



Successful Long-Distance Breeding Range Expansion of a Top Marine Predator

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Little is known about the effects of large-scale breeding range expansions on the ecology of top marine predators. We examined the effects of a recent range expansion on the breeding and foraging ecology of Laysan albatrosses (*Phoebastria immutabilis*). Laysan albatrosses expanded from historical breeding colonies in the Central Pacific Ocean to the Eastern Pacific Ocean around central Baja California, Mexico, leading to a 4,000-km shift from colonies located adjacent to the productive transition zone in the Central Pacific to colonies embedded within the eastern boundary current upwelling system of the Eastern Pacific California Current. We use electronic tagging and remote sensing data to examine the consequences of this range expansion on at-sea distribution, habitat use, foraging habitat characteristics, and foraging behavior at sea by comparing birds from historic and nascent colonies. We found the expansion resulted in distinct at-sea segregation and differential access to novel oceanographic habitats. Birds from the new Eastern Pacific colony on Guadalupe Island, Mexico have reduced ranges, foraging trip lengths and durations, and spend more time on the water compared to birds breeding in the Central Pacific on Tern Island, United States. Impacts of the range expansion to the post-breeding season were less pronounced where birds maintained some at-sea segregation but utilized similar habitat and environmental variables. These differences have likely benefited the Eastern Pacific colony which has significantly greater reproductive output and population growth rates. Laysan albatrosses have the plasticity to adapt to distinctly different oceanographic habitats and also provide insight on the potential consequences of range shifts to marine organisms.

Keywords: biogeography, colonization, North Pacific, climate change, albatross, top marine predator, range expansion

INTRODUCTION

Species distributions are changing rapidly (Hughes, 2000; Walther et al., 2002; Doney et al., 2011). While recent human activities and ecological change have contributed to the contraction of many species' ranges (Vitousek et al., 1997; Lambrinos, 2004; Thomas et al., 2006), other species have simultaneously shifted or expanded their ranges (Thomas and Lennon, 1999; Chen et al., 2011;

Chan et al., 2019). Recent breeding range expansions have been documented for a diversity of terrestrial birds (Thomas and Lennon, 1999; Hitch and Leberg, 2007; Chen et al., 2011). Even though 65% of the earth's surface is pelagic marine habitat and most seabirds have broad foraging ranges, there are few examples of breeding range expansions among seabirds (Dunlap, 1988; Wynn et al., 2007).

Seabirds generally breed on remote islands, forage across wide areas of the ocean, exhibit high breeding site philopatry, and have low annual reproductive rates (Gaston, 2004). This makes them vulnerable to natural and anthropogenic stressors including incidental take by fisheries (Furness and Camphuysen, 1997; Brothers et al., 1999; 2003; Finkelstein et al., 2006; Wren et al., 2019), invasive species (Jones et al., 2008), habitat loss (Kavelaars et al., 2020), overexploitation (Meldgaard, 1988), pollution (Finkelstein et al., 2003), and climate change (Baker et al., 2006; Gremillet and Boulinier, 2009; Maxwell et al., 2013). Bottom-up processes, such as climate-driven changes in oceanographic processes can impact seabird species by shifting prime foraging locations, especially during the breeding period (Ainely and Divoky, 2001; Gremillet and Boulinier, 2009; Wolf et al., 2009; Thorne et al., 2016). Consequently, seabird populations may relocate to new islands where possible. If the current breeding location is remote with few other suitable breeding locations nearby, or populations are unable to adapt to regional oceanographic change, relocation to suitable breeding sites may require large shifts in breeding range.

Among seabirds, albatrosses exhibit extreme life-history patterns including delayed maturity, long lives, and low annual fecundity (Warham, 1990, 1996). Of all albatrosses, Laysan (*Phoebastria immutabilis*) and black-footed (*Phoebastria nigripes*) albatrosses are perhaps the most likely candidates for long-distance displacement of breeding colonies because they primarily nest on low-lying islands less than 2 m in elevation. Laysan albatrosses are more numerous with 70% of the global population nesting on five islands in the central North Pacific Ocean with a maximum elevation of 6 meters above sea-level (masl; Naughton et al., 2007; Arata et al., 2009). These colonies are adjacent to a singularly productive feature in the Central North Pacific region, the North Pacific Transition Zone (Polovina et al., 2001; Seki et al., 2004; Palacios et al., 2006; Kappes et al., 2010, 2015; **Figure 1**).

Within the last 30 years, Laysan albatrosses have expanded their range by 4,000-km from historical breeding colonies in the Northwest Hawaiian Islands to breed on islands off Mexico in the California Current System of the Eastern Pacific Ocean (Pitman, 1985; Dunlap, 1988). This highly productive eastern boundary current is fed by a coastal upwelling front (Huyer, 1983; Checkley and Barth, 2009). Being a recent expansion, little is known about the foraging ranges and habits of Laysan albatrosses from this population. We had a unique opportunity to examine the consequences of large-scale range shifts by comparing the foraging ecology of two Laysan albatross populations: the recently expanded Eastern Pacific population in Mexico and a population from one of the historic colonies in the Central Pacific on the Northwest Hawaiian Islands. This was accomplished by studying both

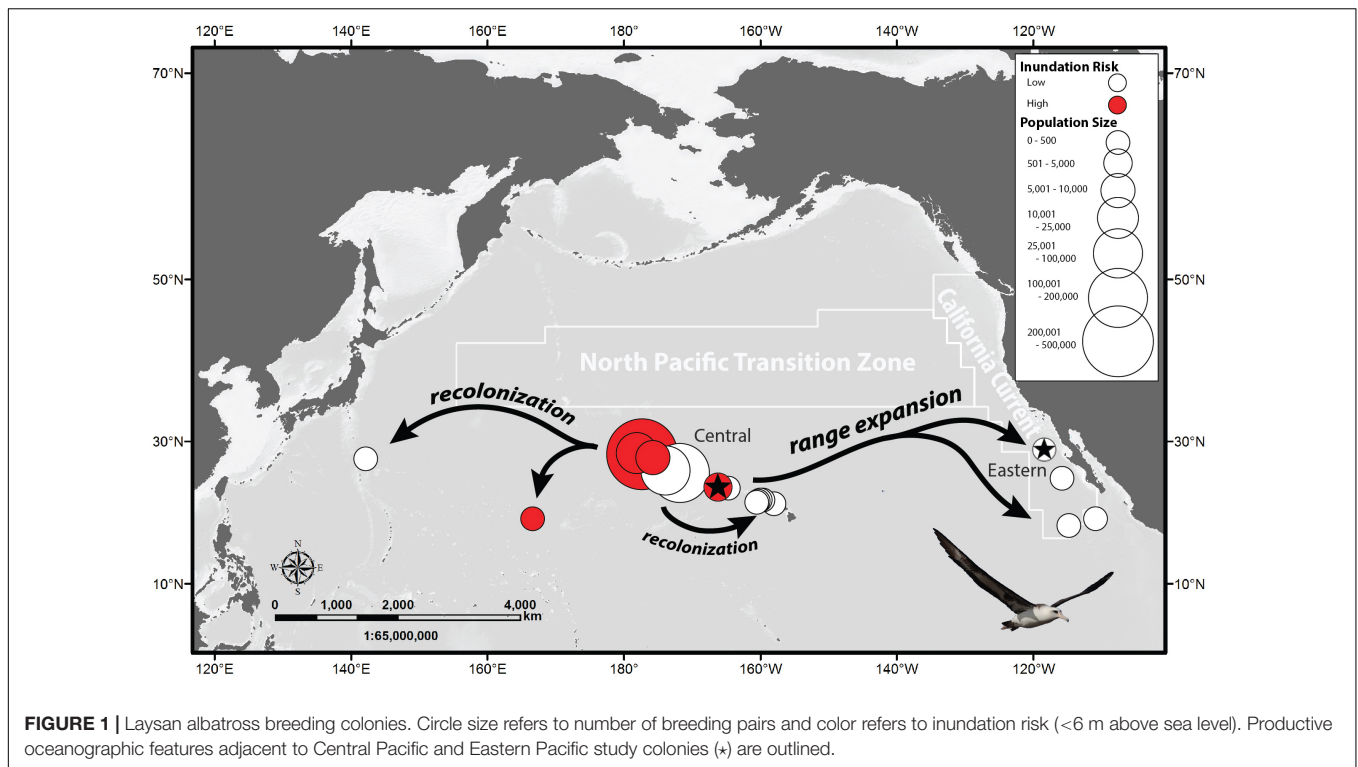
colonies simultaneously using a combination of tracking and biologging methods to capture the behavior and distribution, and remotely sensed data to characterize the physical environment where albatrosses foraged. To explore the consequences of range expansion, our objectives were to compare: (1) at-sea distribution and behavior, (2) habitat use, (3) foraging habitat characteristics in relation to proximity to breeding colonies, and (4) differences in breeding performance. Finally, we explore the consequences of this range expansion on population growth. We found that these top marine predators used distinct oceanographic habitats through foraging plasticity and can provide insight on the types of range shifts that may occur as marine organisms respond to future climate and oceanographic change scenarios.

MATERIALS AND METHODS

Historical Overview of Breeding Colonies

Three species of albatrosses breed in the North Pacific: Laysan albatross, black-footed albatross, and short-tailed albatross (*Phoebastria albatrus*), with colonies historically located in the Western (off Japan) and Central North Pacific Ocean. In the late 1800s and early 1900s, overexploitation of albatross feathers, eggs, and guano resulted in significant declines and several local extirpations (Rice and Kenyon, 1962). Laysan albatrosses were extirpated in the Western Pacific and severely reduced in the Central Pacific by over 99%. Historic numbers for Laysan albatrosses are unknown but were likely greater than present estimates, with one colony having over 2 million birds (Nutting, 1904). Laysan albatross population numbers have steadily increased from a low of approximately 18,000 to the present number of 600,000 breeding pairs, with growth having now plateaued (Arata et al., 2009). In the late 1970s and early 1980s Laysan albatrosses began to recolonize historically occupied sites in the Western Pacific on Mukokima, Japan and Wake Island, United States, and in the Central Pacific on the Main Hawaiian Islands (Chiba et al., 2007; Young, 2010). They also expanded their range to four Eastern Pacific sites off Mexico: Guadalupe, Alijos, Clarion, and San Benedicto Islands where prior breeding had not been documented (Pitman, 1985; Dunlap, 1988; Howell and Webb, 1990, 1992). Core Laysan albatross nesting colonies remain located in the Central Pacific Ocean (Arata et al., 2009; **Figure 1**).

We compared a population of Laysan albatrosses from Tern Island, French Frigate Shoals, in the Northwest Hawaiian Islands of the Central Pacific (23.87°N 166.28°W) with a recently established population on Guadalupe Island, Mexico in the Eastern Pacific (28.88°N 118.29°W) (**Figure 1**). Tern Island (10.5 ha) is part of a group of low-lying atolls (<6 masl) centrally located within other Central Pacific colonies. Neighboring Whale-Skate Island recently eroded away resulting in the loss of breeding habitat for multiple species (Baker et al., 2006), including colony of Laysan Albatrosses (Young et al., 2009). Additional Laysan albatross nesting habitat was lost on East Island due to heavy erosion following a 2018 hurricane. In 2009, Tern Island had approximately 3,000



breeding pairs compared to Island with 457 breeding pairs. Guadalupe is larger (24,300 ha), higher (1,300 masl) and has a rapidly expanding population which grew to more than 1,200 breeding pairs by 2019, despite having an introduced cat population that preyed upon the albatross for over 20 years (Hernández Montoya et al., 2014, 2019).

Tagging

We deployed two types of tags on breeding Laysan albatrosses December to June from 2002 through 2006 at Tern and Guadalupe Islands: 6 g archival global location sensing (GLS; LTD 2400, Lotek Wireless, St Johns, NF, Canada, GLS tags here after) and 35 g satellite platform terminal transmitters (PTTs; Pico-100, Microwave Telemetry, Columbia, MD, United States or Cricket, Wildlife Computers, Redmond, WA, United States). Deployments consisted of PTTs deployed in tandem with GLS tags (Tern $n = 69$, Guadalupe $n = 99$), PTT tags only (Tern $n = 7$), or GLS tags only (Tern $n = 50$, Guadalupe $n = 65$). The combined mass of PTT and GLS tags was less than 2.5% of the ~ 3.2 kg adult body mass, as required by our permits. A summary of tags recovered with viable data by colony and period is shown in **Table 1**.

Global location sensing tags provided long-term movement and temperature data and were attached to plastic leg bands via epoxy and cable ties. These tags captured multiple trips to sea and were deployed both within-breeding period (tags recovered during the same breeding period), inter-annually (tags recovered the following breeding period), and in some cases, recovered two years after deployments. They were programmed to record light level, pressure, and environmental temperature ($\pm 0.1^\circ\text{C}$)

at intervals ranging from 4 to 540 s to accommodate memory capacity for different deployment lengths.

We attached PTTs to dorsal feathers using Tesa® 4651 waterproof adhesive tape (Hamburg, Germany) and programmed them to transmit every 90 s, except for 31 deployments where tags were programmed to duty cycle (either 6:18; 20:4; or 9:15 h on:off) to maximize battery longevity. Satellite transmissions were downloaded via the Argos satellite system (Service Argos, Inc., Largo, MD, United States) using designated accuracy error classes (0–3, A and B).

Location Data Post Processing

Tracking data were analyzed with purpose-built routines created in MATLAB R2007b (The Mathworks, Natick, MA, United States). Location data from GLS tags were post-processed following methods described in Shaffer et al. (2005) to yield two locations per day (local noon and midnight). PTT data were processed and analyzed following methods in

TABLE 1 | Summary of Laysan albatross tracking dataset, number of individuals tracked (number of trips included in the analysis) during breeding and post-breeding periods at Central Pacific and Eastern Pacific colonies.

| | Central | Eastern |
|---------------|-----------|----------|
| Incubation | 58 (72) | 44 (126) |
| Guarding | 39 (41) | 37 (49) |
| Chick-rearing | 26 (157) | 38 (222) |
| Post-breeding | 19 (19) | 32 (45) |
| Total | 104 (289) | 76 (442) |

Kappes et al. (2010). In order to use both types of location data comparably, the PTT data were interpolated using a Hermite spline following methods in Tremblay et al. (2006) and then subsampled to provide two locations per day (like the GLS data) sampled at local noon and midnight.

Distribution and At-Sea Behavior

Utilization distribution (UD) kernel estimates were used to determine spatial habitat distribution (Worton, 1989) for each combination of location/species/breeding period (e.g., incubation, chick-rearing). Laysan albatrosses are known to adjust their range according to ocean conditions and breeding period (Kappes et al., 2010, 2015), we treated each bird \times breeding period \times breeding year as the sample unit for kernel distribution and bootstrap analyses (described below). Utilization distributions (95, 50, and 25%) were calculated in MATLAB using methods in Kappes et al. (2010). For each trip, we estimated the maximum distance from the breeding colony, total distance traveled (km), duration at sea (days), mean percent time on water (the ratio of sea surface to non-sea surface temperatures recorded by GLS tags), and mean distance to shore.

Oceanographic Habitat

Habitat was characterized by matching individual bird location with spatially and temporally referenced remotely sensed oceanographic data following methods described elsewhere (Shaffer et al., 2005, 2006; Kappes et al., 2010, 2015; Conners et al., 2015). We acknowledge that there may be some disconnect between what the birds perceive is good habitat versus what we were able to measure and describe with albatross distribution and remotely sensed data. This disconnect could be applied to virtually any seabird tracking study. Nevertheless, we feel that our study with large sample sizes provides a meaningful characterization of foraging by Laysan albatrosses.

Remotely sensed data were obtained from the NOAA's Environmental Research Division's Thematic Real-time Environmental Distributed Data Service (THREDDs) system.¹ Oceanographic variables were selected based on established associations between albatross distribution and environmental covariates (Waugh et al., 1999; Hyrenbach et al., 2002; Suryan et al., 2006; Kappes et al., 2010; Wakefield et al., 2011; Thorne et al., 2016). For each albatross location at sea, we included variables for: wind speed (m/s), a blended 5-day sea surface temperature (SST) product (SST, °C), chlorophyll-a (CHL, mg/m³), eddy kinetic energy (EKE, J/kg), Ekman transport (WEKM, m/s), and sea surface height (SSH, m).

To characterize the habitats of the Central and Eastern Pacific Ocean, we created a composite for years 2003–2008 by averaging the means of extracted remotely sensed oceanographic data for each of the four breeding periods in 1° longitude \times 1° latitude boxes across the North Pacific Ocean (Shaffer et al., 2005, 2006). These periods approximate annual Laysan albatross breeding phenology as follows: incubation (November 1–January 31), brooding (February 1–21); chick-rearing (February 22–June 15); and post-breeding (June 16–October 31). Climatology

values contained in the 50% UD contour were used to compare habitats available to each population and to define the standard extent of accessibility as a function of distance to colony. To characterize the environmental variables experienced by tracked albatrosses, we extracted, filtered, and selected remotely sensed oceanographic variables for each at-sea location following Henry (2011).

Reproductive Metrics

For each population, we determined annual breeding success (proportion of chicks fledged per eggs laid) and population counts (number of breeding pairs). Data for Tern Island was sourced from the US Fish and Wildlife Service (2003–2009) and published data (Arata et al., 2009; BirdLife International, 2021). Guadalupe Island data were compiled from the literature for years prior 2003 (Dunlap, 1988; Pitman, 1988; Gallo-Reynoso and Figuero-Carranza, 1996; Pitman and Ballance, 2002) and by the authors for 2003–2010. Chicks were considered fledged if observed in a healthy condition at the colony within a month of the average estimated fledging date. We compared the fledging success between colonies (2002–2010) and slopes of the natural log of the breeding population size (1992–2009).

Statistical Analyses

Statistical tests were performed in MATLAB and R (R Development Core Team, 2010). To compare ocean habitats surrounding each colony, we used the oceanographic climatology data bounded by the respective albatross 50% utilization distributions for each colony. Analysis of variance was used to test the dependent environmental variable (contained within the 50% albatross utilization distribution) and covariate distance to colony for each 1° \times 1° grid cell with an interaction of breeding location (Central Pacific or Eastern Pacific).

Albatross habitats were modeled across wind speed, SST, CHL, EKE, WEKM, and SSH using the maximum entropy (MaxEnt version 3.3.3e)² GUI-based approach (Phillips et al., 2006; Elith et al., 2010, 2011). We used resampling (10,000 iterations with replacement) to test the null hypothesis of no difference between Central Pacific and Eastern Pacific locations (Henry, 2011).

RESULTS

Distribution

The core distributions of both Laysan albatross populations had minimal overlap at sea during breeding and non-breeding with only 2.6% of 50% UD kernel overlap during the incubation period, 0% overlap during the chick brooding and rearing periods, and 23% overlap during the non-breeding period (Figure 2). The at-sea distribution of Central Pacific albatrosses was centered north of the breeding colony in the Central North Pacific, near the North Pacific Transition Zone. In contrast, Eastern Pacific albatrosses foraged mainly within the California Current System when breeding. Central Pacific birds moved north and west during the post-breeding period, residing along

¹<http://oceanwatch.pfeg.noaa.gov/thredds/catalog.html>

²<http://www.cs.princeton.edu/~schapire/maxent/>

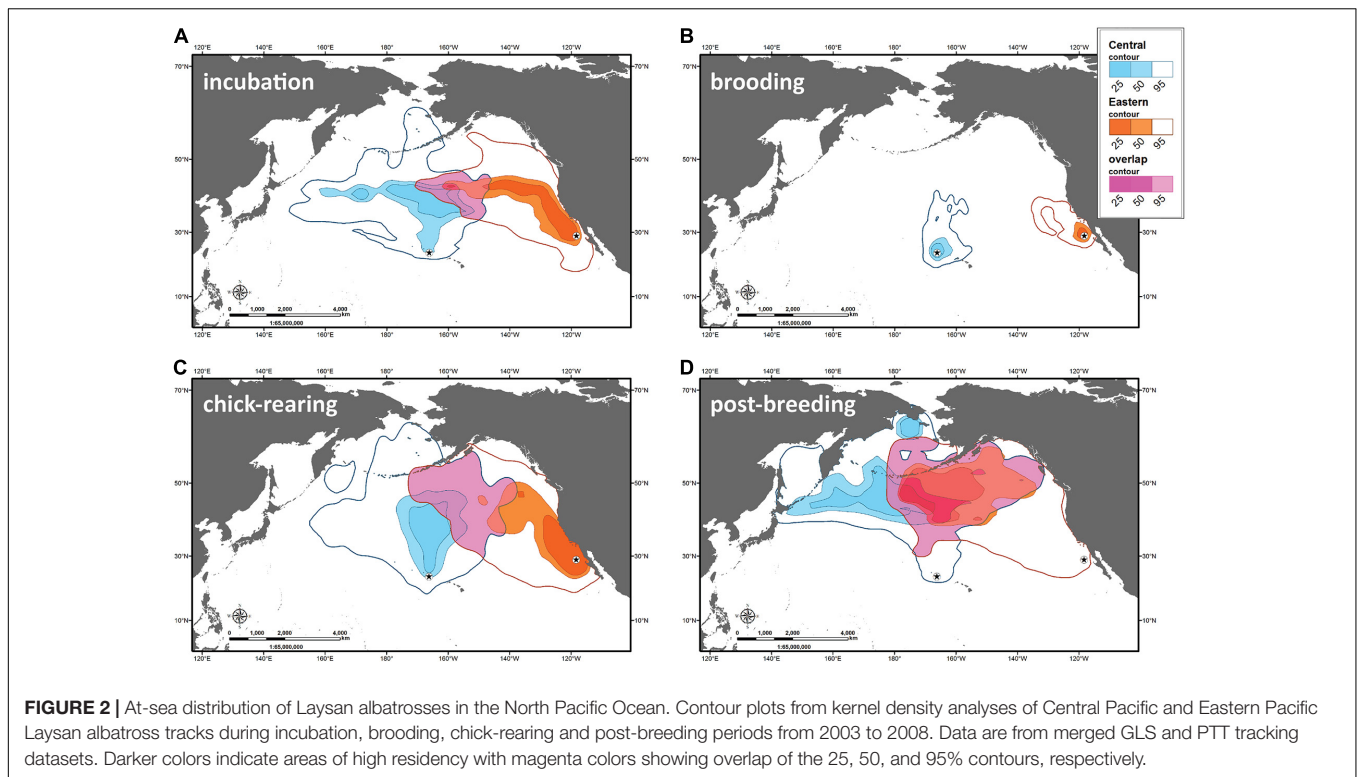


TABLE 2 | Behavior variables from Central Pacific and Eastern Pacific albatross tracks (mean and 95% confidence intervals).

| Period | Location | Distance to colony (km) | Total distance traveled (km) | Duration (days) | Time on water (%) |
|---------------|----------|--------------------------------------|---|-------------------------------------|-------------------------------------|
| Incubation | Central | 1646 (1538, 1774) | 6444 (5455, 7406) | 16.2 (14, 18.9) | 11.9 (9.8, 17.5) |
| | Eastern | 861 (601, 1196) ($P < 0.001$) | 4633 (3413, 6530) ($P = 0.029$) | 12.1 (9.5, 15) ($P = 0.011$) | 16.8 (12.2, 22) ($P = 0.001$) |
| Brooding | Central | 164 (125, 210) | 821 (548, 1049) | 2.7 (2.2, 2.9) | 4 (1.9, 6.5) |
| | Eastern | 93 (58, 129) ($P = 0.005$) | 554 (433, 722) ($P = 0.056$) | 2.4 (2, 2.8) ($P = 0.19$) | 13.4 (7.2, 20.8) ($P = 0.001$) |
| Chick-rearing | Central | 1550 (1364, 1792) | 7299 (5615, 8136) | 13.9 (12.8, 15.6) | 11.4 (6.7, 18.5) |
| | Eastern | 458 (319, 601) ($P < 0.001$) | 3014 (2227, 3524) ($P = 0.004$) | 8 (6.5, 10) ($P = 0.001$) | 17.3 (9.8, 24.4) ($P = 0.123$) |
| Post-breeding | Central | 3090 (2916, 3358) | 42231 (34879, 45707) | 149.7 (142, 158) | 64.6 (60, 70.7) |
| | Eastern | 3855 (3673, 4054) ($P = 0.002$) | 44950 (42624, 48219) ($P = 0.681$) | 161 (158, 165.5) ($P = 0.014$) | 71 (68.3, 73.2) ($P = 0.001$) |

the northern edge of the North Pacific Transition Zone, into the Western Subarctic Gyre with portions of the population residing along the Aleutian Chain and into polar waters. Eastern Pacific birds retained a more easterly distribution during this period, frequenting the northeastern North Pacific Transition Zone, Eastern Subarctic Gyre and along the inner and middle reaches of the Aleutian Chain.

At-Sea Behavior

During the incubation and chick-rearing periods, Central Pacific birds traveled significantly farther from the colony, covered

greater distances, and spent more time at sea than Eastern Pacific birds (Table 2). Trip duration was not significantly different between sites during the brooding period where Central Pacific albatrosses remained closer to and spent less time away from their colony than did Eastern Pacific albatrosses. Central Pacific birds spent less time on the water during incubation, brooding, and post-breeding, but not during chick-rearing. The Eastern Pacific population remained relatively close to the coast of western North America, with mean distance to shore being 483, 268, and 283 km during incubation, brooding, and chick-rearing, respectively.

Habitat Preferences

Birds from each colony used distinctly different habitats during breeding and post-breeding (Table 3). SST, wind speed, and CHL were the most important habitat predictors (Table 3). The relative importance of these and other variables changes with breeding location and period. The values of multi-year composites of habitat predictors change with distance from the colony (Figures 3–5).

Central Pacific albatross at-sea distribution was most closely associated with CHL values during incubation and chick-rearing. Their presence was correlated with the Transition Zone Chlorophyll Front located at the 0.2 mg/m³ surface CHL contour (Polovina et al., 2001). In contrast, during the same periods Eastern Pacific birds associated with SST values such as those found in the edges of filaments and eddies of the coastal upwelling

front of the California Current System (Brink and Cowles, 1991; Strub et al., 1991; Castelao et al., 2006).

During incubation, both CHL and SST had significantly different interaction effects with colony location ($F_{3,627} = 843$, $P < 0.001$ and $F_{3,627} = 79.7$, $P < 0.001$; Figures 4A, 5A). Wind speed did not show a significant interaction effect and had a similar positive relationship with distance to the colony ($F_{3,627} = 1808$, $P = 0.12$; Figure 3A). However, wind speeds were greater surrounding the Central Pacific colony ($F_{3,627} = 1808$, $P < 0.001$). Central Pacific birds accessed regions of higher wind speed, cooler SSTs, and higher CHL as they ranged farther from the colony (Table 3 and Figures 3A, 4A, 5A). Eastern Pacific birds were also associated with cooler SSTs, encountering cooler waters as they traveled further from the colony (Table 3 and Figure 4A). They experienced lower wind speeds and accessed regions with a

TABLE 3 | Summary of MaxEnt model results for Central Pacific and Eastern Pacific colonies.

| incubation | Central | | | | Eastern | | | | |
|----------------------|---------------|----------------------|------------------------|--------------|-------------|----------------------|------------------------|--------------|----------|
| | Variable | Percent contribution | Permutation importance | Relationship | Variable | Percent contribution | Permutation importance | Relationship | |
| AUC = 0.783 | CHL | 37.1 | 42.9 | - | AUC = 0.829 | SST | 28.3 | 32.4 | - |
| | Windsp | 32 | 18.8 | +++ | | Windsp | 24.3 | 17.4 | - |
| | SST | 19.1 | 26.5 | 0 | | CHL | 20.5 | 21.5 | - |
| | EKE | 6.3 | 5.4 | | | WEKM | 20.3 | 19.3 | 0 |
| | SSH | 4 | 3.9 | | | EKE | 3.4 | 3 | |
| | WEKM | 1.5 | 2.6 | | | SSH | 3.3 | 6.4 | |
| brooding | | | | | | | | | |
| AUC = 0.832 | SST | 89.1 | 80.3 | +++ | AUC = 0.777 | SST | 95.3 | 71.7 | - |
| | EKE | 3.4 | 2.6 | | | EKE | 1.5 | 2.9 | |
| | WEKM | 2.8 | 2.9 | | | CHL | 1 | 9.9 | |
| | SSH | 2.8 | 2.5 | | | WEKM | 1 | 0 | |
| | CHL | 1.7 | 9.2 | | | SSH | 0.6 | 10.6 | |
| | Windsp | 0.3 | 2.6 | | | Windsp | 0.5 | 4.9 | |
| chick-rearing | | | | | | | | | |
| AUC = 0.812 | CHL | 32.6 | 56 | 0 | AUC = 0.787 | SST | 58.4 | 43.1 | 0 |
| | EKE | 20.2 | 8.2 | +++ | | SSH | 15.1 | 13.6 | 0 |
| | Windsp | 19.2 | 1.6 | + | | CHL | 13.6 | 20.2 | - |
| | SST | 14.3 | 21.8 | 0 | | Windsp | 6.4 | 8.2 | |
| | WEKM | 7 | 9.2 | | | EKE | 3.4 | 4.4 | |
| | SSH | 6.7 | 3.1 | | | WEKM | 3.1 | 10.4 | |
| post-breeding | | | | | | | | | |
| AUC = 0.798 | SST | 45.3 | 31.5 | +++ | AUC = 0.855 | SSH | 42 | 47.4 | 0 |
| | Windsp | 26.2 | 15.8 | - | | CHL | 21.1 | 31.4 | - |
| | SSH | 10.3 | 18.5 | - | | Windsp | 16.5 | 6.3 | - |
| | WEKM | 9.8 | 28.5 | 0 | | SST | 15.1 | 10.4 | - |
| | EKE | 7 | 5.3 | | | EKE | 2.9 | 3.8 | |
| | CHL | 1.4 | 0.3 | | | WEKM | 2.4 | 0.8 | |

Area under the receiver operating characteristic curve (AUC – a measure of explanatory power) and percent contribution of each environmental variable to the model are listed for each breeding period. Environmental variables include wind speed (Windsp), sea surface temperature (SST), chlorophyll-a (CHL), eddy kinetic energy (EKE), Ekman vertical transport (WEKM), and sea surface height (SSH). Important predictive variables are shown in bold. The association and strength between albatross presence and environmental variables are indicated with +, 0, and – (positive, neutral, and negative).

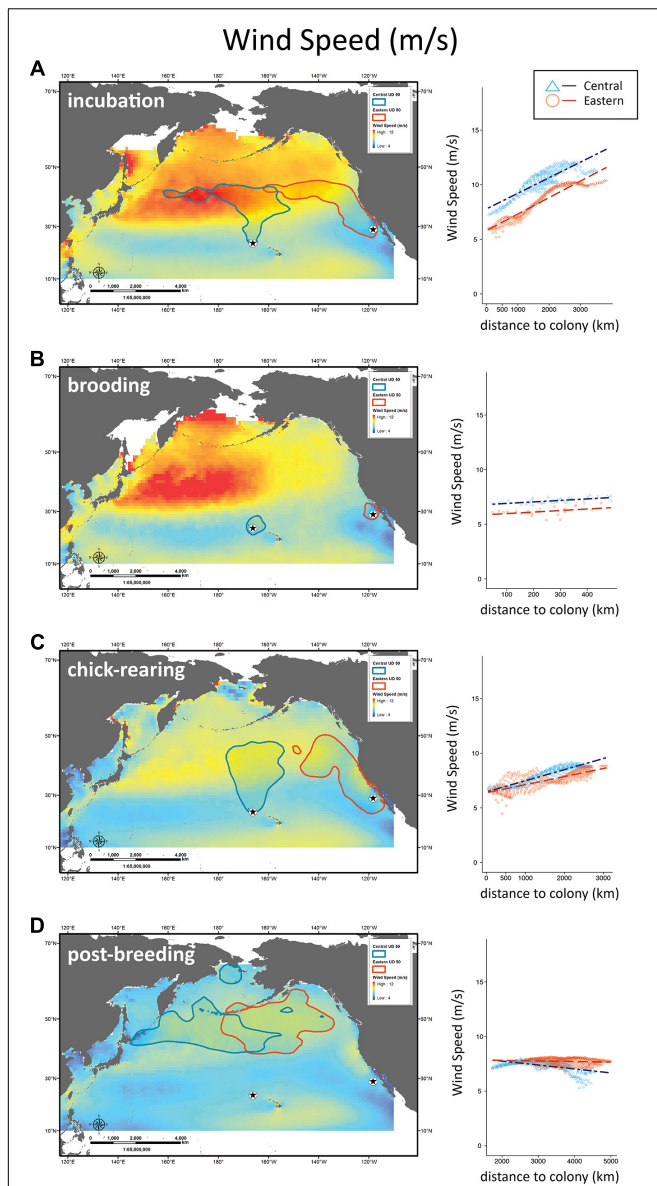


FIGURE 3 | Distribution of Laysan albatrosses in relation to wind speed. Maps and scatter plots of wind speed (m/s) climatologies during incubation, brooding, chick-rearing, and post-breeding for years of albatross tracking (2003–2008). Scatter plots to the right show wind speeds for 1° longitude \times 1° latitude boxes contained within the 50% UD tracking contour as a function of distance to colony with regression lines for Central Pacific and Eastern Pacific colonies.

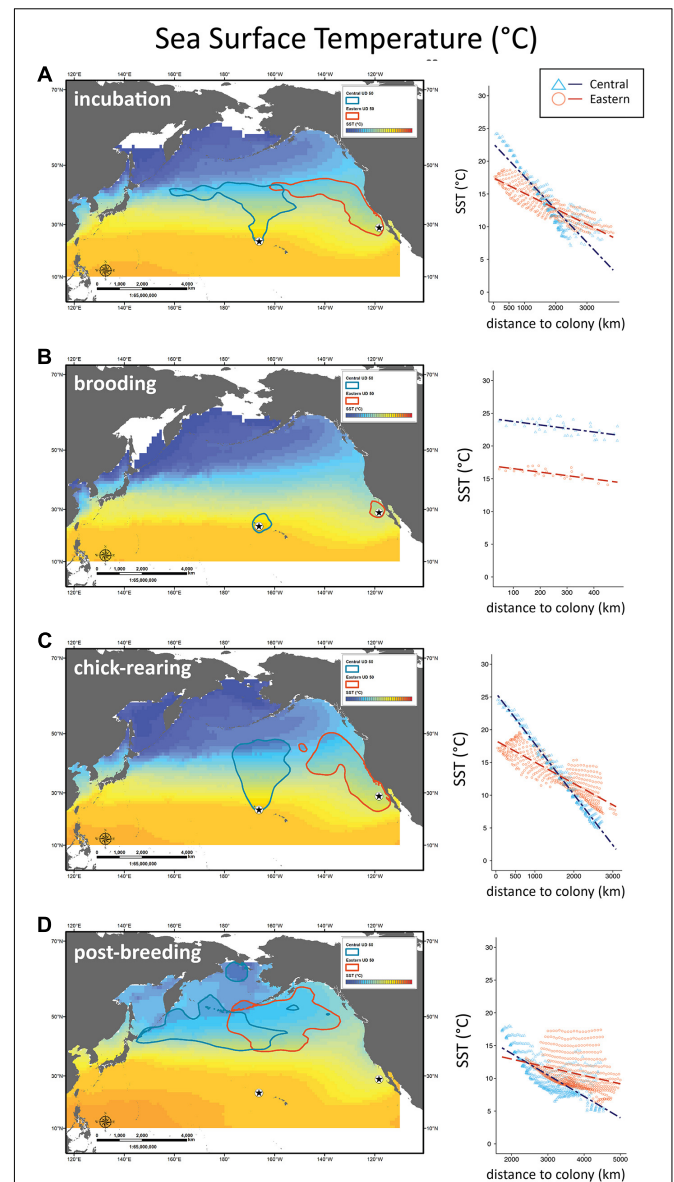


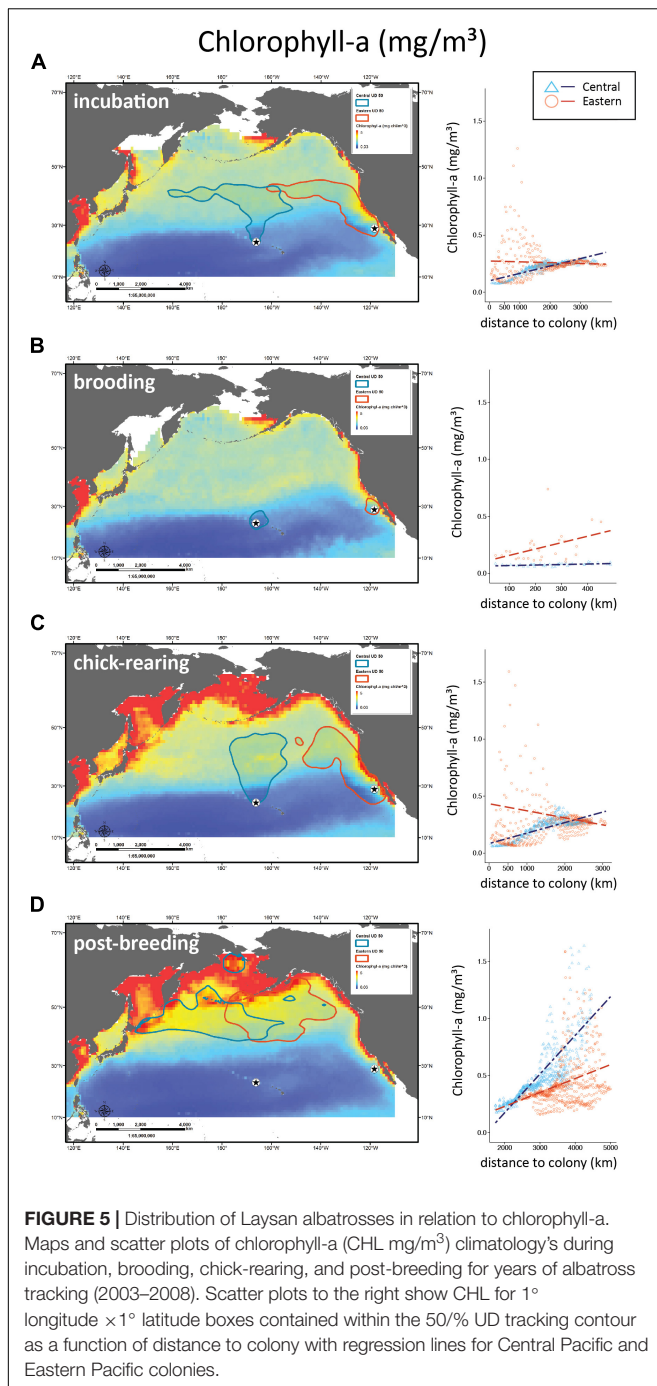
FIGURE 4 | Distribution of Laysan albatrosses in relation to sea surface temperature. Maps and scatter plots of sea surface temperature (SST °C) climatologies during incubation, brooding, chick-rearing, and post-breeding for years of albatross tracking (2003–2008). Scatter plots to the right show SST for 1° longitude \times 1° latitude boxes contained within the 50% UD tracking contour as a function of distance to colony with regression lines for Central Pacific and Eastern Pacific colonies.

broader range of CHL values than Central Pacific birds (**Table 3** and **Figures 3A, 5A, 6A**).

During brooding SST was the sole predictive variable for both populations, with Central Pacific albatrosses utilizing warmer waters compared to Eastern Pacific birds (**Table 3**). Brooding adults are highly constrained by trip duration and distance from the breeding colony (**Figure 2**). Wind speed and SST had similar relationships ($F_{3,62} = 143$, $P = 0.98$ and $F_{3,62} = 440$, $P = 0.96$) but were both significantly greater surrounding the

Central Pacific colony ($F_{2,63} = 143$, $P < 0.001$ and $F_{2,63} = 440$, $P < 0.001$); CHL had different relationships with distance to each colony and was greater in waters near the Eastern Pacific colony ($F_{3,62} = 22.4$, $P < 0.001$; **Figures 3B, 4B, 5B**).

During chick-rearing both Central and Eastern Pacific birds accessed regions of similar wind speeds and encountered higher wind speeds as they ranged farther from the colony. Adults can range more widely at this time because chicks are larger and are able remain alone at the colony for weeks. The relationship



between wind and distance to colony was steeper for the Central Pacific colony ($F_{3,754} = 802$, $P < 0.001$; **Figure 3C**). Eastern Pacific birds had access to regions of lower SST and higher CHL in close proximity to the colony while Central Pacific birds had to travel farther to access regions of low temperatures and higher productivity ($F_{3,754} = 802$, $P < 0.001$ and $F_{3,754} = 8.92$, $P < 0.001$; **Figures 4C, 5C**). Central Pacific birds were more closely associated with specific CHL values while Eastern Pacific birds visited waters with specific SST values. In addition, Central

Pacific albatrosses frequented regions of high eddy kinetic energy during this period (**Table 3**).

Despite greater overlap between at-sea distribution during nonbreeding (**Figure 2**), the Central Pacific birds associated with SSTs characteristic of temperature fronts in the western North Pacific, while Eastern Pacific birds associated with SSHs of large eddies and fronts in the Central North Pacific (**Table 3**).

Reproductive Metrics

Population growth for Guadalupe differed significantly from Tern Island ($F_{3,23} = 157$, $P < 0.001$) (**Figure 7**). There was no significant population growth at Tern Island ($P = 0.286$, $R^2 = 0.08$, slope = 0.016), however during this same time the Eastern Pacific colony grew from 4 pairs to 457 pairs over 26 years ($P < 0.001$, $R^2 = 0.87$, slope = 0.194). Combined data for major Central Pacific colonies (Midway, Kure, and French Frigate Shoals) show a stable population growth trend (pooled data: 1992–2005, $P = 0.596$, $R^2 = 0.08$, slope = 0) (Arata et al., 2009).

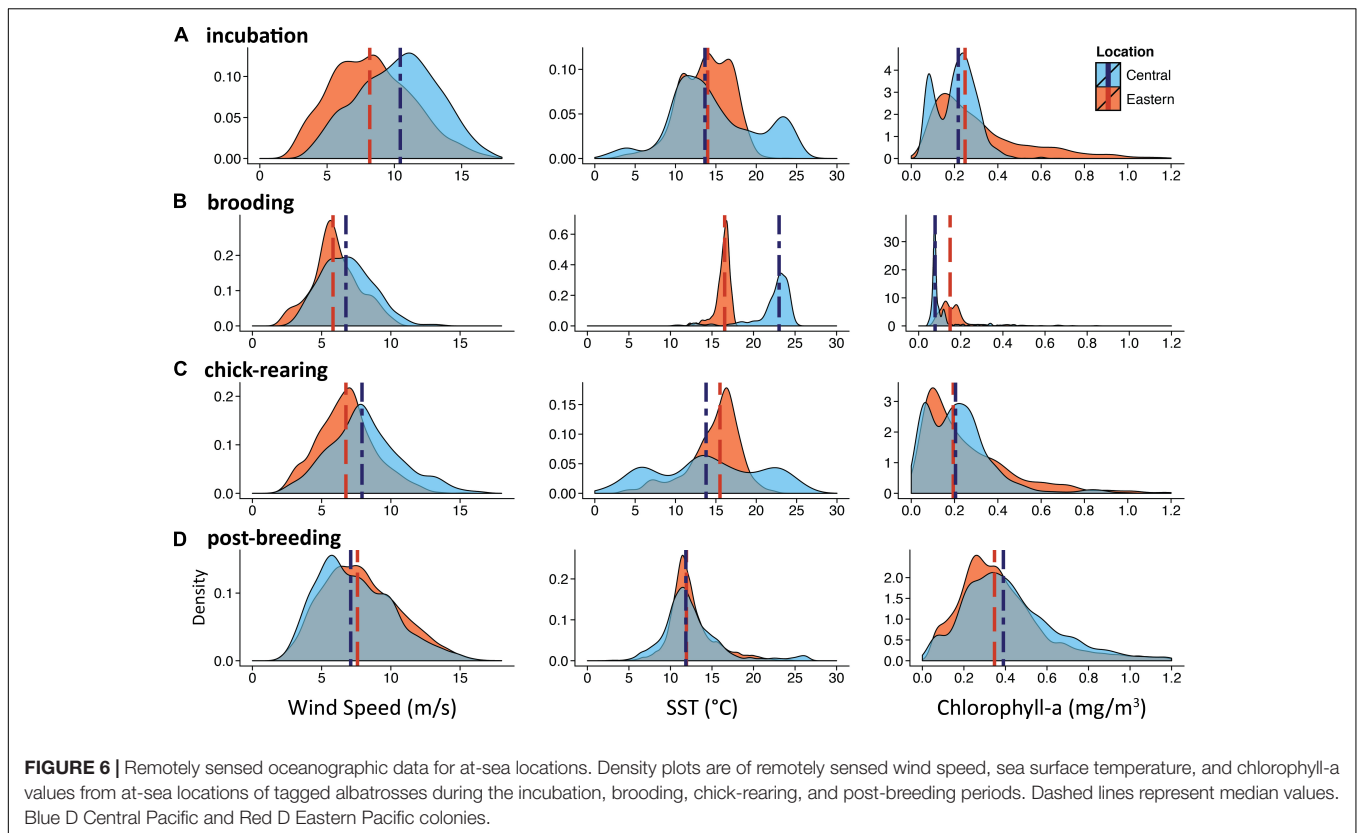
Breeding success was greater at the Eastern Pacific (mean = 0.79 chicks fledged/egg, range = 0.69–0.87, $n = 5$ years) compared to the Central Pacific colony (mean = 0.66 chicks fledged/egg, range = 0.43–0.73, $n = 9$ years, Wilcoxon-Rank Sum $W = 44$, $P = 0.005$) (**Figure 8**).

DISCUSSION

The results of our study show a clear delineation of foraging distribution and oceanic resource use between Laysan albatrosses from a former historic range contrasted by that of a recent range expansion. The oceanic conditions differ markedly in core areas when albatrosses are most constrained by breeding activities, but our results also demonstrate that overlap still occurs outside the breeding period when most individuals aggregate in the central North Pacific. Finally, our comparison of breeding performance between populations suggests that Laysan albatrosses benefited from range expansion to the Eastern Pacific where rapid population growth may be attributed to a combination of available nest sites and high biological productivity in the California Current System.

Population-Level Differences in Foraging Distribution and Habitat Use

Our results show fundamental differences in the distribution of albatrosses from both populations (**Figure 2**). For example, there is little overlap in foraging ranges when breeding but these differences become reduced after breeding when birds are no longer tied to a colony. A primary reason for these differences occurs because the Central Pacific populations breed in tropical/subtropical conditions. Therefore, individuals must commute northward to more productive regions along the North Pacific Transition Zone by exploiting faster wind speeds that were observed over the study period (**Figures 3A–C, 6**). In contrast, the Eastern Pacific population at Guadalupe Island is situated within the productive California Current System, where food resources are closer to the colony. As such, we observed different foraging behavior where Guadalupe albatrosses remained closer to the



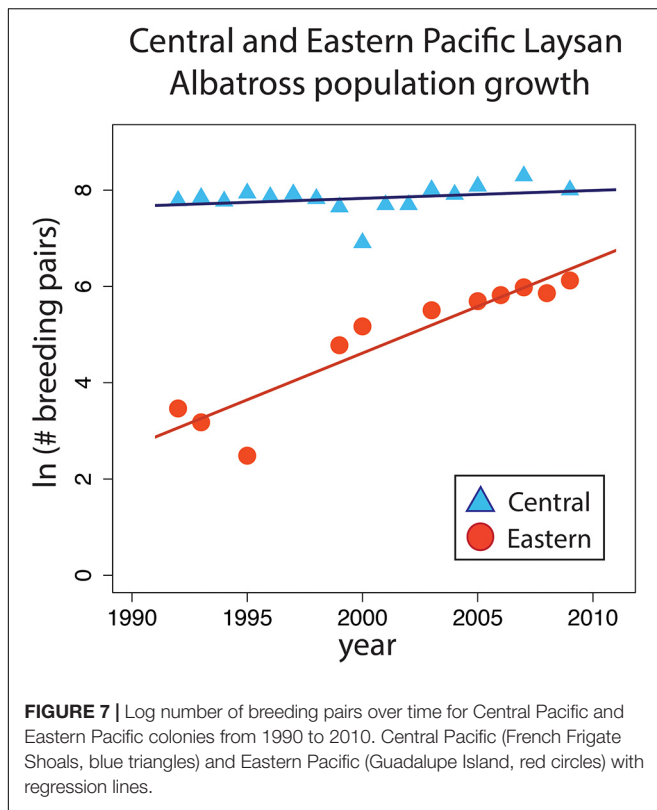
colony, traveled shorter distances, had shorter trip durations, and spent more time on the water (**Table 2**), presumably feeding (Connors et al., 2015).

The profound difference in distribution between albatross populations resulted in the use of oceanic habitats that are influenced by markedly distinct physical processes (**Figures 3–6**). For example, the dominant oceanographic feature exploited by Central Pacific albatrosses was the North Pacific Current and associated North Pacific Transition Zone that forms large eddies and fronts (Polovina et al., 2001; Seki et al., 2004; Palacios et al., 2006; Kappes et al., 2010). Here, the Transition Zone Chlorophyll Front forms important albatross foraging grounds (Fernandez et al., 2001; Hyrenbach et al., 2002; Kappes et al., 2010, 2015). To access productive foraging areas Central Pacific birds utilize the Trades, Westerlies, and transient winter low-pressure systems to transit across oligotrophic subtropical waters (Fernandez et al., 2001; Kappes et al., 2015). Consequently, we observed that habitat use of Tern Island albatrosses was associated with CHL and wind speed and to a lesser extent EKE and SST (**Table 3**).

In contrast, the population breeding at Guadalupe Island in the Eastern Pacific foraged predominantly in the California Current System, among the most consistent and productive ocean systems on earth (Olson, 2002). Here, productivity is heavily influenced by wind-driven upwelling that is seasonally regenerated and characterized by strong cross-shore biological gradients (Bograd et al., 2004; Palacios et al., 2006; Checkley and Barth, 2009). Coastal wind stress from seasonal winter storms

and spring northwesterly winds drive upwelling, establishing density fronts that form filaments and jets that propagate eddy kinetic energy and water masses offshore from spring to fall (Strub et al., 1997; Strub and James, 2000). These frontal features develop meanders and form closed eddies that persist into the following winter (Strub et al., 1987; Lynn et al., 2003). These factors concentrate and transport nutrients, primary production, and secondary production westward (Hickey and Banas, 2008), forming important foraging habitat for coastal and pelagic fish species and a suite of apex predators, including albatrosses (Laurs et al., 1984; Block et al., 2011; Childers et al., 2011; Reese et al., 2011). Here, we observed that habitat use of Guadalupe Island albatrosses was most strongly associated with SST.

Wind enables albatrosses to efficiently travel long distances (Warham, 1996). Wind speed data (**Figure 6** and **Table 4**) support Central Pacific birds' utilization of the strong winter Westerly wind current maxima. Eastern Pacific birds experience reduced winds from transient eastward-moving winter polar low-pressure systems and less intense winter poleward winds of the California Current System (Longhurst, 1998). Later, during brooding and chick-rearing, Central Pacific wind speeds diminish as the frequency of winter low-pressure systems and intensity of the Westerlies decrease toward summer lows (Longhurst, 1998). At this same time, winds for East Pacific albatross also decrease but to a lesser extent because the strong equatorward winds that drive the California Current begin to ramp up



(Bograd et al., 2009). This late-season shift in wind patterns could disproportionately impact the mobility of Central Pacific birds, compromising their ability to provision older chicks late in the chick-rearing period.

Sea surface temperatures accessed by Eastern Pacific albatrosses during rearing may result from utilization of the Coastal Upwelling Front's offshore edge following the collapse of offshore jets and filaments during the California Current System spring transition. This phenomenon is supported by a reduction in mean distance to shore (483 km incubation to 283 km chick-rearing) and consistent with the California Current core position as it moves closer to shore during the spring-summer (Bograd and Lynn, 2003). During this time the Central Pacific birds are visiting the cold side of the Transition Zone Chlorophyll Front. These observations suggest the birds have plasticity in the use of SST as a cue for foraging habitat.

Eastern Pacific birds accessed waters with a broad distribution of CHL values likely due to high variability in CHL productivity across eddies and jets of the California Current System (Thomas et al., 2001). These filament and jet features can have high CHL values that support large zooplankton volumes and aggregate biomass and higher trophic organisms such as fishes, seabirds and cetaceans (Hayward and Mantyla, 1990; Huntley et al., 1995; Sakuma and Ralston, 1997; Logerwell and Smith, 2001; Yen et al., 2006; Henson and Thomas, 2007; Wakefield et al., 2009, 2011; Tynan et al., 2005). Temporal and spatial lags between primary and secondary production in the California Current System can separate higher trophic organisms from

phytoplankton (Smith and Lane, 1991), which may be responsible for the variance in CHL density plots. Access to these features that are located near breeding colonies is likely advantageous for Eastern Pacific albatrosses.

Despite minimal overlap when breeding, Laysan albatrosses from both populations overlapped to a greater extent (>20% of the 50% UD) during the boreal summer/autumn when birds are recovering after breeding. Interestingly, both populations converged in the cooler pelagic waters of the subarctic gyre in the North Pacific (Figure 2D), an area characterized by Aleutian passes where strong currents mix Bering Sea waters with subarctic gyres and large numbers of albatrosses are known to aggregate (Suryan and Fischer, 2010). Differences in distribution during this period may be tied to different Western and Eastern North Pacific features, including the strong eddies and mesoscale energy of the Kuroshio Extension in the West compared to the large Haida-type eddies and the Gulf of Alaska in the East (Longhurst, 1998). Given that albatrosses from the Central Pacific exploit this region while breeding, their return to the colony to begin another breeding cycle is shorter in duration with more time in flight compared to albatrosses from the Eastern Pacific. Interestingly, while Guadalupe birds traveled greater distance from the colony, the overall distances traveled during post-breeding were not different between the populations. Albatrosses from Guadalupe Island may rely on specific wind features such as late fall cold fronts that move towards Western North America to make a rapid return to the colony from the post-breeding oceanic habitats.

Drivers of Range Expansion

Stable population numbers suggest that the Central Pacific albatross populations are near carrying capacity. While historical estimates of Laysan albatross population size are disputed, those for just one Central Pacific colony were reportedly as high as 2 million birds prior to feather hunting (Nutting, 1904), far exceeding current numbers. Although nest site availability may be limiting for Laysan albatrosses on some Central Pacific islands, it is not a major limiting factor for the size of the Eastern Pacific population (Arata et al., 2009). Laysan albatross have also likely experienced reduced inter-specific competition with sympatrically breeding species as population numbers for short-tailed and black-footed albatrosses have dramatically decreased during the 20th century (Hasegawa and Degange, 1982; Arata et al., 2009). This decline may have decreased competition at sea, increasing available foraging habitat for Laysan albatrosses, as suggested by their expansion into waters historically occupied by short-tailed albatrosses (Yesner, 1976). Range expansion into the Eastern Pacific may also entail a diet change, which warrants further research. Because Central Pacific populations of short-tailed albatrosses have not rebounded to historical levels despite reductions in intra- and inter-specific competition, it could be that conditions have changed at sea, altering the timing, availability, and access to prey. Laysan albatrosses may have capitalized on such changes in climatological factors and/or human impacts.

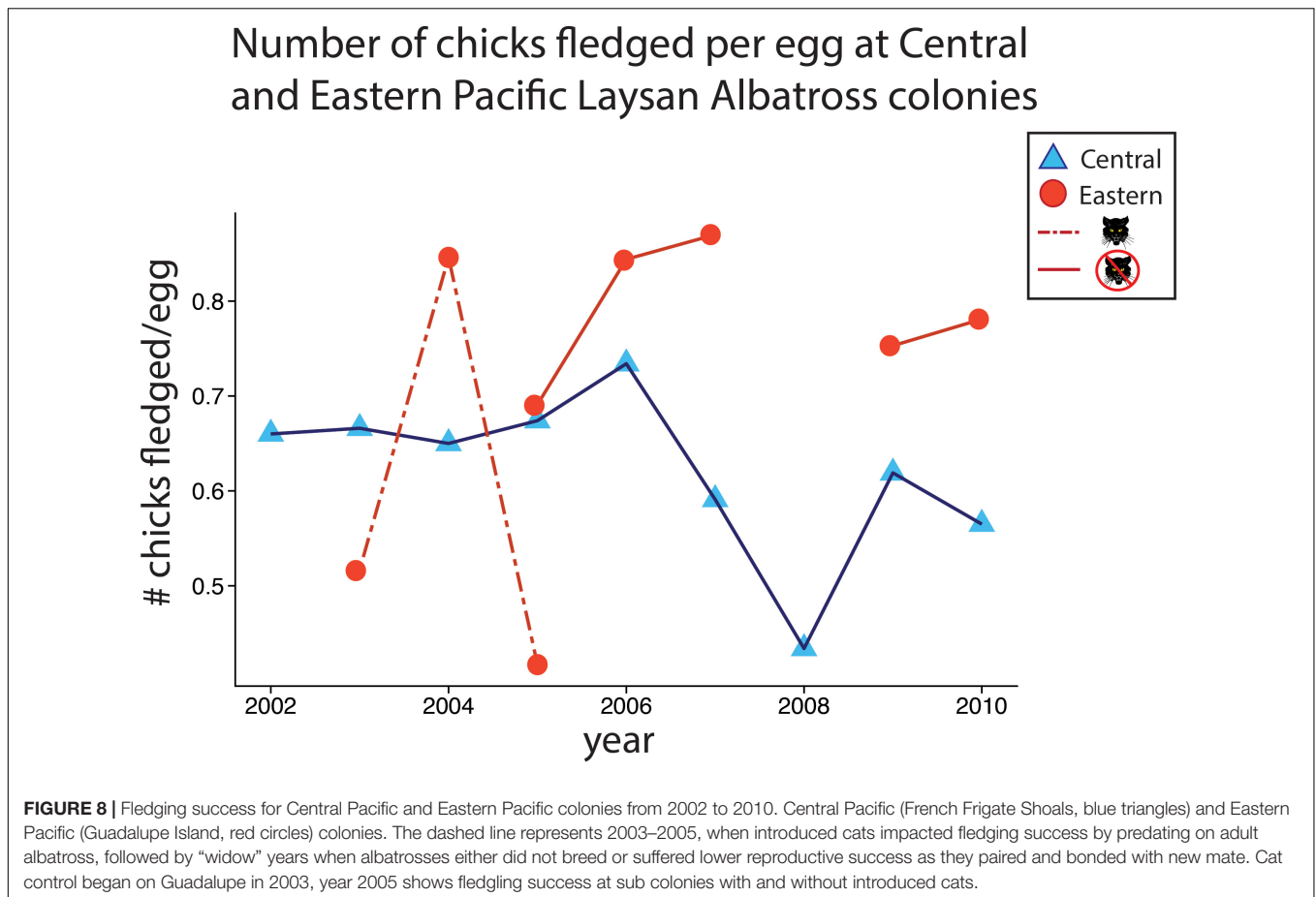


TABLE 4 | Mean and standard error values for oceanographic variables from at-sea locations of tagged albatrosses from Central Pacific and Eastern Pacific colonies during the incubation, brooding, chick-rearing, and post-breeding periods.

| | | Wind speed (m/s) | Sea surface temp (°C) | Chlorophyll (mg/m ³) × 10 ⁴ | Eddy kinetic energy (J/kg) | Ekman transport (m/s) × 10 ⁷ | Sea surface height (m) |
|---------------|---------|------------------|-----------------------|--|----------------------------|---|------------------------|
| Incubation | Central | 10.3 (0.06) | 14.7 (0.11) | 0.21 (0.002) | 14.23 (0.43) | −8.36 (0.68) | 0.015 (0.001) |
| | Eastern | 8.3 (0.07) | 13.7 (0.07) | 0.32 (0.005) | 8.56 (0.27) | −7.93 (0.57) | 0.015 (0.001) |
| Brooding | Central | 6.8 (0.11) | 22.3 (0.15) | 0.1 (0.004) | 18.97 (1.32) | −21.92 (0.84) | 0.007 (0.004) |
| | Eastern | 6 (0.1) | 16.3 (0.05) | 0.17 (0.006) | 11.87 (0.62) | −0.64 (0.65) | −0.021 (0.002) |
| Chick-rearing | Central | 8.1 (0.1) | 14.1 (0.24) | 0.2 (0.006) | 12.09 (0.72) | −12.71 (0.78) | −0.014 (0.002) |
| | Eastern | 6.8 (0.06) | 14.8 (0.1) | 0.19 (0.016) | 12.36 (0) | −0.32 (0.6) | −0.019 (0.001) |
| Post-breeding | Central | 7.5 (0.04) | 12.5 (0.05) | 0.46 (0.005) | 8.12 (0.15) | −5.9 (0.26) | 0.041 (0.001) |
| | Eastern | 7.9 (0.02) | 12.5 (0.02) | 0.41 (0.003) | 5.89 (0.07) | −3.16 (0.16) | 0.023 (0.0004) |

Changes in the North Pacific Ocean and Range Expansion

The phenology of albatross reproduction at both colonies coincide with those of large-scale seasonal oceanographic patterns. Both the southward migration of the Transition Zone Chlorophyll Front and the south to north renewal of coastal upwelling correspond with albatross hatch's onset (Bograd et al., 2004, 2009; Awkerman et al., 2008). This shift in productivity reduces foraging travel during hatching and brooding, a critical point in the albatross breeding cycle. This synchrony of breeding with predictable seasonal productivity and prey availability can

be important to top consumers (Cushing, 1990; Sydeman and Bograd, 2009). The Pacific Decadal Oscillation shift of the late 1970s/early 1980s (Ebbesmeyer et al., 1991; Holt, 1996; McGowan et al., 1998; Mantua and Hare, 2002; Bograd and Lynn, 2003) coincided with the Laysan albatross colonization of the Eastern Pacific (Pitman, 1985; Dunlap, 1988). Climatic phenomena such as the deeper eastward shift of the Aleutian Low-pressure system accompanied by a southward shift in storm tracks likely influenced wind patterns (Trenberth and Hurrell, 1994) and may have contributed to colonization by this wind-dependent species.

Several changes have occurred in the California Current System since the inception of the Eastern Pacific albatross colonies in the early 1980s, including a significant trend toward a longer upwelling season (Bograd et al., 2009), upper-ocean warming, increased stratification, decreased offshore seasonal signal (Bograd and Lynn, 2003), and increases in eddy kinetic energy in summer/fall (Stammer and Wunsch, 1999). The net effects of these changes on albatross habitat are unclear. Some changes, such as the recent shoaling of the hypoxic layer in the California Current System (Bograd et al., 2008; Howard et al., 2020), may enhance cephalopod habitat, a primary prey of the Eastern Pacific Laysan albatrosses (Pitman et al., 2004). Additionally, other surface-feeding seabird species with similar foraging techniques as Laysan albatrosses [black-footed albatross, black-winged petrel (*Pterodroma nigripennis*), California gull (*Larus californicus*), northern fulmar (*Fulmarus glacialis*), pink-footed shearwater (*Puffinus creatopus*), western gull (*Larus occidentalis*), and wedge-tailed shearwater (*Puffinus pacificus*)] have also increased in the California Current System (Hyrenbach and Veit, 2003). Collectively, these large-scale spatio-temporal changes in oceanographic patterns and productivity in the North Pacific may have played a significant role in the initial colonization and subsequent persistence of the Eastern Pacific Laysan albatross colony. Additional effects brought on by global climate change may further influence the metapopulation structure of this species.

Climate Change, Range Expansion, and the Metapopulation

Climate change scenarios forecast increases in Central Pacific El Niño events (Yeh et al., 2009; Wang et al., 2019), which are associated with decreases in the southerly migration of the Transition Zone Chlorophyll Front (Polovina et al., 2001) and reduction of Central North Pacific prey fields (Chen et al., 2007; Tseng et al., 2011). Historically, El Niño events are followed by La Niña conditions when Central Pacific Laysan albatrosses experienced significant decreases in productivity (Dearborn et al., 2001; Seki et al., 2002; Kappes et al., 2010), which is linked to changes in wind fields that impact albatross mobility (Thorne et al., 2016). Furthermore, Bograd et al. (2004) found long-term changes in the timing of the southerly maximum of the Transition Zone Chlorophyll Front, a seasonal phenomenon important to the reproduction of Central Pacific albatrosses. Central Pacific birds may be increasingly competing for dwindling at-sea resources (Hazen et al., 2013). This scenario could be compounded by the impacts of sea-level rise in reducing breeding area on low-lying atolls (Baker et al., 2006; Webb and Kench, 2010; Reynolds et al., 2015), the core breeding habitat for Central Pacific populations.

The recently established Eastern Pacific colony on Guadalupe Island has high reproductive success and is growing rapidly (Figure 7). In addition to a location embedded in favorable foraging conditions, this colony is buffered from sea-level rise by elevated breeding sites, with thousands of hectares of nesting habitat. With low intra-specific competition at sea, it is improbable that density-dependent processes will soon

regulate this Eastern Pacific population. We have observed young born in the Eastern Pacific return to breed. Central Pacific birds founded the Eastern Pacific colonies, and bidirectional visitations occur between these populations. During 8 years of observation, we observed 3 adults banded as chicks or loafers at the Central Pacific colonies breeding on Guadalupe. Researchers have sighted Guadalupe born birds at Central Pacific colonies (Lindsay Young, personal communication). These observations indicate that Eastern Pacific albatrosses interchange with the Central Pacific colonies and may play an important role in metapopulation dynamics under future climate change scenarios.

Invasive Species

While ample breeding habitat exists in the Eastern Pacific, introduced species such as feral cats (*Felis domesticus*) are present on many of these islands including Guadalupe. Cats prey on seabirds (Medina et al., 2011), and, in years when Guadalupe albatrosses were exposed to introduced cat predation, productivity decreased (Figure 8). This illustrates the impact that introduced species can have on nascent seabird populations and underscores the role of invasive species eradications in supporting seabird (meta)populations.

CONCLUSION

In summary, Laysan albatrosses recently expanded their range from colonies on small low-lying subtropical atolls where birds make long foraging commutes to large tall volcanic islands in the Eastern Pacific embedded within a highly productive eastern boundary current. During the breeding period, this expansion has resulted in: (a) low spatial overlap, (b) access to novel oceanographic habitats, and (c) differential utilization of oceanic habitats/features. Birds from the new colony have reduced ranges, foraging trip lengths and duration, and spend more time on the water. These factors undoubtedly contribute to the observed higher reproductive output and population growth rate for the Eastern Pacific colony. Immigration of Central Pacific-born birds may also play a role in these patterns. The range expansion did not impact the post-breeding period as heavily where birds largely utilized habitats with similar environmental variables. Climate change (oceanographic processes and sea-level change) may reinforce this range expansion. In seabirds, the degree to which range expansion will synergize with exposure to other threats on land (e.g., predators and habitat degradation) and at sea (e.g., contaminants and fisheries interactions) is largely unknown. This phenomenon has the potential to dramatically alter static management strategies and warrants further study.

Species are increasingly adjusting their ranges in response to rapidly changing environments. This will inevitably result in novel distributions and changes of the “realized” within the “fundamental” niche (Hutchinson, 1957). The differences we found in model ranking of environmental variables between populations cautions against using predictive habitat modeling based on current populations, as results may not be transferrable under different environmental conditions (e.g.,

oceanographic systems), particularly for highly mobile species with relatively broad diets. It is important to recognize the destination habitats that receive immigrants are rapidly changing as well. For example, Bograd et al. (2009) suggested recent changes in the phenology of upwelling in the California Current System may spawn greater mismatches in predator needs and prey availability. Perhaps the Laysan albatrosses, buffered by plasticity in their opportunistic palate, ability to move large distances, and lack of intraspecific competition in the Eastern Pacific, are well positioned to capitalize on this change.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <http://www.seabirdtracking.org>, searchable by species, location, or investigator. All data analysis codes are available by reasonable request to the lead author.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care & Use Committee, University of California, Santa Cruz.

AUTHOR CONTRIBUTIONS

RH and SS designed the experiment, collected, analyzed, interpreted the data, and wrote the manuscript. MA collected, analyzed, and interpreted the data. MF-L collected the data. DF collected and interpreted the data. EH and YT analyzed and interpreted data. DPC designed the experiment and provided the tags. BT designed the experiment and wrote the manuscript. DAC designed the experiment, interpreted the data, and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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