fig. 4).

Chl *a* was greatest over the shelf ($\overline{X} = 1.44$, SE $= 0.23$) and declined linearly to oceanic waters ($\overline{X} = 0.73$, SE $= 0.06$). Areas of greatest concentrated search activity for albatrosses (identified as the upper quartile of FPT, 70-km radius) sometimes coincided with persistent chl *a* hot spots, particularly off the northeast coast of Japan, the Kuril
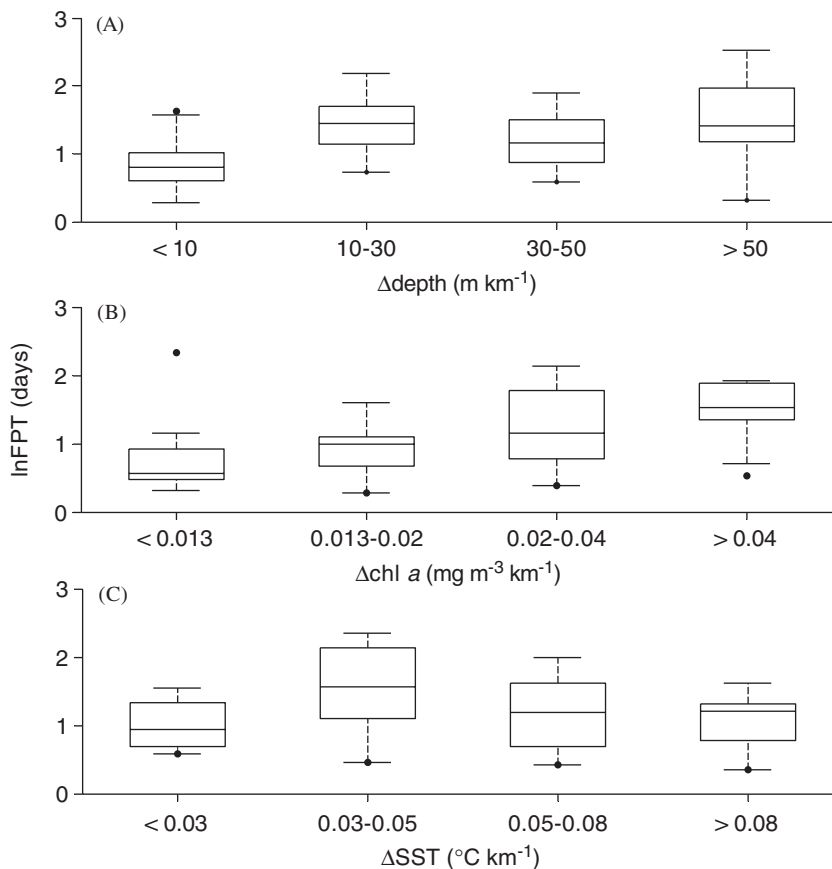

Fig. 7. First-passage time of short-tailed albatrosses at a 70 km search radius in relation to gradients for marine habitat variables of depth (A), chlorophyll *a* concentration (B), and sea surface temperature (C). Bin sizes were selected for each metric to produce approximately equal sample sizes among bins.

Islands, Aleutian Islands, and southeastern Bering Sea shelf (Fig. 8). The Kuroshio Extension was not a prominent feature used by short-tailed albatrosses during their post-breeding season migration from Torishima. In May, some birds crossed the northern part of this region, especially those that moved northeast over oceanic waters when transiting to the Aleutian Islands (Fig. 9). However, these birds engaged in limited ARS behavior in this region (Fig. 8), as evidenced by the small FPT values along this portion of their tracks.

4. Discussion

4.1. Marine habitats

Bathymetric relief (e.g., banks, shelf-breaks) and hydrographic fronts (e.g., eddies, tidal fronts) are commonly associated with productivity hot spots. As such, these features are commonly sought by many foraging seabirds, including albatrosses (Hunt et al., 1996; Rodhouse et al., 1996; Hyrenbach et al., 2002; Yen et al., 2004). Our results suggest that during spring and summer (May–July) surface chl *a* standing stocks are greatest on the shelf and progressively decline with increasing water depth, with few exceptions depending on month. Primary production alone, however, does not explain short-tailed albatross hot spots, as areas of foraging do not always coincide with regions of greatest chl *a* (Fig. 8). This may be explained, in part, by time lags between increased primary productivity and associated increased availability of albatross prey, but also by habitat preferences of prey species consumed (Rodhouse et al., 1996; Waugh et al., 1999; Cherel et al., 2000).

What little information exists on short-tailed albatross diets comes exclusively from the breeding season and suggests that squids, crustaceans, and fishes are important prey (Hattori, 1889; Hasegawa and DeGange, 1982). The Japanese common squid, *Todarodes pacificus* (formerly *Ommastrephes sloani*
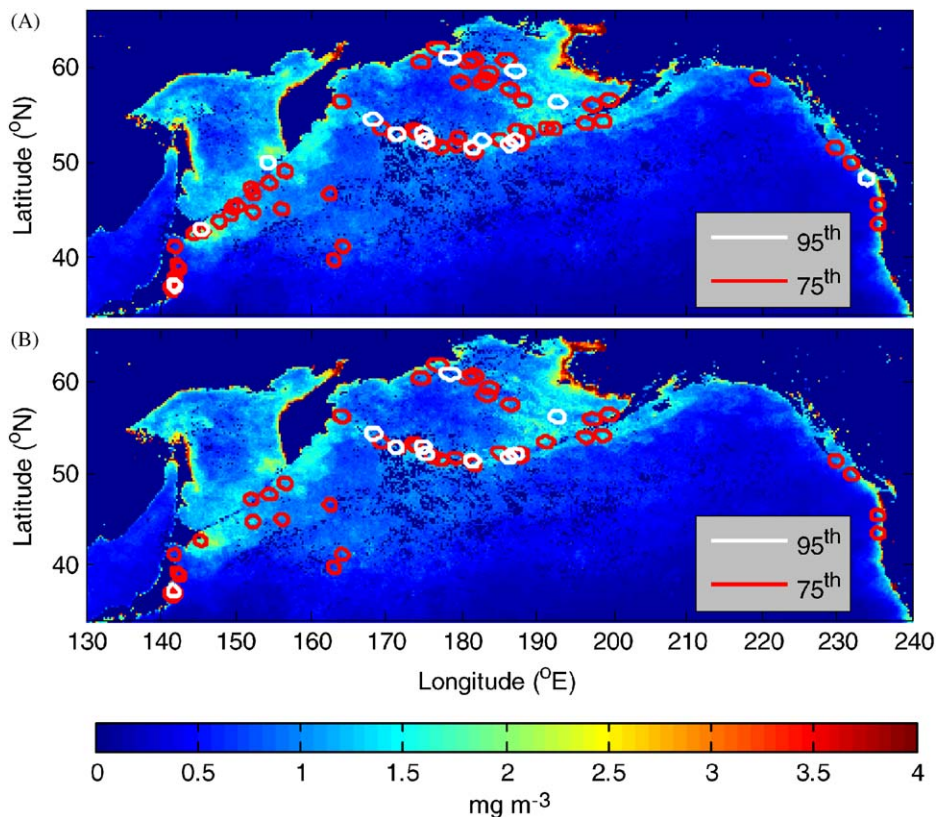

Fig. 8. (A) Locations for 95th and 75th percentile of first-passage time at the 70-km search radius for each of the 14 short-tailed albatrosses tracked. Plot (B) includes only radii where wind speed was ≥4.4 m s^{-1} (the lower quartile of wind speeds for locations in plot a) and, therefore, area-restricted search activity was less likely to be limited by low wind speeds. Radii are superimposed over a composite image of chlorophyll *a* concentration for the study period (May–November, 2002 and 2003).
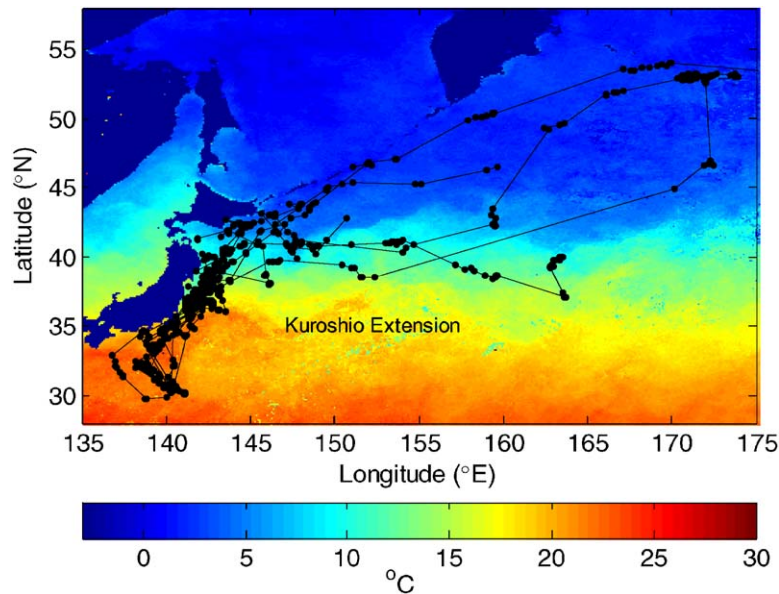
Fig. 9. Average sea-surface temperature and short-tailed albatross satellite telemetry locations in May, 2002 and 2003. Lines connect satellite fixes (points) of individual albatrosses. The confluence of the cooler Oyashio Current and warmer Kuroshio Current is evident and albatrosses tended to only use the northern portion of the Kuroshio Extension.

pacificus), was a common diet item (Hattori, 1889) for short-tailed albatrosses and is common, although variable in abundance, off Japan (Sakurai et al., 2000; Mokrin et al., 2002). *T. pacificus* is particularly abundant within the Kuroshio-Oyahio transition zone west of 160° E longitude (Mori et al., 2002), a region that was visited by all albatrosses tracked from Torishima. In the Bering Sea, midwater squid concentrations (primarily *Berryteuthis magister*, *Gonatopsis borealis* in the upper layer, 200–500 m) were greatest near the outer continental shelf and slope, with the standing stocks in these regions comprising one quarter of the mesopelagic squid biomass in the western Bering Sea (Sinclair et al., 1999). Midwater prey become available to albatrosses through; scavenging on discards from subsurface predators and fisheries, post-mortem individuals that are positively buoyant, and vertical migration (Lipinski and Jackson, 1989; Croxall and Prince, 1994). Therefore, the distribution of squids provides a plausible explanation for the association of short-tailed albatrosses with shelf break and slope regions, which are habitats frequented by other seabird species known to exploit similar niches (e.g., Northern Fulmar, *Fulmarus glacialis*; Shuntov, 1972; Springer et al., 1999).

Wind speed is an important determinant of marine bird distributions at a variety of spatial scales (Spear and Ainley, 1998; Spruzen and Woehler, 2002). Our results underscore the significance of wind speed as an important habitat variable influencing short-tailed albatross movement patterns. The negative relationship between FPT and wind speed and interaction between wind speed and depth suggest that foraging albatrosses "trapped" by low winds slow down their progress, giving rise to tracks potentially reminiscent of ARS behavior. This is evident in Fig. 2A, with one of the upper 50-percentile locations showing little ARS activity, despite having a long FPT. This result is consistent with prior evidence that albatrosses will travel shorter distances and fly slower during high pressure conditions (Jouventin and Weimerskirch, 1990), and they seem to concentrate in areas of low wind conditions (Spruzen and Woehler, 2002). Thus, when attempting to define key foraging areas from residency time alone, it is important to also consider wind speed (e.g., Fig. 8A,B).

4.2. Hot spots

Our telemetry data demonstrate that short-tailed albatrosses did not disperse widely throughout the subarctic North Pacific and are consistent with infrequent ship-based observations in the gyres (Sanger, 1972; McDermond and Morgan, 1993).

The primary hot spots for short-tailed albatrosses in the Northwest Pacific Ocean and Bering Sea occur where a variety of underlying physical processes enhance biological productivity or prey aggregations. Upon departing Torishima, all the tagged albatrosses traveled to the outer continental shelf off northeast Honshu, a convergence region of the Kuroshio and Oyashio currents, with some influence of the Tsugaru warm current (Qu et al., 2001; Shimizu et al., 2001; Qiu, 2002). Albatross activity in this boundary region (36–40°N) was greatest in May and June along the shelf break. Primary production in this region was evident in chl *a* imagery for May and June, but it was not persistent through the remaining study months. However, the northern convergence region to the east of northern Japan and the southern Kuril Islands was evident as a persistent chl *a* hot spot (Fig. 8) and a region of extensive use by albatrosses (Fig. 9). Such turbulent mixing and eddy formation within the Kuroshio and Oyashio convergence region extends into the western central gyre (Qu et al., 2001; Shimizu et al., 2001; Qiu, 2002). However, in our study, albatrosses made mainly transitory excursions along the northern boundary of the Kuroshio Extension and Oyashio Front while in-route to the Aleutian Islands and Bering Sea. It is intriguing that the satellite-tracked albatrosses did not venture into the sub-arctic gyre or forage along the Transition Domain, like other North Pacific pelagic predators including species known also to feed on squid, such as Dall's porpoises (*Phocoenoides dalli*), sperm whales (*Physeter catodon*), fur seals (*Callorhinus ursinus*), and Laysan albatrosses (*Poebastria. immutabilis*; Springer et al., 1999; Hyrenbach et al., 2002; Ream et al., 2005).

The Aleutian Islands, in particular, were a primary foraging destination for short-tailed albatrosses, with the maximum FPT for eight of the 14 birds occurring in this region. Passes within the Aleutian Islands with the greatest albatross ARS activity included Near, Buldir, Shumagin, and Seguam. Currents flowing through these relatively narrow and shallow passes cause localized upwelling, frontal zone formation, and eddies that enhance mixing, nutrient supply, and productivity (Shuntov, 1993; Reed and Stabeno, 1994; Lapshina, 1996; Coyle et al., 1998). The significance of passes as feeding zones for breeding and migratory seabirds, is well documented (Springer et al., 1996b; Hunt et al., 1998) and their use by short-tailed albatrosses have been described from ship-based

observations (Piatt et al., 2006) and historically by their prevalence in middens of native Aleut communities (Yesner, 1976).

Within the Bering Sea, short-tailed albatross locations were most associated with the shelf break and slope, excursions over deeper water were typically transitory. The Bering Sea shelf break and slope and associated currents are well defined features of enhanced productivity and use by upper trophic level predators (Shuntov, 1972; Springer et al., 1999; Robson et al., 2004). The intrusion of the Alaska Stream through the Aleutian Islands creates an along shelf current (Stabeno and Reed, 1991, 1994) that fuels elevated primary productivity, particularly in the early spring. The few excursions of albatrosses onto the Bering Sea shelf occurred in the region south of St. Matthew Island and in the southeast, both areas where frontal zones commonly occur (Hunt, 1997; Belkin, 2003). The fact that short-tailed albatrosses spent little time in the central Bering Sea is consistent with ship-based observations indicating low seabird densities over deeper waters of the central Bering Sea (Shuntov, 1972; Wahl et al., 1989; Springer et al., 1999).

4.3. The scale of habitat associations and first passage time analysis

Identifying the spatial and temporal scales at which animals respond to environmental cues is a central issue in ecology (Fauchald, 1999; Fauchald et al., 2000; Schneider, 2001). Our results confirm the use of FPT as a valuable analytical tool for identifying the spatial scales of foraging activities and habitat associations of continuously tracked, free-ranging animals. Habitat use models at a scale of 70-km search radius best explained variation in FPT of short-tailed albatrosses. Previous studies have documented strong seabird–habitat associations over tens of kilometres, both in the sub-arctic North Pacific and the Bering Sea (Schneider, 1991; Gould and Piatt, 1993). The prevalence of spatial patterns over intermediate scales (e.g., shelf-breaks, frontal systems) may partly explain why our finer-scale models (10 km and 40 km search radius) explained less variation in short-tailed albatross habitat associations (Table 2). It also is important to consider how the resolution of sampling instruments can affect these scale-dependent patterns; for example, a mean of five locations per animal-day obtained in this study vs. global positioning system receivers that provide up to tens of thousands of

locations per day (Weimerskirch et al., 2002; Fritz et al., 2003). Nevertheless, FPT identified appropriate spatial scales for our application, which we used to create general habitat use models capable of explaining half of the variation in short-tailed albatross movements. These results are particularly encouraging given that we did not include other variables such as prey distribution and occurrence of fishing vessels, which are known to attract short-tailed albatrosses.

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