



Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses *Phoebastria nigripes* in the North Pacific

SARAH E. GUTOWSKY,^{1*} YANN TREMBLAY,^{2,3} MICHELLE A. KAPPES,^{2,4} ELIZABETH N. FLINT,⁵
JOHN KLAVITTER,⁶ LEONA LANIAWE,⁶ DAN P. COSTA,² MAURA B. NAUGHTON,⁷
MARC D. ROMANO⁷ & SCOTT A. SHAFFER^{8,9}

¹Department of Biology, Dalhousie University, Halifax, NS, Canada

²Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, USA

³Institut de Recherche pour le Développement (IRD/IFREMER/UM2), Sète Cedex, France

⁴Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

⁵USFWS, Pacific Reefs Islands National Wildlife Refuge Complex, Honolulu, HI, USA

⁶USFWS, Midway Atoll National Wildlife Refuge, Midway Atoll, HI, USA

⁷USFWS, Pacific Region, Migratory Birds and Habitat Programs, Portland, OR, USA

⁸Department of Biological Sciences, San Jose State University, San Jose, CA, USA

⁹Institute of Marine Sciences, University of California, Santa Cruz, CA, USA

Past tracking studies of marine animals have primarily targeted adults, biasing our understanding of at-sea habitat use toward older life stages. Anthropogenic threats persist throughout the at-sea ranges of all life stages and it is therefore of interest to population ecologists and managers alike to understand spatiotemporal distributions and possible niche differentiation between age-classes. In albatrosses, particularly little is known about the juvenile life stage when fledglings depart the colonies and venture to sea with no prior experience or parental guidance. We compared the dispersal of 22 fledgling Black-footed Albatross *Phoebastria nigripes* between 2006 and 2008 using satellite telemetry and 16 adults between 2008 and 2009 using geolocators from Midway Atoll National Wildlife Refuge, Northwest Hawaiian Islands. Following tag deployment, all fledglings spent several days within the calm atoll waters, then travelled northward until reaching 750–900 km from the colony. At this point, fledgling distributions approached the productive North Pacific Transition Zone (NPTZ). Rather than reaching the high chlorophyll *a* densities on the leading edge of this zone, however, fledglings remained in areas of low productivity in the subtropical gyre. In contrast, adult albatrosses from the same breeding colony did not utilize the NPTZ at this time of year but rather ranged throughout the highly productive northern periphery of the Pacific Ocean Basin among the shelf regions off Japan and the Aleutian Islands. The dichotomy in habitat use between fledglings and adults from Midway Atoll results in complete spatial segregation between age-classes and suggests ontogenetic niche separation in this species. This research fills a large knowledge gap in at-sea habitat use during a little known yet critical life stage of albatrosses, and contributes to a more comprehensive understanding of differential mortality pressure between age-classes and overall conservation status for the vulnerable Black-footed Albatross.

Keywords: dispersal, geolocators, habitat use, juvenile, Procellariiform, satellite telemetry, seabird.

Management and conservation of animal populations require an understanding of where an

organism is found in space and time, and the associated habitat characteristics influencing this spatiotemporal distribution (Costa *et al.* 2012). However, for most far-ranging migratory species, this spatial information can be difficult to obtain.

*Corresponding author.

Email: sarahegutowsky@gmail.com

With roughly 1800 migratory bird species globally, gathering comprehensive information on the distribution of any species throughout the entire annual and life cycle poses a common challenge (Sekercioglu *et al.* 2004). This is especially true of long-distance migratory marine species, for which direct observation over long periods for the majority of the life cycle is often logistically impossible (Hazen *et al.* 2012).

Many pelagic seabirds range across extraordinary oceanic distances spanning multiple management jurisdictions and anthropogenic threats, and thus encounter a wide range of risks to survival and reproduction throughout their lifetime (Shaffer *et al.* 2006, Egevang *et al.* 2010, Fijn *et al.* 2013). Of all seabird families, albatrosses (Diomedidae) are the most threatened, with 18 of 22 species listed as Globally Threatened by the IUCN and the remainder Near Threatened (IUCN 2012). Investigations of at-sea distributions throughout all seasons and life stages are therefore critical in building a spatially and temporally integrated survey useful for conservation and management applications.

Little information exists on the juvenile life stages of albatrosses, despite representing nearly half the total population of many species (Weimerskirch *et al.* 2006). When fledging occurs, juvenile albatrosses depart to sea, seemingly without parental influence (Tickell 2000). Hence, they must develop and refine their skills at flying as well as their ability to successfully search for and capture prey without guidance from experienced adults. It is unclear how fledglings are able to find food, navigate in a pelagic environment or assess how temporal and environmental cues such as season, lunar cycles, currents or dynamic features associated with biological productivity may affect prey availability. It is therefore not surprising that mortality rates of albatrosses are generally highest during the first few years of life at sea (Fisher 1975, Warham 1990, Weimerskirch & Jouventin 1997).

Information on the spatial distribution of juveniles is difficult to obtain due to high mortality rates and an extended multi-year at-sea period following fledging, precluding the retrieval of expensive electronic tracking devices. Our current understanding of juvenile albatross postnatal dispersal and at-sea behaviour is based on only three previously studied species (Weimerskirch *et al.* 2006, Alderman *et al.* 2010, Riotte-Lambert &

Weimerskirch 2013, Deguchi *et al.* in press). These studies tracked fledgling Wandering Albatross *Diomedea exulans*, Shy Albatross *Thalassarche cauta* and Short-tailed Albatross *Phoebastria albatrus* for periods of 10 days to one full year. Wandering and Shy Albatross juvenile core areas did not overlap spatially with adults; however, the nature of this segregation differed between species. Wandering Albatross fledglings appear to concentrate into much less productive regions but overlap more with fishing operations compared with adults (Weimerskirch *et al.* 2006, Riotte-Lambert & Weimerskirch 2013), whereas young Shy Albatrosses exhibit the opposite pattern, exploiting more productive oceanic areas than adults (Alderman *et al.* 2010). Short-tailed Albatross juvenile distributions have not been directly compared with those of adults but were found to range widely throughout the entire North Pacific rim, as did older age-classes (Deguchi *et al.* in press). Documenting differential habitat use has important implications for population ecology and conservation biology due to the potential consequences for niche width and differential mortality pressures faced by different age-classes (Weimerskirch *et al.* 1997, 2006).

Black-footed Albatross *Phoebastria nigripes* in the North Pacific Ocean exhibit some age-related differences in distribution at sea (Hyrenbach *et al.* 2002). Although the at-sea movements of adults from some colonies have been studied previously (Fernández *et al.* 2001, Hyrenbach *et al.* 2002, Shaffer *et al.* 2005, Fischer *et al.* 2009, Kappes *et al.* 2010), nothing is known about patterns of juvenile dispersal from the natal colony. The IUCN listed Black-footed Albatrosses as Vulnerable in 2012, based on a projected rapid decline over the next three generations due primarily to incidental fisheries mortality (Lewison & Crowder 2003, IUCN 2012). Therefore, it is critical to assess whether differential mortality of juveniles due to distribution at sea may be contributing to this decline. Unfortunately, because the distribution of juveniles has not been directly studied, little can be said about the influence of at-sea habitat use on the mortality of juvenile North Pacific albatrosses. In the present study, we identify for the first time the initial dispersal, at-sea distributions and habitat associations of fledglings of this vulnerable North Pacific albatross species. By combining concurrent fledgling and adult tracking data (from satellite transmitters and light-sensing archival tags) during the first month of post-fledging life out to sea, we

assess how Black-footed Albatross fledglings and adults from the same colony segregate at sea over large spatial scales.

METHODS

Study site and tracking

We followed 22 fledgling Black-footed Albatross departing from Midway Atoll National Wildlife Refuge, Northwest Hawaiian Islands (28.21°N, 177.40°W, Fig. 1) between 2006 and 2008 (2006 $n = 10$, 2007 $n = 4$, 2008 $n = 8$). Roughly 96% of the world population of this species breed at colonies in the Northwest Hawaiian Islands, with over one-third nesting at Midway Atoll (Arata *et al.* 2009). This species has a well-defined breeding cycle with little documented annual or inter-colony variation. The majority of eggs are laid before mid-December, followed by an average incubation period of 66 days and hatching occurs before early February. The chick-provisioning period averages 150 days, during which adults spend most of their time foraging at sea, returning to the colony only to briefly feed chicks until fledging from mid-June to mid-July (Arata *et al.* 2009). All Albatross fledglings in this study were captured near their nests or on the beach adjacent to their colony during the months of June and July, when adults have completed provisioning. All birds were nearly (99%) free of down and were considered near fledging age and in good condition when captured. Each bird was equipped with a c. 20–35 g satellite Platform Terminal Transmitter (PTT, SPOT4/SPOT5; Wildlife Computers, Redmond, WA, USA). The mass of these devices was approximately

1% of total bird body mass, well below the suggested maximum (Phillips *et al.* 2003). Satellite transmitters were attached to dorsal feathers with Tesa[®] tape (Weimerskirch *et al.* 1994) and were programmed to transmit a radio signal every 90 s, for 8 h a day, operating for 33% of the total time that they were deployed. Due to the tag duty cycle encompassing a 24-h period and the spatio-temporal scale of factors considered in this study, the duty cycle of the tags did not limit broad-scale characterization of postnatal dispersal and distribution. Tag transmissions were localized by orbiting satellites of the Argos System (Fancy *et al.* 1988). We received an average of 6 ± 2.3 (sd) locations per transmitter per day and a total of 6577 locations during the tracking durations across all 3 years. All transmitters were expected to last 8–14 months (given the manufacturer's battery power specifications) and were intended to be lost at sea when fledglings underwent the first moult, some time between 16 and 21 months after fledging (Awkerman *et al.* 2008).

For macro-scale comparison of distributions and habitat associations between age-classes, we followed adults from the same colony at Midway Atoll using Global Location Sensing (GLS) tags that allow estimates of latitude and longitude based on ambient light levels, providing a lower location accuracy (c. 200 km, Phillips *et al.* 2004, Shaffer *et al.* 2005). We deployed and successfully retrieved 16 GLS on breeding adults in 2008 ($n = 7$) and 2009 ($n = 9$). Each year, adults were captured on the nest during the incubation period (late December to mid-January) and equipped with a c. 6-g Lotek LTD 2500 geolocation archival data logger (Lotek Wireless, St. John's, Newfoundland)

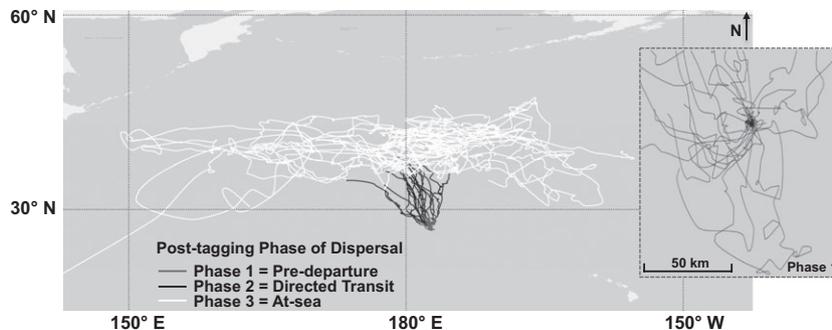


Figure 1. Dispersal of 22 Black-footed Albatross *Phoebastria nigripes* fledglings departing from Midway Atoll between 2006 and 2008 during June and July, as determined by satellite telemetry. Each individual's track is divided into three distinct phases of post-tagging dispersal.

mounted on a plastic identification leg band using UV-resistant cable ties and quick-setting epoxy, resulting in a total package < 10 g. GLS archival tags use light sensors autonomously to log ambient light levels to on-board memory. During the incubation period of the following breeding season (November to January), birds were recaptured and devices retrieved. Equinox periods do not overlap with the time period of interest for this study and did not pose a problem. The timing of local noon and midnight were used to estimate longitude and day length to estimate latitude, providing a single daily location.

Track processing and analysis

Location data obtained from PTT and GLS tags were filtered using purpose-built routines from the Iknos toolbox (Y. Tremblay unpubl. data) developed with MATLAB software (The MathWorks, Natick, MA, USA). Unrealistic locations in the dataset were removed in cases of excessive flight speeds and track spikes by applying the following filters: (1) flight speeds, calculated as transit rates between successive locations, of > 80 km/h were filtered out, and (2) successive locations with an azimuth change of > 170° were removed. To avoid simultaneous location fixes from overlapping satellite transmissions, successive points < 10 min apart were removed. Adult GLS positions with major interference to the light sensor resulting in unrealistic locations were removed. All fledgling satellite tracks were interpolated at hourly intervals using a piecewise cubic Bézier curve with $\mu = 0.3$ (following Tremblay *et al.* 2006, where the parameter μ controls curve elasticity and a value of 0.3 allows high curvature) to create even sampling in time between all birds, which is necessary to obtain representative kernel density utilization distributions. The same interpolation scheme was used to produce two locations per day at 12-h intervals for each GLS-tracked adult bird.

Visual inspection of interpolated tracks of fledglings revealed that each undertook a consistent post-tagging dispersal pattern, delineated into three distinct phases: (1) the resident pre-departure phase, (2) the directed northward transit phase and (3) the at-sea phase (Fig. 1). Each phase was identified by rapid shifts in travel rate and bearing between consecutive locations, along with total distance reached from the colony. For the purposes of this study, a series of rules was applied to

delimit each track into these three phases for later analyses. Phase 1 was marked by low travel rates (< 10 km/h) without directed travel within a 50-km radius of the colony. We defined the beginning of Phase 2 as the location at which travel rates began to increase to > 10 km/h in one direction (most commonly due north) consistently for a minimum of five consecutive hours. We defined Phase 3 as the point in the track where both travel rate slowed markedly (determined relative to an individual's average Phase 2 travel rate but generally to < 15 km/h) and where consistent northward directionality dissipated, occurring for all fledglings between 750 and 900 km from the colony (Fig. 1).

All fledglings entered the at-sea Phase 3 of post-tagging dispersal by July 28, and all adults began the post-breeding period, when they were no longer tied to the colony, by the same date. Fledgling PTT tags ceased transmission between 7 July and 14 November, with most terminating in late August or early September. Thus, for adults, only locations from the month of August were used in the analyses (resulting in 1037 total locations). This ensured that adult at-sea locations represented those of post-breeding adults at maximum temporal overlap with fledglings, while avoiding errors in GLS estimates from the September equinox period. Four fledgling tracks failed to enter Phase 2 due to early loss of tag transmission and were therefore not included in any analyses. To assess behaviour, descriptive track characteristics for each of the remaining 18 fledglings and 16 adults were calculated from filtered and interpolated data. Small sample sizes within each year for both fledglings and adults necessitated pooling data within age-classes across years. Approximate travel rates (km/day) and maximum range reached from the colony (km) were calculated for all birds. In addition, we tabulated the number of days spent in each post-tagging phase of dispersal for fledglings and the track duration for each bird (Table 1).

To determine patterns of at-sea distribution, we employed a kernel density analysis (Worton 1989) to pooled fledgling Phase 3 locations and adult August locations. The geographical coordinates of each bird location were transformed to Cartesian coordinates using a Lambert Cylindrical Equal Area projection, and 2D Gaussian kernel densities were computed (1° longitude by 2° latitude grid, accounting for the approximate error

Table 1. Descriptive track characteristics for PTT-tracked fledgling Black-footed Albatross *Phoebastria nigripes* through three phases of post-tagging dispersal from the natal colony at Midway Atoll (2006, 2007, 2008) and GLS-tracked adults from the same colony during their at-sea hiatus from the colony in August (2008, 2009).

	Mean	sd	Min	Max
Fledglings $n = 18$				
Maximum range from colony (km)	2027.8	845.8	820.4	4343.5
Average travel rate (km/day)	137.4	54.7	44.0	226.0
Phase 1 travel rate (km/day)	31.5	15.1	8.5	73.1
Phase 1 duration (days)	8.6	5.7	2.1	22.3
Phase 2 travel rate (km/day)	199.0	46.7	112.1	268.6
Phase 2 duration (days)	5.2	2.4	2.9	13.1
Phase 3 travel rate (km/day)	197.7	57.1	94.1	301.4
Phase 3 duration (days)	42.5	28.2	3.7	113.8
Tracking duration (days)	59.9	26.1	26.5	120.0
Adults $n = 16$				
Maximum range from colony (km)	3699.9	893.6	2188.8	5524.1
Average travel rate (km/day)	268.5	92.1	57.9	431.2

of the least accurate geolocation estimation method, Shaffer *et al.* 2005). The smoothing parameter (h) was estimated using an adaptive method to estimate an optimal local value (Wood *et al.* 2000). The density surface was divided into concentric polygons to calculate utilization distribution (UD) contours of 95% (overall range), 75%, 50% and 25% (core areas). UD kernels were determined using the Ikonos KERNEL toolbox (Y. Tremblay unpubl. data) developed in MATLAB, with a minimum requirement of two individual birds within a grid cell, and each cell was normalized for bird effort by dividing the number of locations within each cell by the number of birds contributing to the cell (Shaffer *et al.* 2009, Kappes *et al.* 2010).

Habitat characterization

To examine the oceanographic characteristics of the core areas and overall range for both fledglings and adults, we used remotely sensed data based on Albatross locations found within each examined UD contour. Oceanographic variables were selected based on demonstrated biological relevance to the species and study area, as factors previously documented to influence foraging conditions and movement (e.g. Hyrenbach *et al.* 2006, Kappes *et al.* 2010). Remotely sensed data were obtained from time series of environmental data (<http://coastwatch.pfel.noaa.gov/>, see website for metadata on satellite sensors and parameters). These datasets included science quality products

for chlorophyll *a* concentrations (Chl *a*, mg/m³) with resolution of 0.1°; multiple-satellite blended sea surface temperature (SST, °C, resolution 0.1°, see Powell *et al.* 2008 for details on specific SST datasets, Chl *a* and SST as proxies for local biochemical regimes influencing presence of prey); and 3-day average surface wind vectors (0.25° resolution, likely to influence both flight conditions and local prey aggregation from surface water convergence/divergence) measured from the Seawinds sensor on the QuickSCAT spacecraft (e.g. Freilich 2000). Data for each environmental parameter were extracted from the global time series within a 1° longitude by 2° latitude grid centred on the location and date of each PTT or GLS location. The mean \pm sd of the data for locations found within the 25% core area density contour and locations found within the 95% overall range density contour (discounting those falling within core areas) were used in subsequent analyses.

Statistical analyses

All statistical comparisons were performed using R 2.15.1 (R Development Core Team 2012). To investigate at-sea habitat preference for each age-class, mixed-effects ANOVAs were used to test for differences between overall range and core areas for a given environmental parameter using individual birds as a random factor. To investigate differential environmental conditions experienced between age-classes, the same approach tested for differences in each oceanographic parameter

between core areas, and also between overall ranges. Restricted maximum likelihood (REML) estimations were used, and Type 3 sums of squares were compared to account for the unbalanced design (unequal number of observations for oceanographic parameters by individual bird and contour; Shaffer *et al.* 2009). To assess the degree of spatial segregation at sea between fledglings and adults, per cent area overlap for 25% and 95% UD contour polygons was calculated by dividing the total area of overlap by the total area of each UD polygon (Kappes *et al.* 2010).

RESULTS

The 22 fledglings were tracked for 6–120 days (mean 46.8 ± 28.4 (sd), Table 1). The tracks of four individuals ceased transmission before 15 days and did not enter post-tagging Phase 2. These four birds were not included in subsequent calculations or analyses. Dispersal behaviour was consistent among most individuals (Fig. 1). Fledglings travelled at an average rate of 137.4 ± 54.7 km/day over the entire duration of tracking, but travel rates and bearings consistently shifted post-tagging,

corresponding to each of three post-tagging phases of dispersal. The birds remained relatively stationary (31.5 ± 15.1 km/day) for the first 8.6 ± 5.7 days after tag attachment, either remaining on shore or near the protected area of the atoll (Fig. 1) before beginning a northerly migration. This shift marked the beginning of postnatal dispersal Phase 2. Directed transit lasted an average 5.2 ± 2.4 days, with travel rates of 200.1 ± 46.7 km/day, in a consistently northward, north-northeast or north-northwest bearing. Upon entering Phase 3, travel rates initially decreased and the sinuosity of movements increased, while maintaining an overall average travel rate of 197.7 ± 57.1 km/day approximately within the bounds of 35–40°N. The number of days spent in Phase 3 differed between individuals due to varying transmission failure dates, with an average of 42.5 ± 28.2 days (Table 1).

Based on kernel density analysis of fledgling Phase 3 locations, core areas (25% UD) were located within 1500 km north of the natal colony in each year (Fig. 2, Table 1). Most birds travelled quickly to deep pelagic waters in a band between 35° and 40°N, before dispersing zonally across the

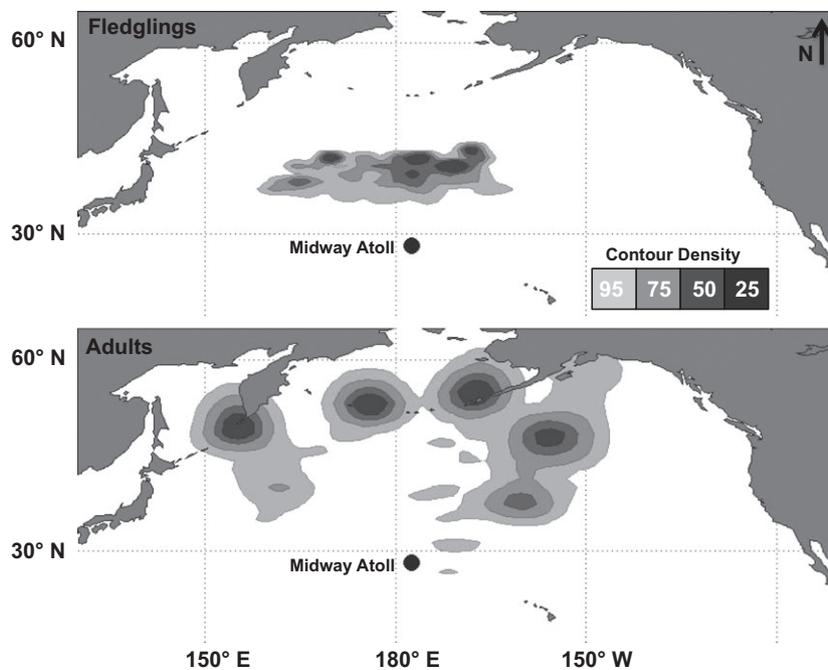


Figure 2. Kernel density analysis of 95%, 75%, 50% and 25% utilization distribution (UD) contours, in increasingly darker shades of grey. Top panel depicts UD contours of 18 PTT-tracked fledgling Black-footed Albatross *Phoebastria nigripes* in Phase 3 of post-tagging dispersal during August to October; bottom panel depicts 16 GLS-tracked non-breeding adults during the month of August.

central North Pacific. Maximum distances reached from the colony ranged from 820 to 4343 km. Core areas fell mainly within 15° on either side of the dateline; however, some individuals travelled beyond 150°E or 160°W (Figs 1 and 2). The overall range of fledglings during Phase 3 was constrained to an area of 4197 km^2 , with core areas of 165 km^2 . Non-breeding adults dispersed widely to the shelf regions along the periphery of the North Pacific Ocean basin, focusing on areas around Japan, the Aleutian Islands and the Gulf of Alaska in both study years. The 16 tracked adults ranged across an area of $15\,580\text{ km}^2$ with core areas of 420 km^2 . Throughout the month of August, adults maintained average daily travel rates of $269 \pm 92\text{ km/day}$ while reaching maximum distances from the colony between 2189 and 5524 km (Table 1). Core areas of fledglings and adults were completely spatially segregated, whereas overall ranges overlapped by $< 2\%$ at the far edges of their distributions (Figs 2 and 3).

Oceanographic conditions experienced by fledglings and adults within core areas and throughout their overall ranges differed markedly between age-classes in both SST and chlorophyll *a* density (Fig. 4). Not all birds contributed equally to the 25% UD contour due to individual variation in tracking duration and distribution, resulting in lower sample sizes representing core areas than overall ranges for both age-classes. Fledglings concentrated into core areas with SST of $20.2 \pm 1.5^\circ\text{C}$ (10 birds, $n = 1965$ locations), whereas adults experienced much lower temperatures of $9.8 \pm 2.3^\circ\text{C}$ (10 birds, $n = 299$ locations) during the same time period (mixed-effects ANOVA, $F_{1,18} = 184$, $P < 0.001$). Throughout their at-sea ranges, SST also differed significantly between age-classes ($F_{1,32} = 93$, $P < 0.001$): fledglings encountered SST of $21.8 \pm 2.2^\circ\text{C}$ (18 birds, $n = 15647$ locations) and adults SST of $12.6 \pm 4.7^\circ\text{C}$ (16 birds, $n = 842$ locations). Chlorophyll *a* also differed significantly between

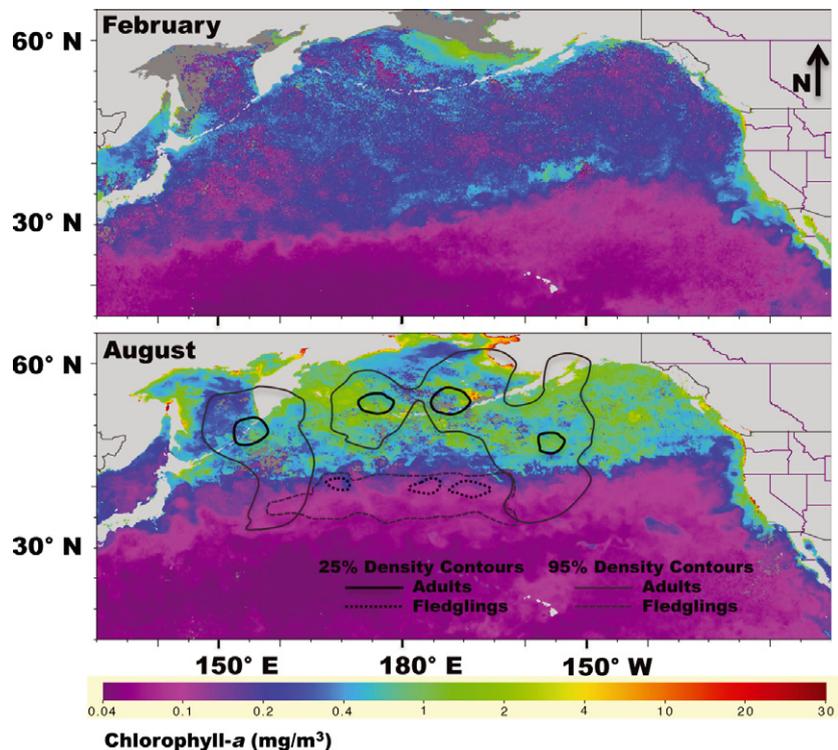


Figure 3. Monthly composites of remotely sensed surface chlorophyll *a* density (mg/m^3) estimated from SeaWiFS ocean colour during February and August in 2008 (imagery courtesy of NOAA CoastWatch, 0.025° resolution). The north-south seasonal migration of the NPTZ chlorophyll front can be seen as the distinct purple to blue transition at 0.2 mg/m^3 (Polovina *et al.* 2001). The bottom panel depicts the association of PTT (fledgling) and GLS (adult) tagged Black-footed Albatross *Phoebastria nigripes* kernel density utilization distributions for locations during August 2008 with areas of particularly low (fledgling) and high (adult) chlorophyll *a* concentrations.

age-class core areas and overall ranges ($P < 0.001$ for all comparisons). Fledgling core areas were characterized by Chl a of $0.148 \pm 0.0425 \text{ mg/m}^3$ and overall range of $0.12 \pm 0.059 \text{ mg/m}^3$. Adult core areas exhibited Chl a of $0.748 \pm 0.53 \text{ mg/m}^3$ and overall range of $0.67 \pm 0.67 \text{ mg/m}^3$. No significant differences were detected between core areas and ranges within age-classes, except for adult SST ($F_{1,24} = 6.7$, $P < 0.001$). Wind vectors did not differ significantly either between or within core areas and overall ranges for adults and fledglings (fledgling's core area: $5.5 \pm 2.1 \text{ m/s}$ and overall range $5.9 \pm 2.1 \text{ m/s}$, adult's core area: $6.0 \pm 1.7 \text{ m/s}$ and overall range $6.2 \pm 1.9 \text{ m/s}$, Fig. 4).

DISCUSSION

Past tracking studies of marine animals have primarily targeted adults, biasing our understanding of at-sea habitat use toward older life stages (Hazen *et al.* 2012). Although tracking durations were short, our results identify for the first time a striking dichotomy in basin-scale patterns of distribution and habitat between fledgling and post-breeding adult Black-footed Albatross tracked concurrently from the same colony. This ontogenetic niche divergence is possibly the product of juvenile naïvety, differential energetic demands and historical competitive interactions between age-classes.

The duration of tracking fell short of expectations given the history of satellite tagging efforts with this and other albatross species, and this may be attributed to several possible causes. First, some fledglings could have perished at sea. Estimates of juvenile survival in Black-footed Albatross from Midway Atoll suggest that only 57% of fledglings survive during the first 1–3 years (Cousins & Cooper 2000). This low survival rate could be influenced by fisheries-related mortality (Cousins *et al.* 2000) but incidental by-catch is not the only source of mortality for fledglings. The initial days (Alderman *et al.* 2010) or months (Weimerskirch *et al.* 2006, Riotte-Lambert & Weimerskirch 2013) are thought to be the point at which juvenile mortality is at its greatest for naïve birds. Many fledglings become waterlogged and drown on ill-fated flight attempts, and others succumb to starvation before successfully departing the colony to begin foraging for themselves. Unique to the Northwest Hawaiian Island colonies, fledglings also face Tiger

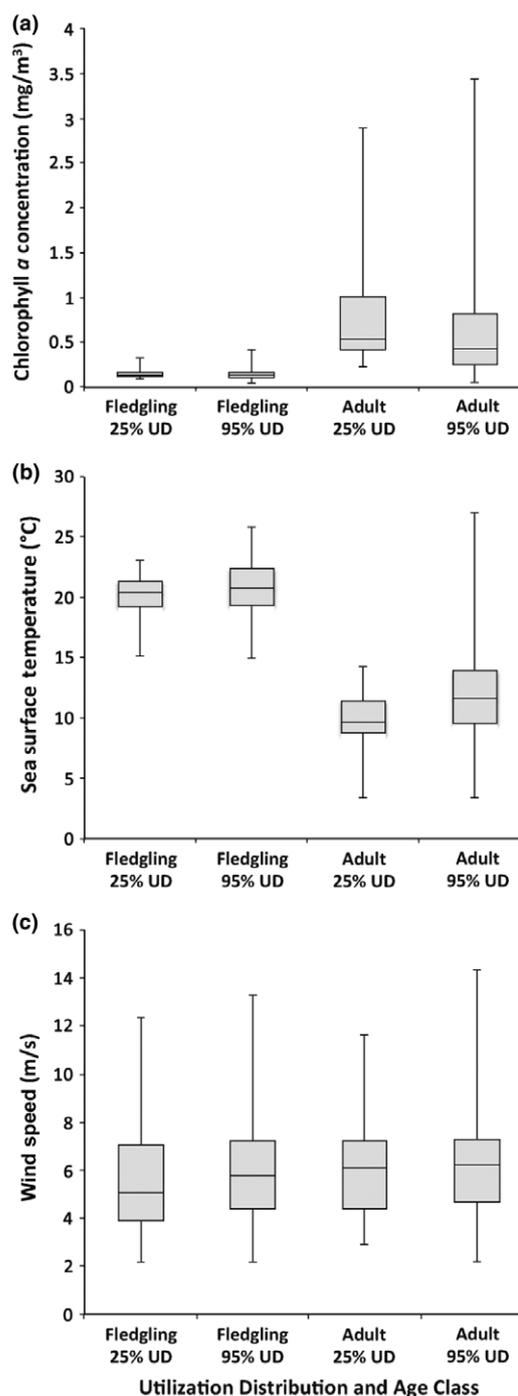


Figure 4. Habitat characteristics of areas visited by fledgling Black-footed Albatross *Phoebastria nigripes* during the at-sea Phase 3 of post-tagging dispersal contrasted with areas visited by non-breeding adults during the same time period. All raw data are shown, extracted for each location of a tracked individual falling within a utilization distribution (UD) contour (25% UD contour: 10 fledglings $n = 1965$ locations, 10 adults $n = 299$ locations; 95% UD contour: 18 fledglings $n = 15\ 647$ locations, 16 adults $n = 842$ locations).

Shark *Galeocerdo cuvieri* predation during this already vulnerable period, as these predators are known to aggregate in the atoll waters during the fledging season awaiting the naïve birds' first incursions to sea (Arata *et al.* 2009). It is also possible that tracking duration was limited by the failure of the satellite tags to transmit before dropping off during moult, where faulty software or hardware could have resulted in transmission loss. Because we did not observe unusual transmission patterns (e.g. weak or loss of signal strength) prior to a loss in signal, it is unlikely that tags failed during the deployments. It is more likely that some short tracks were due to premature loss of the tag itself. Satellite tagging using leg-loop harness attachments on Laysan Albatross *Phoebastria immutabilis* fledglings from Midway Atoll lasted considerably longer (J. Klavitter, pers. comm.). Although Black-footed Albatross fledglings departed with freshly grown plumage, attachment of the tag may have weakened the feathers, causing early tag loss.

For tags that continued to transmit, once beyond 50 km of the Atoll, each fledgling travelled north towards the oceanic region generally characterized as the North Pacific Transition Zone (NPTZ). Breeding Black-footed Albatross are known to exploit the NPTZ (Hyrenbach *et al.* 2002, Kappes *et al.* 2010) along with many other apex predators (e.g. seals, sharks, tuna, Block *et al.* 2011; sea turtles, Polovina *et al.* 2001), where well-known oceanographic processes create generally high biological productivity in an area positioned between 30° and 45°N and biochemically positioned at chlorophyll *a* concentrations of > 0.25 mg/m³ (Polovina *et al.* 2001). Large-scale frontal systems and meso-scale dynamic features create large gradients of horizontal oceanographic variability that heavily influence the NPTZ, enhancing productivity (Seki *et al.* 2004).

Fledglings headed toward the NPTZ but stopped short of oceanographic conditions frequented by adults. Kappes *et al.* (2010) found that SST and to a lesser extent Chl *a* were consistently the best predictors of search effort in breeding Black-footed Albatross adults foraging within the NPTZ despite seasonal and inter-annual variation in their core areas, indicating that adults use specific environmental characteristics as foraging cues to track preferred oceanographic habitat. In contrast, fledglings head to the same broad geographical area but do not appear to seek out equally productive waters. Fledglings congregate too far

south within the subtropical gyre (characterized by Chl *a* ≤ 0.15 mg/m³) to intersect the enhanced productivity beyond the NPTZ chlorophyll front: an area over 8000 km long at the southern edge of the NPTZ that seasonally migrates north and south by about 1000 km (Polovina *et al.* 2001, Fig. 3). During the breeding period, this zone of surface convergence is typically located at about 30–35°N, and during the fledgling at-sea period, can meander to about 40–45°N. The majority of fledgling locations in post-tagging Phase 3 of dispersal were located just below this boundary, and the spatial mismatch is responsible for low average Chl *a* conditions and high SST experienced by fledglings within their core areas (c. 0.15 mg/m³ and 20 °C) and throughout their overall range (c. 0.12 mg/m³ and 22 °C, Figs 3 and 4).

Surprisingly, adults from Midway Atoll were not observed to visit the NPTZ during the first month of their post-breeding exodus. Instead, tracked adults from Midway ranged throughout the far northern reaches of the North Pacific Ocean Basin, probably taking advantage of productive shelf break waters (core areas Chl *a* c. 0.75 mg/m³ and SST 13 °C; Figs 3 and 4), and resulting in complete spatial and niche segregation between age-classes of Black-footed Albatrosses from Midway Atoll. Adult birds of unknown colonial origin captured at sea during the post-breeding period (including July and August) and tagged with PTT-transmitters in Alaska were shown to forage among the Aleutian Islands, Gulf of Alaska, and extensively south of 45°N within the NPTZ but not further west of 170°W (Fischer *et al.* 2009). Mature birds from other colonies are also commonly known to visit the productive areas of the California Current system (Fernández *et al.* 2001, Hyrenbach *et al.* 2006, Kappes *et al.* 2010, Fig. 3), but this behaviour was not observed for any of the fledglings or adults tracked from Midway Atoll during the period of July to August. The observed differences in adult distributions between this and past studies could be the result of the restricted time period investigated in this study or it may suggest colony-specific at-sea habitat use during the post-breeding period. Our results support past reports of immature birds at sea being more commonly observed further south and west than adults (Tickell 2000), and suggest that fledglings probably spend the first year of their life at sea in the southwestern North Pacific, possibly shifting toward adult distributions with age and development in

what is referred to as an 'ontogenetic niche shift' (Werner & Gilliam 1984).

It has long been suggested that younger life stages inherently have different energetic and resource allocation needs than adult stages, as well as different proficiencies in locating and exploiting food resources (Lack 1954). In albatrosses, adults are faced with energetically demanding and lengthy breeding periods, where provisioning for both themselves and their growing chick is made challenging by central-place foraging constraints and results in an unavoidable loss of adult body condition (Jouventin & Dobson 2002). The post-breeding period of only 4 months leaves limited time to recover, while also allocating resources to feather growth for moult and compensating for reduced flight and subsequent foraging performance due to flight feather gaps (Rohwer *et al.* 2011). In contrast, fledglings during their first year at sea must learn to fly, forage and survive but lack the resource demands of breeding and feather replacement, as they will not undergo moult until between 16 and 21 months old (replacing only their distal three or four primaries in a pre-basic I moult; Awkerman *et al.* 2008). Differing energetic demands and flight proficiency are suggested by travel rates and habitat use among age-classes in Black-footed Albatrosses. Fledglings departing the colony at Midway Atoll travelled *c.* 200 km/day, whereas incubating (Kappes *et al.* 2010), brooding and rearing (Hyrenbach *et al.* 2002) adults commuting to the NPTZ from Tern Island, French Frigate Shoals (28.20°N, 177.35°W, approximately 500 km southeast of Midway), covered *c.* 670 km/day. Fledglings on their maiden voyage lack the urgency of temporal and spatial constraints of returning to the colony to relieve a nest-bound partner or provision young, and also lack the learned efficiency of travelling rapidly to productive foraging areas. Furthermore, complete spatial segregation between age-classes at-sea during post-breeding is likely to reflect differing energetic demands and experience. Despite the absence of physical boundaries and central-place foraging impeding their dispersal across the entire North Pacific Ocean basin, fledglings demonstrated a surprisingly restricted oceanic distribution (with an overall utilized area 3.7 times less than that of adults) within mostly forage-poor waters. While young birds are honing flight and foraging skills during this early life stage, experienced adults spread out to recover from the breeding season

and replace plumage in productive waters to the north. It has been suggested that direct or historical competitive exclusion by experienced adults may be responsible for Wandering Albatross fledglings concentrating in significantly less productive waters (Weimerskirch *et al.* 2006). Adults from Midway and other colonies, as well as other congeners, are likely to range within the productive NPTZ at some point throughout the non-breeding season and thus historical or direct interactions may competitively exclude hatch-year juveniles. Differing resource needs, flight and foraging competence, and innate evolved behaviours are all mechanisms likely to shape the divergent ontogenetic niches between age-classes from Midway Atoll.

Prior to attaining the sustained northward flight of true fledging, the initial stationary post-tagging phase represents a period where fledglings spend time practising skills and developing flight muscles in the protected waters of the fringing reef at Midway Atoll (Fig. 1, inset). The success of albatross long-distance travel is attributed to their remarkable adaptations for strategically exploiting wind and wave conditions through dynamic soaring (Suryan *et al.* 2008). Although wind did not have a significant effect on at-sea distributions of fledglings at the macro-scale, wind and waves may influence movement decisions at a finer scale than those considered in the present study, particularly when young birds may be relying on favourable winds for departure but have not yet achieved adult flight proficiency, with the experience necessary to effectively exploit wind conditions (Weimerskirch *et al.* 2006). To test this idea, future efforts could look to more localized analyses of wind effects on fledgling movements in the vicinity of the colony during the early stages of postnatal dispersal.

Previous work has documented early dispersal movements for other fledgling albatross species but those studies covered only the first 10–389 days at sea, with most tags ceasing to transmit after the first 3 months (Weimerskirch *et al.* 2006, Alderman *et al.* 2010, Deguchi *et al.* 2013). Further investigations into differing at-sea distributions and habitat characteristics across age-classes, seasons and colonies should attempt to resolve the mechanisms responsible for observed differential behaviour between age-classes both in our study and for other species of seabirds and marine animals. It is possible that differences in

distributions presented in this study could be influenced by tag-type and inter-annual variability in at-sea habitat use among and between age-classes. Given the high consistency of areas used among years for both fledglings and adults and the vast distance between high-use areas relative to the spatial accuracy of the different tag types, it was considered acceptable to compare location data derived from PTT and GLS tags to assess spatial distributions at the macro-scale presented in this study despite direct temporal overlap in only one of four study years. Small sample size further precluded robust comparison between years within age-classes but future work should investigate whether juveniles predictably follow cues and exhibit the same flexibility as adults in core foraging zones based on environmental signals (Kappes *et al.* 2010) or are generally restricted to settling into smaller and less productive zones relative to waters favoured by adults. This information will indicate age-based sensitivity to future changes in the Earth's climate and related changes in the marine environment. Furthermore, juvenile dispersal data should be integrated into analyses of overlap with fisheries and by-catch data to assess differential vulnerability between age-classes.

Because of the inherent risks that fledgling albatrosses may face during the first few years of life, the fact that they spend the first five or more years at sea before returning to land (Fisher 1975, Weimerskirch *et al.* 1997) and the cost of tracking technology, few studies have been directed at understanding this critical early life stage. Thus many questions remain about fledgling dispersal, distribution, overall movement patterns, habitat use, diet, and temporal and spatial overlap with conspecifics or congeners and anthropogenic threats. In general, our understanding of the early life stages in albatrosses, other seabirds and other marine animals is very poor. Yet it is crucial to study this life stage because it comprises large proportions of the populations of long-lived species and is when the greatest amount of mortality occurs, and thus when natural selective forces are strongest (Fisher 1975). The information obtained from this research fills a large knowledge gap in at-sea habitat use during a critical life stage for this species. The continued vulnerability of this species to interactions with commercial fisheries and the precarious state of most of their breeding habitat in light of climate change-induced sea level rise are arguments for the timeliness of

studying their at-sea behaviour across all life stages.

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