POST-BREEDING DISTRIBUTION OF WEDGE-TAILED SHEARWATERS (*ARDENNA PACIFICA*) NESTING ON O‘AHU, HAWAI‘I AND ASSOCIATED GEOLOCATOR DEVICE EFFECTS

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ABSTRACT

The use of animal-borne sensors, or biologging, has greatly enhanced our understanding of the at-sea ecology of seabirds, improving conservation efforts. In this thesis, I present a literature review on the application of light-level geolocators in shearwater and petrel migration studies and investigate the post-breeding distribution and effects of geolocator deployment on Wedge-tailed Shearwaters (*Ardenna pacifica*) from the Freeman Seabird Preserve in Oʻahu. By deploying geolocators on adult shearwaters across two contrasting El Niño Southern Oscillation (ENSO) phases, La Niña (2022–23) and El Niño (2023–24), my goal was to advance understanding of tropical seabird migration and assess the effects of geolocator attachment under varying oceanographic conditions. Potential device effects were tested by comparing the growth of chicks between tagged and non-tagged parents and the adults' rate of return to the colony across two breeding seasons. Although there were no significant negative effects of geolocators (< 1% body mass) on chick growth or adult return rates, there were lower peak body masses and slower wing chord growth in chicks overall in the El Niño year. While geolocators did not impact adult survival or breeding performance, subtle interactions among device deployment, sex-specific traits, and environmental variability may emerge during periods with more challenging conditions. Following breeding, shearwaters consistently migrated to coastal and pelagic waters off Central America in the eastern tropical Pacific (ETP), irrespective of ENSO phase. However, during the El Niño year, the timing of departure from the breeding colony and arrival to the ETP were delayed. In non-breeding areas, shearwaters shifted to more diurnal foraging and expanded their foraging range during El Niño. Because most of their time was spent within international Exclusive Economic Zone waters, findings highlight the importance of collaborative, multinational conservation efforts.

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CHAPTER 1

Light-level geolocation to study migration and at-sea behaviors of tropical petrels and shearwaters: a review

1.1 Introduction

Seabirds face numerous challenges in a rapidly changing world. Although they are constrained to breed on land, they must forage over vast and dynamic seascapes. Seabirds' reliance on both land and sea exposes them to a wide range of threats, including invasive predators, fisheries bycatch, pollution, and climate change (Croxall et al., 2012; Rodríguez et al., 2017; Dias et al., 2019). Environmental pressures have contributed to population declines in up to 70% of the approximately 368 species, with one-third of species now threatened with (Young and VanderWerf, 2022). Efforts to address population threats at breeding colonies and protect nesting sites have helped slow population declines, but effective conservation planning requires a better understanding of seabird ecology at-sea, which remains limited for many species and ocean regions (Rodríguez et al., 2017; Mott and Clarke, 2018). Mapping foraging ranges, migration routes, and overwintering areas are essential for identifying risks and to facilitate spatially explicit management actions, such as marine protected areas (Gilmour et al., 2022) and fishery closures (McInnes et al., 2024).

Seabirds are also valuable indicators of oceanographic variability and fishery stock health due to their reliance on marine prey. As highly mobile predators, seabird foraging behaviors provide critical insight into changing ocean productivity and prey availability (Cairns, 1987; Piatt and Sydeman, 2007). Many tropical seabirds rely on subsurface predators, like tunas, to locate and access prey, making them convenient focal species for studying the broader food webs and oceanographic features important to other marine predators (Miller et al., 2018; Carreiro et al., 2023).

Studying seabirds in the marine environment is challenging because their wide-ranging habits complicate the study of links between their ecology (e.g., provisioning chicks on land and foraging at sea) and life histories (e.g., breeding and wintering). Many tubenose seabirds (Order Procellariiformes, hereafter tubenoses) undertake extensive migrations during the non-breeding period, dispersing from nesting sites. Biologging—the use of animal-borne sensors to record and transmit information—has greatly improved our understanding of seabird movements, ecology, and physiology (Ainley et al., 2012; Wilson and Vandenabeele, 2012).

Until the recent miniaturization of biologging devices, seabird distribution was described using vessel-based observations, while individual survival was tracked by marking birds with paint or banding them with rings (Murphy, 1914; King, 1974; Bairlein and Schaub, 2009). However, linking individuals observed at-sea to their breeding sites is challenging, offering a limited understanding of seabird movement. Recent advances in biologging technology have transformed seabird research, allowing for detailed studies of at-sea ecology and greatly expanding our knowledge of spatiotemporal distributions.

Given the widespread use of light-level geolocators (hereafter, geolocators) in seabird migration studies, I reviewed the literature to evaluate current knowledge of non-breeding ecology of tropical and subtropical tubenoses. Specifically, my goal was to compare different analytical approaches used in geolocator studies to ensure methods used to study Wedge-tailed Shearwaters (*Ardenna pacifica*) in Hawaiʻi are appropriate and comparable with similar biologging studies.

1.2 Geolocators

The avian biologging toolkit has improved and expanded since its advent, and researchers now can select from a wide range of sensor types depending on their research question and the study species. For instance, studying long-distance migration requires that devices do not exceed 5% (or as little as 1%) of bodyweight (Phillips et al., 2003; Wilson and McMahon, 2006; Casper, 2009), attachment via leg band or harness to accommodate molt during winter and require extended battery life throughout the duration of the non-breeding period (Wilson et al., 2002). For these reasons, geolocators are routinely used to measure and quantify seabird migration (Table 1).

Table 1. Geolocators are currently the optimal biologger to study long-distance migration in seabirds due to their small size, ability for leg attachment, and extended battery life.

	Description	Attachment	Battery life	Number of locations	Minimum tag mass (g)	Location accuracy
Geolocator	Records ambient light levels to determine location	Leg band, Attached to skin, harness	> 1 year	Two locations daily	< 2	100s km
Radio telemetry (VHF)	Transmits unique radio signal to receiver to show time and location if within range	Leg band, Attached to feathers, skin, harness	Few weeks	Only within ~50km of receiver	< 1	1–10s km
Platform terminal transmitter (PTT)	Satellites calculate locations using ARGOS system	Attached to feathers, skin, harness	> 1 month	Satellite-defined (depends on latitude; ~5-15)	5–30	< 5 km
Global positioning system (GPS)	Triangulates location from incoming satellite signals and stores positions	Attached to feathers, skin, harness	> 1 month	User-defined (seconds to days)	< 3	< 20 m

Geolocators store data during deployment (archival) and are used to study long-distance migration due to their prolonged battery life (> two years; Lisovski et al., 2020). Their small size allows them to be attached to animals weighing as little as 10 g, inclusive of 88% of all bird species (Bridge et al., 2011). Geolocators have an onboard clock and record ambient light levels, which can be used to estimate locations based on the timing of sunrise and sunset (Hill, 1994). Light levels provide coarse-scale location estimates, and latitude estimates are less accurate during solar equinoxes (Hill and Braun, 2001; Ekstrom, 2004). Including locations within three weeks of the spring and autumn equinox, spatial accuracy (mean ± SD) for seabirds can range from 304 ± 413 km to 408 ± 473 km with the widely-used probGLS and FLightR geolocation analysis packages, respectively (Halpin et al., 2021). Due to this relatively low resolution, geolocators are best suited for tracking extensive (1000s km) migrations and seasonal distributions, rather than for relating bird movements to small-scale (10-100s km) habitat features. Additionally, geolocators can be equipped with temperature and saltwater immersion sensors which provide insights into activity patterns during the migration period, via the timing and duration of dry/wet periods, and can be used to improve latitudinal accuracy based on SST, respectively (Teo et al., 2004).

The use of geolocators to study seabird distribution has enhanced our understanding of the behaviors and habitats for many seabird species, particularly those of smaller sizes that cannot be easily fitted long-term with GPS and PTT transmitters. While the literature on migration of tubenoses is extensive (e.g., Guilford et al., 2009; Shaffer et al., 2006; Yamamoto et al., 2010), it is biased towards larger-bodied species (e.g., albatrosses, giant petrels), often from subpolar and temperate regions, leaving a knowledge gap among tropical species (Mott and Clarke, 2018; Bernard et al., 2021). Future research on the migration patterns of smaller taxa (e.g., storm-petrels, gadfly petrels) and tropical species is needed for a broader understanding of tubenose ecology. Despite the smaller body of literature focusing on tropical seabird migration, light-level geolocation has provided valuable insights on the year-round distribution and behavior for several species (e.g., Rayner et al., 2012; Jaeger et al., 2017).

1.3 Review of Tropical Seabird Migration

In this review, I examined nine geolocator studies on tropical tubenose migration, published between 2009 and 2022 (Fig. 1, Table 2). While not exhaustive, this review emphasizes single-species studies that addressed research questions about migratory behavior similar to my thesis. I excluded studies that compiled tracking data from various projects to answer broad spatial questions (e.g., identifying regions for marine protection; Le Corre et al., 2012; Trevail et al., 2023).

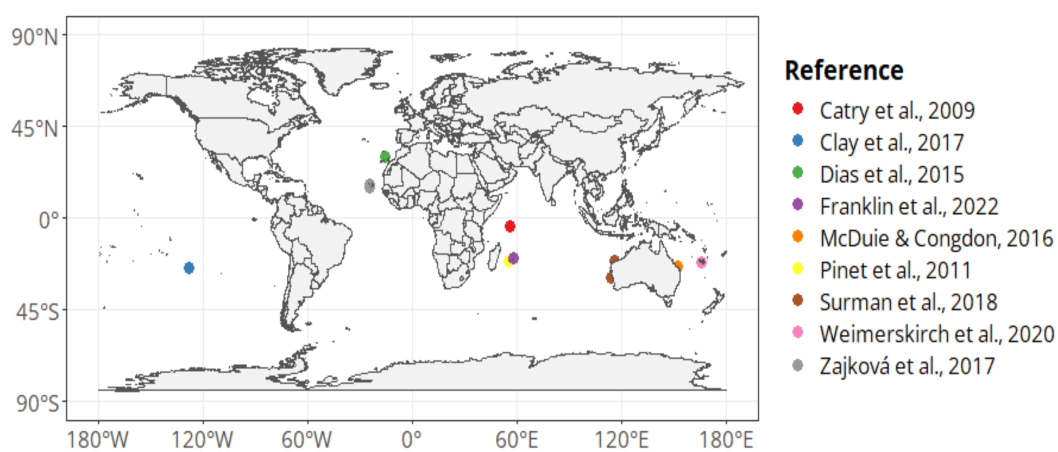


Figure 1. A world map with locations of the nine reviewed geolocator studies.

Table 2. Details of tag deployment and retrieval from nine geolocator studies on tropical and subtropical seabird migration. The number of datasets is the number of recovered tags with movement data that could be downloaded. (-) indicates details were not provided.

Species	Location (Ocean Basin)	Number of tracks (% of total deployed)	Wet/dry sensor	References
Wedge-tailed Shearwater	Aride (Indian)	11 (69%)	Yes	Catry et al., 2009
Barau's Petrel	Reunion (Indian)	23 (66%)	Yes	Pinet et al., 2011
Bulwer's Petrel	Selvagem Grande (Atlantic)	13 (65%)	Yes	Dias et al., 2015
Wedge-tailed Shearwater	Heron (Pacific)	15 (50%)	Yes	McDuie & Congdon, 2016
Boyd's Shearwater	Cape Verde (Atlantic)	38 (42%)	Yes	Zajková et al., 2017
Murphy's Petrel	Henderson Island (Pacific)	18 (72%)	Yes	Clay et al., 2017
Wedge-tailed Shearwater	Varanus & Pelsaert (Indian)	4 (16%)	-	Surman et al., 2018
Wedge-tailed Shearwater	New Caledonia (Pacific)	35 (50%)	Yes	Weimerskirch et al., 2020
Round Island Petrel	Round Island (Indian)	337 (80%)	Yes	Franklin et al., 2022

Tropical seabirds demonstrate flexible migratory behaviors. Wedge-tailed Shearwaters (*Ardenna pacifica*) adapt their behavior during migration to the local environmental conditions within their range. Wedge-tailed Shearwaters breeding in Seychelles and Western Australia moved along an east-west gradient near the equator, between 5° N and 10° S, towards the central Indian Ocean (Catry et al., 2009; Surman et al., 2018). In contrast, without the restriction of continental landmasses, Wedge-tailed Shearwaters from the Great Barrier Reef and New Caledonia made lengthy northern trans-equatorial migrations covering over 40° of latitude

(McDuie and Congdon, 2016; Weimerskirch et al., 2020). These migration patterns highlight the species' adaptability to its environment.

Many tropical seabirds exploit deep, oligotrophic waters during the non-breeding season. Rather than migrating to more productive regions of the Indian Ocean, such as the Arabian Gulf or coastal Somalia upwelling zone, Wedge-tailed Shearwaters and Barau's Petrels (*Pterodroma baraui*) traveled long distances to oligotrophic wintering grounds (Catry et al., 2009; Pinet et al., 2011). Wedge-tailed Shearwaters breeding in the Great Barrier Reef remained in deep (> 6000 m), warm (27.7 - 29.5°C), and unproductive (< 0.05 mg chl a m^{-3}) waters, despite undertaking longer migrations compared to Wedge-tailed Shearwaters in the Indian Ocean (McDuie and Congdon, 2016). These habitat use patterns indicated many tropical seabirds found prey in areas lacking predictable oceanographic features and high productivity, unlike many higher-latitude species (e.g., Shaffer et al., 2006). For example, Bulwer's Petrels (*Bulweria bulwerii*) used deep ocean waters in the tropical Atlantic and spent more time flying at night during the non-breeding period, indicating they exploited mesopelagic, vertically migrating prey (Dias et al., 2015). These migration strategies reflect the seasonal variability of the marine environment, with many species adjusting their activity patterns and habitat throughout the year.

1.3.1 Individual Variation in Migration

One third (3/9) of the reviewed studies considered sex-specific differences in migratory behavior, yet there was no evidence of at-sea segregation of sexes or differences in migratory routes during the non-breeding season (Catry et al., 2009; Clay et al., 2017; Pinet et al., 2011). In contrast, evident patterns of sex-specific behaviors were observed during the breeding season for several petrel species. During the pre-laying exodus, the core use areas of male Barau's Petrels and male Murphy's Petrels (*Pterodroma ultima*) overlapped with those of females by only 2.2% and 0.08%, respectively; males ranged farther from the colony than females (Clay et al., 2017; Pinet et al., 2012). This segregation prior to laying may reflect the different energetic requirements and reproductive roles between males and females (Hedd et al., 2014). During chick-rearing, female Wedge-tailed Shearwater had larger foraging ranges and longer trip durations than males (Peck and Congdon, 2006; Catry et al., 2009). I suggest these results indicate many petrels are constrained during the breeding season to use limited foraging areas, leading to intersexual competition and sex-related differences in space use. Conversely, the absence of sexual segregation may indicate that resources are less limited in wintering areas or that sexes have similar energy requirements outside of the breeding period (Phillips et al., 2011).

Other intrinsic factors, such as breeding status, also influence migratory patterns in tubenoses. Unsuccessful breeders, no longer constrained to a breeding site, may adjust their behavior by migrating to the wintering grounds early or by shifting their geographic distribution to avoid competition with breeding birds. For example, unsuccessful Bulwer's Petrels in the Atlantic departed from their colony and arrived at non-breeding foraging areas three weeks earlier than successful breeders (21 Aug ± 10 days vs. 14 Sep ± 5 days, respectively) (Dias et al., 2015). Additionally, unsuccessful breeders were observed returning earlier to nesting sites the following season, providing evidence of carry-over effects from the costly energy demands of successful breeding (Catry et al., 2013).

Differences in migratory behavior and phenology between and within species can be a response to the widely dispersed prey in tropical waters. Timing of migration and non-breeding destinations may vary among individuals of the same species. For instance, non-breeding Round Island Petrels (*Pterodroma arminjoniana*) tracked over multiple years had high site fidelity, returning to the same locations each year, with different individuals using different over-wintering sites (Franklin et al., 2022). Tubenoses may vary their timing and destinations to reduce competition for limited resources at sea, but familiarity with locations drives fidelity to certain foraging areas at-sea when these resources are heterogenous. It is possible that individuals learn successful foraging areas and strategies over time and choose to return to locations with predictable prey resources (Spear et al., 2007).

1.3.2 Foraging strategies

Foraging strategies are shaped in part by the heterogeneity of prey resources in the marine environment (Weimerskirch, 2007), which influences the global distribution and abundance of seabirds (Ballance, 2007). Because tropical seabirds search vast and oligotrophic oceanic waters, they employ a wide range of strategies to locate dispersed prey, such as relying on subsurface predators to bring prey up to the surface (Ballance and Pitman, 1999), targeting vertically-migrating prey (Bonnet-Lebrun et al., 2021), or covering as much area as possible to maximize chances of finding prey (Ventura et al., 2020; Halpin et al., 2022). Yet, because background prey resources tend to be less predictable in tropical oceans, fundamental questions persist regarding their foraging ecology: do tropical seabirds alter their migration patterns in response to seasonal and inter-annual oceanographic variability, or do they consistently use the same habitat features? Do they exploit vertically migrating prey or do they depend on subsurface predators, such as marine mammals and tunas? The answers to these questions are likely species-specific and may vary among individuals. For instance, while some tropical seabirds, such as Murphy’s petrel, disperse to areas of markedly higher productivity after breeding (Clay et al., 2017), others, like the Wedge-tailed Shearwater, remain in oligotrophic regions (Weimerskirch et al., 2020).

Although a universal pattern does not appear to exist for tropical seabirds, the reviewed studies emphasize the importance of facilitated foraging and diel vertically migrating prey, reflected in the way tropical seabirds use deep and oligotrophic waters for at least a part of their annual cycle. In the eastern tropical Pacific, seabirds exploit feeding opportunities in association with other taxa for greater success in finding widely dispersed prey (Au and Pitman, 1986; Spear et al., 2007). Subsurface predators drive prey towards the surface, enabling seabirds to access them. This dependence on other species is seldom a major foraging strategy in higher-latitude seabirds (Ballance & Pitman 1999). Similarly, diel vertical migration of mesopelagic prey may also be of importance to several tropical species. Both the Bulwer's and Black-winged Petrel (*Pterodroma nigripennis*) become predominantly nocturnal while in their non-breeding areas (Bonnet-Lebrun et al., 2021), indicating these species may exploit vertically migrating prey more over winter.

1.4 Methods for Light-level Geolocation

Light-level geolocation enables the estimation of one or two daily locations, with latitude derived from day length and longitude from the timing of local midday and midnight relative to Greenwich Mean Time and Julian day (Hill, 1994). Initially, geolocators were applied to larger marine species, such as elephant seals (Delong et al., 1992) and tuna (Block et al., 1998). As these devices have become increasingly smaller, their use has expanded to include a growing variety of smaller taxa (e.g., Dias et al., 2015; Militão et al., 2022).

There is now a diverse range of tools and methods commonly used to derive and refine estimated locations from geolocator data. The choice of tools to calculate latitude and longitude typically depends on the quality of data around defined twilight events (Lisovski et al., 2020). High-quality light data refer to the consistency of twilight times between days when the tag carrier is relatively stationary (i.e., not migrating). Ultimately, choosing a method depends on the research question, the species' life history, the tag's sampling regime, and the researcher's preference for additional tools to refine location data.

An important aspect of geolocator analysis is defining breeding stages, which can be challenging due to the relatively low accuracy of locations derived from geolocator data. Moreover, large location errors are also influenced by latitude and by species-specific behaviors (Lisovski et al., 2020; Halpin et al., 2021). Accordingly, visual inspection of tracks is not sufficient to identify the start and end of the migration period, since these location errors often match the size of the foraging range during the breeding period. Thus, the timing of seabird migration can be determined through direct nest observation at the colony, inferred from immersion (wet/dry sensor) data, or interpreted based on directional movement. For tubenoses with distinct breeding and non-breeding areas, the non-breeding period can be divided into three phases: 1) outward migration, 2) non-breeding, and 3) return migration. Since the timing of migration is integral for delineating the non-breeding range, most studies explicitly state how they determined these arrival / departure dates (Table 3).

The most common spatial analysis tool used in the reviewed studies is kernel density estimation (KDE). KDE is used to identify utilization distributions (UD) that depicts the areas of frequent use, typically visualized using several isopleths of varying quantiles. All studies used 50% and 95% isopleths to represent the core and general use areas, respectively, following a common standard used in many animal home range estimation studies (Ford and Krumme, 1979; Soanes et al., 2013). To ensure equal representation and control for differing numbers of locations among individuals, all studies developed separate UDs for each bird, which were merged to obtain an overall wintering distribution (Clay et al., 2017).

To quantify overlap among individuals, sexes, colonies, or years, studies have used Bhattacharyya's affinity (BA) index (Clay et al., 2017; Weimerskirch et al., 2020) or the earth mover's distance (EMD) (Franklin et al., 2022). The BA index, which ranges from 0 (no overlap) to 1 (complete overlap), provides an objective assessment of similarity between distributions (Fieberg & Kochanny, 2005). EMD is a parallel method to evaluate overlap by calculating how much "effort" it takes to transform one UD into another, while considering spatial proximity between UDs (Kranstauber et al., 2017).

Table 3. Methods used to determine start and end dates of migration in reviewed geolocator studies on tropical seabirds.

Start of outward migration	End of outward migration	Start of return migration	End of return migration	References
Direct nest monitoring	Combination of movements and activity patterns	Combination of movements and activity patterns	Activity patterns	Catry et al., 2009
Last day bird in burrow: dry at night/no light during day & direct nest monitoring	Cessation in rapid directed movement	Rapid directed movement	First day bird in burrow: dry at night/no light during day	Pinet et al., 2011
First day further than 200 km of the colony	Cessation in rapid directed movement	Rapid directed movement	First day within 200 km of the colony	Dias et al., 2015
Last day bird in burrow: dry at night	Cessation in rapid directed movement	Rapid directed movement	First day bird in burrow: dry at night and location indicates return	McDuie & Congdon, 2016
Combination of movements and activity patterns	Combination of movements and activity patterns	Combination of movements and activity patterns	Dry night within 500 km of the colony	Clay et al., 2017
Logger dry at night indicating last night in colony followed by directed movement away from colony	First day the bird entered the cluster of positions at non-breeding area	First day the bird’s location was outside the cluster of previous positions and followed by directed movement away	First day bird in burrow: dry at night/no light during day	Zajková et al., 2017
Not stated	Not stated	Not stated	Not stated	Surman et al., 2018
Rapid directed movement	Cessation in rapid directed movement	Rapid directed movement	Cessation in rapid directed movement	Weimerskirch et al., 2020
Hidden Markov model	Hidden Markov model	Hidden Markov model	Hidden Markov model	Franklin et al., 2022

Reviewed studies characterized non-breeding habitats using oceanographic parameters, expanding the scope of seabird research through the integration of remotely-sensed data (Tremblay et al., 2009). The use of satellite data has enabled detailed examination of non-breeding seabird ecology (Table 4), with sea surface temperature (SST), surface chlorophyll-a concentration, bathymetry, and wind speed emerging as the most frequently used parameters in reviewed studies to describe seabird habitats.

Although relative contributions of the top four oceanographic parameters outweighs other less commonly used habitat variables (e.g., sea-level anomaly SLA), two studies evaluated mesoscale oceanographic features (McDuie and Congdon, 2016; Clay et al., 2017). Positive SLA values, which may indicate presence of eddies, were the strongest determinants of Wedge-tailed Shearwater distribution in the western Pacific (McDuie and Congdon, 2016). In the subtropical Indian Ocean, Wedge-tailed Shearwater were observed more frequently within convergence zones of higher SLA during vessel surveys (Hyrenbach et al., 2006). Evidence that dynamic features influence where Wedge-tailed Shearwater are distributed indicates that large-scale characteristics of oceanographic water masses (e.g., SST) may be relatively unimportant drivers of seabird presence in warm tropical waters. Since many tropical seabirds rely on multiple foraging strategies (including subsurface predators), the association between foraging seabirds and tuna and marine mammals may also influence seabird distribution.

Table 4. Description of the oceanographic parameters used in the nine reviewed sub- and tropical seabird geolocator studies.

Variable	Description	Studies that summarized values	Studies that modelled parameter
Bathymetry	Bathymetry, depth, bathymetry gradients	4	2
Temperature	Sea surface temperature, temperature gradients	3	2
Chlorophyll	Chlorophyll-a concentration at surface, chlorophyll gradients	2	2
Wind	Wind speed, wind direction	2	1
Sea-level anomaly	Measure of mesoscale turbulence	0	2
Net primary productivity	How much carbon dioxide is taken in during photosynthesis minus how much carbon dioxide is released during respiration per unit area and time	1	0
Salinity	Sea surface salinity, salinity gradients	0	1
Eddy kinetic energy	Measure of mesoscale turbulence	0	1
Distance to seamount	Nearest seamount	0	1

1.5 Conclusion

Although geolocator studies of tropical tubenoses are relatively few compared to those of higher-latitude species, consistent behavioral patterns have been observed across studies. In these reviewed studies, tubenoses remained within tropical and subtropical waters during one or more stages of the annual cycle, having evolved foraging strategies to successfully exploit warm oligotrophic waters. Nonetheless, there is no universal pattern of migration or single foraging strategy among tropical seabirds, as the reviewed studies reveal considerable variation at the individual, population, and species level. Variability in migration and foraging strategies likely reflect adaptations that optimize foraging success for the vastly distributed and patchy prey in tropical oceans.

My thesis focuses on Wedge-tailed Shearwater migration using a breeding colony on the island of Oʻahu, Hawaiʻi. Wedge-tailed Shearwaters are widely distributed in the tropical and subtropical Pacific and Indian Oceans (King, 1974; Whittow, 2020) with > 87,000 breeding pairs estimated on the main Hawaiian Islands (Pyle and Pyle, 2017). Though abundant, the post-breeding movements of this population remain largely unknown. Shipboard surveys have documented abundant Wedge-tailed Shearwaters in the eastern and western tropical Pacific, but these observations have not yet been linked to specific breeding sites (Jenkins, 1979; Ballance et al., 2006; Duffy and Frazier, 2014; Young and Zook, 2016; Marín, 2024). Geolocator studies in the South Pacific and the Indian Ocean demonstrate Wedge-tailed Shearwaters have varied migration patterns. Additionally, they are known to associate with tunas, especially Skipjack Tuna (*Katsuwonus pelamis*) around Hawai'i and in the tropical North Pacific (King, 1974; Hebshi et al., 2008). Following dispersal from the Hawaiian Islands, it is possible that they seek out areas of high Skipjack Tuna biomass either in the warm pool or in the eastern tropical Pacific (Blackburn and Williams, 1975; Lehodey et al., 1997).

1.6 References

Ainley, D., Ribic, C., and Woehler, E. (2012). Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. *Mar. Ecol. Prog. Ser.* 451, 231–243. doi: 10.3354/meps09524

Au, D. W. K., and Pitman, R. L. (1986). Seabird Interactions with Dolphins and Tuna in the Eastern Tropical Pacific. *Condor* 88, 304–317. doi: 10.2307/1368877

Bairlein, F., and Schaub, M. (2009). Ringing and the study of mechanisms of migration. *Ring. Migr.* 24, 162–168. doi: 10.1080/03078698.2009.9674387

Ballance, L. T. (2007). Understanding seabirds at sea: why and how? *Mar. Ornithol.* 35, 127–135.

Ballance, L. T., and Pitman, R. L. (1999). Foraging ecology of tropical seabirds. *In: Adams, N.J. & Slotow, R.H. (eds) Proc. 22 Int. Ornithol. Congr., Durban*, 2057–2071.

Ballance, L. T., Pitman, R. L., and Fiedler, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Prog. Oceanogr.* 69, 360–390. doi: 10.1016/j.pocean.2006.03.013

Bernard, A., Rodrigues, A. S. L., Cazalis, V., and Grémillet, D. (2021). Toward a global strategy for seabird tracking. *Conserv. Lett.* 14, e12804. doi: 10.1111/conl.12804

Blackburn, M., and Williams, F. (1975). Distribution and ecology of skipjack tuna, *Katsuwonus pelamis*, in an offshore area of the eastern tropical Pacific Ocean. *Fish. Bull.* 73, 382–411. doi: 10.1111/j.1095-8649.1974.tb01338.x.

Block, B. A., Dewar, H., Williams, T., Prince, E. D., Farwell, C. J., and Fudge, D. (1998). Archival Tagging of Atlantic Bluefin Tuna (*Thunnus thynnus thynnus*). *Marine Technology Society Journal* 32, 37–46.

Bonnet-Lebrun, A.-S., Dias, M. P., Phillips, R. A., Granadeiro, J. P., Brooke, M. de L., Chastel, O., et al. (2021). Seabird Migration Strategies: Flight Budgets, Diel Activity Patterns, and Lunar Influence. *Front. Mar. Sci.* 8, 683071. doi: 10.3389/fmars.2021.683071

Bridge, E. S., Thorup, K., Bowlin, M. S., Chilson, P. B., Diehl, R. H., Fléron, R. W., et al. (2011). Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience* 61, 689–698. doi: 10.1525/bio.2011.61.9.7

Cairns, D. K. (1987). Seabirds as Indicators of Marine Food Supplies. *Biol. Oceanogr.* 5, 261–271. doi: 10.1080/01965581.1987.10749517

Carreiro, A. R., Ramos, J. A., Mata, V. A., Almeida, N. M., Rodrigues, I., Dos Santos, I., et al. (2023). DNA metabarcoding to assess prey overlap between tuna and seabirds in the Eastern tropical Atlantic: Implications for an ecosystem-based management. *Mar. Environ. Res.* 187, 105955. doi: 10.1016/j.marenvres.2023.105955

Casper, R. M. (2009). Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour* 78, 1477–1483. doi: 10.1016/j.anbehav.2009.09.023

Catry, P., Dias, M. P., Phillips, R. A., and Granadeiro, J. P. (2013). Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecol.* 94, 1230–1235. doi: 10.1890/12-2177.1

Catry, T., Ramos, J., Le Corre, M., and Phillips, R. (2009). Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Mar. Ecol. Prog. Ser.* 391, 231–242. doi: 10.3354/meps07717

Clay, T., Phillips, R., Manica, A., Jackson, H., and Brooke, M. (2017). Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Mar. Ecol. Prog. Ser.* 579, 139–155. doi: 10.3354/meps12244

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., et al. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* 22, 1–34. doi: 10.1017/S0959270912000020

Delong, R. L., Stewart, B. S., and Hill, R. D. (1992). Documenting migrations of northern elephant seals using day length. *Marine Mammal Science* 8, 155–159. doi: 10.1111/j.1748-7692.1992.tb00375.x

Dias, M. P., Alho, M., Granadeiro, J. P., and Catry, P. (2015). Wanderer of the deepest seas: migratory behaviour and distribution of the highly pelagic Bulwer's petrel. *J Ornithol* 156, 955–962. doi: 10.1007/s10336-015-1210-9

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., et al. (2019). Threats to seabirds: A global assessment. *Biol. Conserv.* 237, 525–537. doi: 10.1016/j.biocon.2019.06.033

Duffy, D. C., and Frazier, J. G. (2014). A census of Tehuantepec and Papagayo eddies in the northeastern tropical Pacific. *Geophys. Res. Lett.* 32, 2005GL024324. doi: 10.1029/2005GL024324

Ekstrom, P. A. (2004). An advance in geolocation by light. *Mem. Natl Inst. Polar Res. Spec. Issue* 58, 210–226.

Ford, R. G., and Krumme, D. W. (1979). The Analysis of Space use Patterns. *J. Theor. Biol.* 76, 125–155. doi: 10.1016/0022-5193(79)90366-7

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., et al. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.* 10, 13. doi: 10.1186/s40462-022-00311-y

Gilmour, M. E., Adams, J., Block, B. A., Caselle, J. E., Friedlander, A. M., Game, E. T., et al. (2022). Evaluation of MPA designs that protect highly mobile megafauna now and under climate change scenarios. *Global Ecology and Conservation* 35, e02070. doi: 10.1016/j.gecco.2022.e02070

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., et al. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proc. R. Soc. B.* 276, 1215–1223. doi: 10.1098/rspb.2008.1577

Halpin, L. R., Mott, R., Clay, T. A., Humphries, G. R. W., Chatwin, T. A., Carlile, N., et al. (2022). Predicting the Foraging Habitats of Sympatrically Breeding Gadfly Petrels in the South Pacific Ocean. *Front. Mar. Sci.* 9, 853104. doi: 10.3389/fmars.2022.853104

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., et al. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods Ecol. Evol.* 12, 2243–2255. doi: 10.1111/2041-210X.13698

Hebshi, A., Duffy, D., and Hyrenbach, K. (2008). Associations between seabirds and subsurface predators around Oahu, Hawaii. *Aquat. Biol.* 19, 89–98. doi: 10.3354/ab00098

Hedd, A., Montevecchi, W. A., Phillips, R. A., and Fifield, D. A. (2014). Seasonal Sexual Segregation by Monomorphic Sooty Shearwaters *Puffinus griseus* Reflects Different Reproductive Roles during the Pre-Laying Period. *PLoS ONE* 9, e85572. doi: 10.1371/journal.pone.0085572

Hill, R. D. (1994). “Twelve. Theory of geolocation by light levels,” in *Elephant Seals*, eds. B. J. Le Boeuf and R. M. Laws (University of California Press), 227–236. doi: 10.1525/9780520328150-014

Hill, R. D., and Braun, M. J. (2001). “Geolocation by Light Level – The Next Step: Latitude,” in *Electronic Tagging and Tracking in Marine Fisheries*, eds. J. R. Sibert and J. L. Nielsen (Dordrecht: Springer Netherlands), 315–330. doi: 10.1007/978-94-017-1402-0_17

Hyrenbach, K., Veit, R., Weimerskirch, H., and Hunt GL, J. (2006). Seabird associations with mesoscale eddies: the subtropical Indian Ocean. *Mar. Ecol. Prog. Ser.* 324, 271–279. doi: 10.3354/meps324271

Jaeger, A., Feare, C. J., Summers, R. W., Lebarbenchon, C., Larose, C. S., and Le Corre, M. (2017). Geolocation Reveals Year-Round at-Sea Distribution and Activity of a Superabundant Tropical Seabird, the Sooty Tern *Onychoprion fuscatus*. *Front. Mar. Sci.* 4, 394. doi: 10.3389/fmars.2017.00394

Jenkins, J. A. F. (1979). Observations on the Wedge-tailed shearwater *(Puffinus pacificus)* in the South West Pacific. *Notornis* 26, 331–348.

King, W. B. (1974). Pelagic studies of seabirds in the central and eastern Pacific Ocean. *Smithsonian Contributions to Zoology*, 1–277. doi: 10.5479/si.00810282.158

Kranstauber, B., Smolla, M., and Safi, K. (2017). Similarity in spatial utilization distributions measured by the earth mover's distance. *Methods Ecol. Evol.* 8, 155–160. doi: 10.1111/2041-210X.12649

Le Corre, M., Jaeger, A., Pinet, P., Kappes, M. A., Weimerskirch, H., Catry, T., et al. (2012). Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. *Biological Conservation* 156, 83–93. doi: 10.1016/j.biocon.2011.11.015

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., and Picaut, J. (1997). El Niño Southern Oscillation and tuna in the western Pacific. *Nature* 389, 715–718. doi: 10.1038/39575

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., et al. (2020). Light-level geolocator analyses: A user's guide. *J. Anim. Ecol.* 89, 221–236. doi: 10.1111/1365-2656.13036

Marín, M. (2024). Status and occurrence of Wedge-tailed Shearwater *Ardenna pacifica* in waters of the northwestern coast of South America. *Mar. Ornithol.* 52, 81–84. doi: 10.4319/mo.2021.49.1.071

McDuie, F., and Congdon, B. (2016). Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas. *Mar. Ecol. Prog. Ser.* 550, 219–234. doi: 10.3354/meps11713

McInnes, A. M., Weideman, E. A., Carpenter-Kling, T., Barham, P., Christian, M., Day, K., et al. (2024). Commercial fishery no-take zones for African penguins minimize fisheries losses at the expense of conservation gains. *ICES Journal of Marine Science* 81, 1632–1646. doi: 10.1093/icesjms/fsae109

Militão, T., Sanz-Aguilar, A., Rotger, A., and Ramos, R. (2022). Non-breeding distribution and at-sea activity patterns of the smallest European seabird, the European Storm Petrel (*Hydrobates pelagicus*). *Ibis* 164, 1160–1179. doi: 10.1111/ibi.13068

Miller, M., Carlile, N., Scutt Phillips, J., McDuie, F., and Congdon, B. (2018). Importance of tropical tuna for seabird foraging over a marine productivity gradient. *Mar. Ecol. Prog. Ser.* 586, 233–249. doi: 10.3354/meps12376

Mott, R., and Clarke, R. H. (2018). Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu - Austral Ornithology* 118, 235–246. doi: 10.1080/01584197.2017.1416957

Murphy, R. C. (1914). Observations on Birds of the South Atlantic. *Auk* 31, 439–457. doi: 10.2307/4072006

Peck, D. R., and Congdon, B. C. (2006). Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Puffinus pacificus*. *J. Avian Biol.* 37, 245–251. doi: 10.1111/j.2006.0908-8857.03558.x

Phillips, R. A., McGill, R. A. R., Dawson, D. A., and Bearhop, S. (2011). Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Mar Biol* 158, 2199–2208. doi: 10.1007/s00227-011-1725-4

Phillips, R. A., Xavier, J. C., and Croxall, J. P. (2003). Effects of Satellite Transmitters on Albatrosses and Petrels. *Auk* 120, 1082–1090. doi: https://doi.org/10.2307/4090279

Piatt, I., and Sydeman, W. (2007). Seabirds as indicators of marine ecosystems. *Mar. Ecol. Prog. Ser.* 352, 199–204. doi: 10.3354/meps07070

Pinet, P., Jaquemet, S., Pinaud, D., Weimerskirch, H., Phillips, R., and Le Corre, M. (2011). Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. *Mar. Ecol. Prog. Ser.* 423, 291–302. doi: 10.3354/meps08971

Pyle, R. L., and Pyle, P. (2017). The Birds of the Hawaiian Islands: Occurrence, History, Distribution, and Status. *B.P. Bishop Museum, Honolulu, HI, U.S.A.* Available at: http://hbs.bishopmuseum.org/birds/rlp-monograph/

Rayner, M. J., Taylor, G. A., Gummer, H. D., Phillips, R. A., Sagar, P. M., Shaffer, S. A., et al. (2012). The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). *Emu - Austral Ornithology* 112, 107–116. doi: 10.1071/MU11066

Rodríguez, A., Holmes, N. D., Ryan, P. G., Wilson, K.-J., Faulquier, L., Murillo, Y., et al. (2017). Seabird mortality induced by land-based artificial lights: Seabird Mortality and Artificial Lights. *Conserv. Biol.* 31, 986–1001. doi: 10.1111/cobi.12900

Shaffer, S. A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D. R., Sagar, P. M., et al. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc. Natl. Acad. Sci. U.S.A.* 103, 12799–12802. doi: 10.1073/pnas.0603715103

Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Sumner, M. D., and Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *J. Appl. Ecol.* 50, 671–679. doi: 10.1111/1365-2664.12069

Spear, L. B., Ainley, D. G., and Walker, W. A. (2007). *Foraging dynamics of seabirds in the eastern tropical Pacific Ocean*. Camarillo, CA: Cooper Ornithological Society.

Surman, C. A., Nicholson, L. W., and Phillips, R. A. (2018). Distribution and patterns of migration of a tropical seabird community in the Eastern Indian Ocean. *J. Ornithol.* 159, 867–877. doi: 10.1007/s10336-018-1556-x

Teo, S., Boustany, A., Blackwell, S., Walli, A., Weng, K., and Block, B. (2004). Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Mar. Ecol. Prog. Ser.* 283, 81–98. doi: 10.3354/meps283081

Tremblay, Y., Bertrand, S., Henry, R. W., Kappes, M. A., Costa, D. P., and Shaffer, S. A. (2009). Analytical approaches to investigating seabird–environment interactions: a review. *Mar. Ecol. Prog. Ser.* 391, 153–163. doi: 10.3354/meps08146

Trevail, A. M., Nicoll, M. A. C., Freeman, R., Le Corre, M., Schwarz, J., Jaeger, A., et al. (2023). Tracking seabird migration in the tropical Indian Ocean reveals basin-scale conservation need. *Current Biology* 33, 5247-5256.e4. doi: 10.1016/j.cub.2023.10.060

Ventura, F., Granadeiro, J. P., Padget, O., and Catry, P. (2020). Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales. *Proc. R. Soc. B.* 287, 20191775. doi: 10.1098/rspb.2019.1775

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Res. Part II.* 54, 211–223. doi: 10.1016/j.dsr2.2006.11.013

Weimerskirch, H., de Grissac, S., Ravache, A., Prudor, A., Corbeau, A., Congdon, B., et al. (2020). At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. *Mar. Ecol. Prog. Ser.* 633, 225–238. doi: 10.3354/meps13171

Whittow, G. C. (2020). Wedge-tailed Shearwater *(Ardenna pacifica)*. version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: https://doi.org/10.2173/bow.wetshe.01

Wilson, R., Grémillet, D., Syder, J., Kierspel, M., Garthe, S., Weimerskirch, H., et al. (2002). Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Mar. Ecol. Prog. Ser.* 228, 241–261. doi: 10.3354/meps228241

Wilson, R. P., and McMahon, C. R. (2006). Measuring Devices on Wild Animals: What Constitutes Acceptable Practice? *Frontiers in Ecology and the Environment* 4, 147–154. doi: https://doi.org/10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2

Wilson, R., and Vandenabeele, S. (2012). Technological innovation in archival tags used in seabird research. *Mar. Ecol. Prog. Ser.* 451, 245–262. doi: 10.3354/meps09608

Yamamoto, T., Takahashi, A., Katsumata, N., Sato, K., and Trathan, P. N. (2010). At-Sea Distribution and Behavior of Streaked Shearwaters (Calonectris leucomelas) During the Nonbreeding Period. *Auk* 127, 871–881. doi: 10.1525/auk.2010.10029

Young, B. E. Y., and Zook, J. R. (2016). Observation frequency and seasonality of marine birds off the Pacific coast of Costa Rica. *RBT* 64, 235. doi: 10.15517/rbt.v64i1.23453

Young, L. C., and VanderWerf, E. A. (2022). *Conservation of Marine Birds*. Cambridge, MA: Elsevier.

CHAPTER 2

Geolocator device effects on chick-provisioning and overwinter survival of Wedge-tailed Shearwaters: does interannual oceanographic variability matter?

2.1 Abstract

Although biologging has transformed the study of seabird ecology, unintended negative effects of device deployments can alter the very behaviors being studied. These impacts can vary by species, device type, and, less commonly explored, by year. In this study, I tested for potential effects of archival light-level geolocator deployment (< 1% of body mass) on the chick growth and overwinter survival of Wedge-tailed Shearwaters (*Ardenna pacifica*) during two contrasting El Niño Southern Oscillation (ENSO) years. Accounting for hatching phenology, I compared chick growth rates between individual nestlings provisioned by tagged and non-tagged adults and assessed adult return rates in the following breeding season. My results revealed no significant negative or sex-specific effects of adults carrying geolocators on chick growth or adult return rates in either year. However, oceanic conditions during the 2023 El Niño may have influenced chick development; chicks from both tagged and non-tagged adults had lower peak body mass and slower wing chord growth compared to the La Niña year. Despite these ENSO-driven differences, geolocator deployment and interannual variability did not cumulatively affect breeding performance or adult return rates. My findings indicate that geolocator deployment did not adversely impact the survival and breeding success of Wedge-tailed Shearwaters, but subtle interactions between tagging, sex-specific traits, and oceanographic conditions may emerge during periods with more challenging conditions. As biologging technology continues to evolve, my study emphasizes the importance of ongoing assessments of device effects, particularly with varying ocean conditions.

2.2 Introduction

Advancements in biologging technology have facilitated an increasing number of tagging studies aimed at understanding the movements, behaviors, and physiology of a growing number of animals (Burger and Shaffer, 2008). This research has broadened our knowledge of migrations, foraging ecology, and specific habitats used by individuals from different breeding sites. However, carrying these devices can influence the natural behavior of the tagged individuals, with serious implications for their overall fitness and for the interpretation of collected data (Paton et al., 2020; Clewley et al., 2021).

Tagged birds (i.e., birds fitted with telemetric devices) may alter their behavior and expend more energy due to discomfort from the added mass and increased drag when flying or diving (Vandenabeele et al., 2012). For instance, Black-legged Kittiwakes (*Rissa tridactyla*) fitted with global-positioning system (GPS) loggers increased their foraging trip durations and ranges compared to non-tagged individuals, likely compensating for increased energy demands as a result of carrying devices (Heggøy et al., 2015). For species that travel long distances to locate dispersed prey, these device effects can indirectly impact breeding success and survivorship through reduced foraging performance. Specifically, there are a variety of adverse effects on body condition, chick-provisioning, and foraging behavior (Paredes et al., 2005; Adams et al., 2009; Schacter and Jones, 2017). Ultimately, the duration of the deployment and the birds' ability to buffer these impacts (e.g., higher energetic costs, lower food acquisition) influence whether they exhibit behavioral, physiological, or demographic responses. Because seabirds exhibit short-term responses (days – weeks) (Chivers et al., 2016; Gillies et al., 2020) and long-term responses (months – one year) (Elliott et al., 2012), researchers should consider the ethical and scientific implications of device effects and the associated potential biases in the context of the broader research question.

Despite the growing number of seabird tracking studies that use biologging tools, a relatively small proportion investigate device effects (Vandenabeele et al., 2012; Geen et al., 2019). Many researchers rely on long-standing published guidelines, such as the ‘tag weight not exceeding 5% (or 3%) of the body mass’, or assume that the absence of detectable negative impacts on a closely-related species applies to their study species (Phillips et al., 2003; Wilson and McMahon, 2006; Casper, 2009). However, meta-analyses have highlighted that these impacts vary in relation to species-specific traits (such as flying style and body size), attachment methods, and tag weight (Barron et al., 2010; Costantini and Møller, 2013). Moreover, (Bodey et al., 2018) suggested that the variable outcomes reported in tracking studies are likely due to species- and individual-specific traits and behavior, as their meta-analysis found little evidence that phylogenetically related species were similarly affected by device deployment. Device effects may also vary interannually, becoming more pronounced during years of reduced food availability and challenging environmental conditions. For instance, the winter conditions that seabirds experience after energy-intensive breeding and migration play a key role in influencing future survival and breeding phenology (Schroeder et al., 2009; Sydeman and Bograd, 2009). Yet, previous studies that quantified breeding success and chick-provisioning as measures of device effects rarely evaluated the role of sub-optimal foraging conditions, particularly those that carry over from the non-breeding season. Accordingly, the cumulative effects of device deployment and stressful environmental conditions on the fitness of seabirds have not been widely explored.

To test whether deployment of biologging devices can have a synergistic effect on breeding performance during years with contrasting oceanographic conditions, I conducted an experimental study to evaluate the potential effects of geolocators on Wedge-tailed Shearwaters (*Ardenna pacifica*). This medium-sized tropical shearwater is capable of diving to depths exceeding 10 m, with average maximum dive depths of 4 m (Hyrenbach et al., 2014; Felis et al., 2019). Geolocators are small archival data loggers, typically measuring 14 to 17 mm by 8 to 19 mm by 6 to 8 mm and weighing between 0.4 and 3 g. These devices can be mounted to the tarsus using a metal or darvic band and a cable tie. In previous Wedge-tailed Shearwater studies, tarsus geolocator deployments did not deter adults from returning to feed their chicks during the breeding season, indicating handling and tag deployment did not cause nest abandonment (Catry et al., 2009; McDuie and Congdon, 2016). Additionally, chicks of tagged birds fledged at similar body masses compared to chicks of the same age raised by non-tagged parents (Catry et al., 2009).

Effects of winter foraging conditions and energetics during the non-breeding season can carry over to affect breeding performance in the following season (Shoji et al., 2015; Fayet et al., 2017). Therefore, it is important to understand these overwinter device impacts, especially during years with varying environmental conditions and prey availability. Because chick-rearing Wedge-tailed Shearwaters experience lower provisioning rates and meal sizes during periods with warmer sea-surface temperature (Peck et al., 2004), they may be particularly sensitive to interannual changes in ocean climate. To explore the potential influence of climatic variations, I measured the growth rates of chicks raised by geolocator-tagged and non-tagged adults during two years with contrasting oceanographic conditions: the 2022 La Niña and the 2023 El Niño.

Sex-specific differences in Wedge-tailed Shearwater chick-provisioning behavior were previously documented; females have greater foraging ranges (Catry et al., 2009) and longer trip durations than males, resulting in males feeding chicks more frequently (Peck and Congdon, 2006). Yet, despite sex-specific morphometric differences in Wedge-tailed Shearwaters, with males having larger bill-depth , there is no evidence of strong sexual dimorphism in this species (Bull et al., 2005). Sex differences in foraging behavior of monomorphic species can arise due to varying energetic or nutritional needs between the sexes, influenced by factors like the costs of egg production (Monaghan et al., 1998), or unequal incubation shifts (Hatch, 1990; Creelman and Storey, 1991). Although the contributions of each sex to incubation in Wedge-tailed Shearwaters are not well-documented, the observed differences in foraging behavior during chick provisioning indicate the possibility of sex-specific tagging effects.

The objectives of this study were to test geolocator device effects on adult shearwaters and whether effects vary (becoming detectable or intensified) during years of sub-optimal oceanographic conditions. Specifically, I tested: 1) if chicks provisioned by tagged adults grew at the same rate as chicks provisioned by non-tagged but handled adults, 2) if chick growth rates vary in La Niña and El Niño years, and 3) if there are sex-related differences in device effects. I hypothesize lower growth rates and survivorship in chicks with a tagged parent versus those with non-tagged parents, and lower return rates of tagged adults the following year.

2.3 Methods

2.3.1 Study site and device attachment

I studied Wedge-tailed Shearwaters breeding at the Freeman Seabird Preserve (21°15.36' N, 157°47.51' W) on the island of Oʻahu, Hawaiʻi during the 2022 and 2023 breeding seasons

(August – November). Wedge-tailed Shearwaters nest in this one-acre private preserve between March and November in artificial rock and brick structures and ceramic nest modules, which facilitate easy capture of shearwaters by hand through the burrow entrance. In this colony, multiple pairs often share large rock formations for nesting, resulting in intermingling of chicks. To minimize complications associated with the high density of nesting birds, I only selected isolated burrows with a single entrance.

I deployed Lotek MK4093 light-level geolocators (25 in 2022 and 30 in 2023, hereafter, tags) on adults provisioning chicks during the early chick rearing period in August, and I retrieved tags upon return to the colony in April the following breeding season. Tags were fixed to a metal incoloy band on the right tarsus with a single nylon cable tie. The total attachment mass was 2.6 g, equivalent to < 1 % of adult body mass (mean mass ± SD: 393 ± 30.7 g; $n = 113$; Whittow, 2020). The dimensions of the tags, excluding the communication pins, were 15 mm × 10 mm × 6 mm (L × W × D). The incoloy band was flattened into a “D” shape to prevent the tag from rotating towards the interior side of the leg. I deployed tags during the brooding period (i.e., shortly after chicks hatched) because nest abandonment is more likely to occur during incubation (Sun et al., 2020), and because it is the window of time an adult is most likely to be present in the burrow after hatching. Only one adult from each pair was tagged in a single year to reduce any potential effects on chicks. Mean handling time ± SD during deployment was 7.58 ± 1.92 minutes for banding and tagging and was 5.33 ± 1.88 minutes for the banding only comparison group.

2.3.2 Comparison groups and breeding success

I assessed breeding success and adult return rates by comparing two groups: a tagged group (banded and tagged) and a non-tagged group (banded only). I evaluated breeding success during the 2022 and 2023 chick-provisioning season using two criteria: (i) three chick growth metrics—body mass (grams), unflattened wing chord (mm), and tenth primary length (mm), and (ii) chick survivorship to fledging. I also compared adult return rates to the colony in the following breeding seasons (2023 and 2024), confirmed through recapture. Searching effort involved checking inside every burrow and adjacent areas within the colony to maximize chances of recapture. I tested the sex-specific proportion of returning birds in each group (tagged or non-tagged) every year using Chi-square tests.

Over the course of two chick rearing seasons (2022 and 2023), I visually inspected burrows, weighed chick body mass, and measured the length of chick wing chords and tenth primary feathers (P10) weekly in the evenings (16:00 – 19:00 local time), starting one week after tag deployment (20 – 21 August 2022 and 18 – 20 August 2023) and until the third week of November when the chicks reached fledging stage. A chick was presumed to have fledged when it was no longer found in the burrow, and at least 100 days old, based on Wedge-tailed Shearwater mean fledging age in Hawaiʻi (Pettit et al., 1984). Chicks were weighed inside a draw-string polyester bag using a digital hanging scale (American Weigh Scale SR-1), with a 1-gram resolution. A ruler was used to measure wing chord and P10 length to the nearest millimeter.

To determine if there were sex-specific device effects, I sampled a drop of blood from the foot webbing vein of handled adults in both comparison groups during recaptures the following breeding season. Blood was preserved on Flinders Technology Associate (FTA) cards and molecular identification of sex was carried out by the Pacific Center for Molecular Biodiversity.

2.3.3 Chick growth

Only the chicks that fledged were included in the analysis of growth rates. For each chick, I focused on the linear phase of growth and fitted linear regressions to three response variables—mass (g), wing chord length (mm), and P10 length (mm)—using chick age as the predictor variable. To ensure that the analyses captured the linear portion of the growth curves, I evaluated the R^2 values of the linear regressions and tested the residuals of each model for normality. I used the significant best-fit slopes to estimate daily growth rates for mass (g/day), wing chord (mm/day), and P10 (mm/day). While one chick for wing chord growth, three chicks for P10 growth, and five chicks for mass gain had non-normal residuals, these individuals were retained in the analysis because excluding these chicks did not affect subsequent test results.

Because many Procellariform chicks are irregularly fed large food loads and lose mass prior to fledging, I evaluated the linear growth portion between 10% and 90% of the peak mass each chick attained (Huin and Prince, 2000). Due to the weekly oscillations in body mass, several chicks reached 90% of their peak mass twice. In these instances, I fit a separate linear regression to each time the 90% of peak mass was reached, resulting in two slope estimates per chick. When I compared these two slopes across all chicks with two peak masses, the second (occurs later in time) slope was always smaller than the first (occurs earlier in time). To make the growth rates of these chicks comparable to the chicks with a single peak mass, I estimated their daily mass growth rate using their first peak mass.

The fixed factor effects of tagging (tagged vs. non-tagged), year (2022 El Niño vs. 2023 La Niña), and sex (male vs. female) on growth rates, and their interaction, were assessed with separate ANOVAs for each of the three growth metrics. I conducted a power analysis using the R package "pwrss" to determine the ability of my sample size (100 chicks) to detect device effects on growth rates (Bulus, 2023). I used the function 'DurgaDiff' in the package Durga to calculate mean differences and bootstrapped confidence intervals for growth rates (Khan and McLean, 2024). All statistical analyses were completed using R version 4.3.3, and significance was assessed at the alpha = 0.05 level.

2.3.4 Estimates of hatch date

Because chicks that hatch sooner reach higher peak masses in this colony, the hatching phenology was considered in the analysis of the growth rates (Hyrenbach, 2011). To assess if chick growth rates are influenced by hatch date, I estimated median hatch dates (MHD) and hatch date intervals (HDI). Unless the exact date was determined from seeing a hatching or pipping egg, I define the median hatch date (in julian day) as:

$$(date\ chick\ first\ seen - \ date\ egg\ last\ seen)\ /\ 2$$

To account for instances when I could not confirm if a chick had hatched that week due to being hidden by the adult, I defined a hatch date interval as the number of days in between the date the chick was first seen and the date the egg was last seen. The relationship between MHD and HDI was tested each year with a Spearman's rank correlation. General linear models were used to evaluate the influence of hatch date on growth rate, using three predictors: a tagging factor (tagged versus non-tagged), the MHD covariate, and the HDI covariate.

Comparison groups (tagged versus non-tagged), years (2022 versus 2023), and hatch dates (MHD and HDI) were compared using independent *t*-tests, when the data met the assumptions of normality and homoskedasticity, and using Mann-Whitney *U* tests when these assumptions were not met.

2.4 Results

Overall, I recaptured 52 out of 55 (94.5%) of the tagged individuals and 45 out of 49 (91.8%) of the non-tagged individuals (Table 1). Return rates did not differ between tagged and non-tagged groups in either year (2023: $\chi^2 = 0.01$, df = 1, $p = 0.92$, 2024: $\chi^2 = 0.002$, df = 1, $p = 0.96$), nor did they differ between sexes during either year (2023: $\chi^2 = 0.01$, df = 1, $p = 0.90$, 2024: $\chi^2 = 0.03$, df = 1, $p = 0.85$). Upon tag retrieval, one adult in 2024 had a small abrasion on its leg from the band with attached geolocator. Otherwise, no other injuries were observed and no leg bands needed replacement upon recapture.

The total tag deployment was 236 ± 5 (mean ± SD) days, when both years were combined (n = 51). This estimate excludes one individual tagged in August 2022 and recaptured in August 2023, whose tag deployment was 364 days and was not sampled for molecular sexing. Recapture success over time was similar between tagged and non-tagged groups each year, with the maximum number of study birds resighted after 25 hours of cumulative survey effort in 2023 and 27 hours in 2024 (Figure 1).

Table 1. Sample sizes of Wedge-tailed Shearwaters in each comparison group over the two study years. Adults were recaptured at the beginning of the following breeding season (in 2023 and 2024). Unknown sex is due to the inability to sample blood.

Year	Group	N	Chicks fledged	Adults returned	Sex		
					F	M	Unknown
2022	Tagged	25	23	24	9	14	1
	Non-tagged	25	23	23	9	13	1
2023	Tagged	30	30	28	12	16	0
	Non-tagged	24	24	22	10	12	0

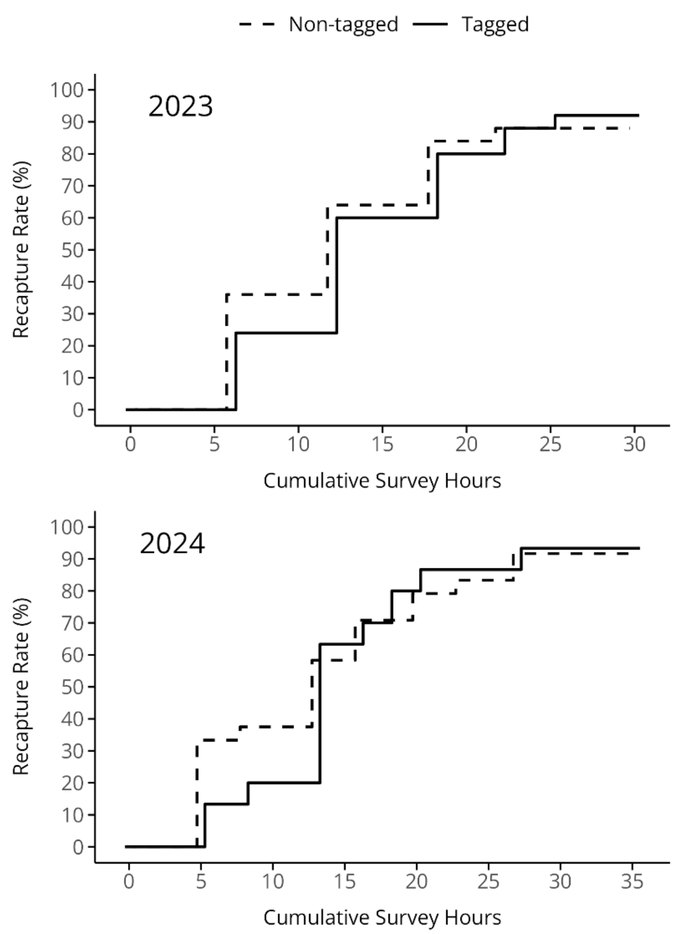


Figure 1. Similar recapture success rate of tagged versus non-tagged adults each year with increasing cumulative survey hours.

2.4.1 Chick growth

Breeding success was equal between the tagged and non-tagged groups at the end of the two seasons. In 2022, 92% of chicks raised by both tagged and non-tagged adults fledged, while in 2023, 100% of chicks raised by both tagged and non-tagged adults fledged (Table 1).

I used significant best-fit linear regression slopes to estimate daily growth rates of mass, wing chord, and P10 with age (Table 2). There were 22 chicks (15 in 2023 and 7 in 2022) with two slope estimates, because they reached the same peak mass twice. In 2022, the first slope did not differ significantly from the second, though it was 24.1% greater (Paired *t*-test, $t_6 = 2.37$, $p = 0.056$). However, in 2023, there was a significant difference between the two slopes, as the first was 26.8% greater than the second slope (Paired *t*-test, $t_{14} = 6.28$, $p < 0.001$). In subsequent analysis, I used the first slope of mass each year because it was consistently greater than the second slope for every chick and more accurately captured the linear phase of chick growth. Two chicks were excluded from the mass analysis: one in 2022 due to a non-significant regression slope, and another in 2023 because it had only two mass measurements.

Table 2. Summary of linear relationships between the chick growth metrics and age (days). Sample sizes for wing chord and P10 in 2022 and 2023 were 46 and 54 chicks, while samples sizes for mass were 45 and 53, respectively.

Metric	Year	Min num of measurements	Max num of measurements	R^2 (min – max)
Mass	2022	4	9	0.78 – 0.98
	2023	5	9	0.75 – 0.95
Wing chord	2022	10	13	0.92 – 0.98
	2023	9	15	0.93 – 0.98
P10	2022	5	9	0.96 – 0.99
	2023	4	9	0.92 – 0.99

I found no effect of tagging ($F_{1,81} = 0.101$, $p = 0.75$), year ($F_{1,81} = 3.269$, $p = 0.07$), and sex ($F_{1,81} = 0.022$, $p = 0.88$) on the rates of daily mass gain in chicks (Figure 2a). While there was no interaction between tagging and sex ($F_{1,81} = 0.054$, $p = 0.82$), there were significant interactions between tagging and year ($F_{1,81} = 4.409$, $p = 0.04$) and between year and sex ($F_{1,81} = 4.363$, $p = 0.04$). Though these yearly mass differences were not significant, there were negative effect sizes for both the tagged and non-tagged groups in 2023. Moreover, the tagged group had a greater negative mean effect between years, compared to the non-tagged group (Figure 2a). Overall, when all chicks were combined, they reached lower peak masses (6.25% lower) in 2023 than in 2022 (Welch's *t*-test, $t_{89.8} = 3.49$, $p < 0.001$). There was no significant difference in the age chicks reached peak mass between years (Mann-Whitney, $U = 1480$, $p = 0.10$). However, the age of the last feeding (inferred using the last gained mass during weekly monitoring) was greater in 2023 than in 2022 (Mann-Whitney, $U = 775$, $p = 0.001$).

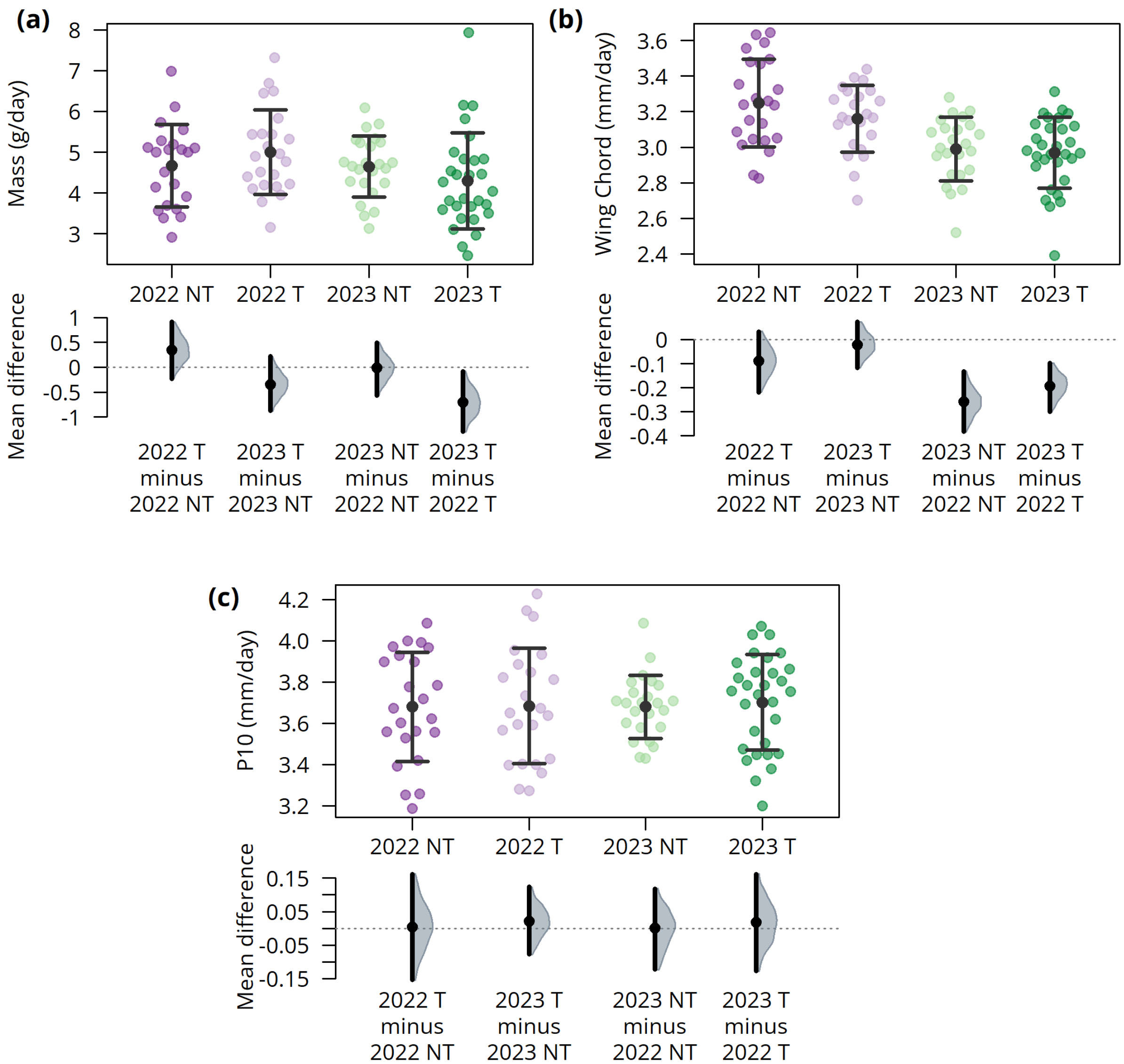


Figure 2. Growth rates of Wedge-tailed Shearwater chicks across tagged (T) and non-tagged (NT) groups and year (2022 or 2023) measured through (a) mass gained per day, (b) length of wing chord grown per day, (c) length of P10 grown per day. In the top panels, each colored dot represents a chick's growth rate, black dots and error bars represent mean ± standard deviation. The effect sizes (bottom panels), quantified as the mean differences, are depicted as black dots, 95% confidence intervals of mean difference as vertical lines, and half violins as sampling distribution (1000 replicates) of bootstrapped differences.

While there was no effect of tagging on the growth rate of chick wing chord ($F_{1,83}$ = 3.751, p = 0.06), there was a significant effect of year ($F_{1,83}$ = 29.741, p < 0.001). In 2023 the mean wing chord growth rate was 6.48% lower for the tagged group and 7.97% lower for the non-tagged group, compared to 2022 (Figure 2b). There were no significant interactions between tagging and year ($F_{1,83}$ = 0.373, p = 0.543), between tagging and sex ($F_{1,83}$ = 3.793, p = 0.055), and between year and sex ($F_{1,83}$ = 2.709, p = 0.104) in the wing chord growth rate, as evidenced by the pairwise comparisons of the mean differences across groups and years (Table 3). Furthermore, the peak wing chord length was not different between years (Mann-Whitney, U = 1295, p = 0.72), nor was the age of the chicks when they reached that peak wing chord length (Mann-Whitney, U = 1348, p = 0.46).

The chick P10 growth rates varied the least between tagging groups and between years. There was no effect of tagging ($F_{1,83}$ = 0.000, p = 0.984), no effect of year ($F_{1,83}$ = 0.040, p = 0.843), and no effect of sex ($F_{1,83}$ = 0.872, p = 0.353) on the growth rates of P10 (Figure 2c). While there was no significant interaction of tagging and year ($F_{1,83}$ = 1.653, p = 0.202), or tagging and sex ($F_{1,83}$ = 1.802, p = 0.183), there was a significant interaction between year and sex ($F_{1,83}$ = 4.259, p = 0.04).

Table 3. Pairwise comparisons of mean differences and bootstrapped 95% confidence intervals using adjusted bootstrap percentile method for tagged (T) and non-tagged (NT) comparison groups.

	Mass		Wing chord		P10	
	Mean diff	95% CI	Mean diff	95% CI	Mean diff	95% CI
2023 T – 2023 NT	-0.35	-0.83, 0.20	-0.02	-0.12, 0.07	0.02	-0.09, 0.12
2022 T – 2022 NT	0.34	-0.26, 0.91	-0.08	-0.21, 0.03	0.004	-0.13, 0.17
2023 T – 2022 T	-0.70	-1.26, -0.16	-0.19	-0.31, -0.10	0.02	-0.13, 0.15
2023 NT – 2022 NT	-0.02	-0.49, 0.48	-0.26	-0.39, -0.13	0.0002	-0.13, 0.13

The power analysis indicated that I had 80% power to detect small ($\eta^2 \geq 0.075$) effects in the ANOVA tests for differences in chick growth rates (Figure 3). Tagging on wing chord growth had an observed effect size of $\eta^2 = 0.043$, a small but detectable effect with moderate power (~ 56%). Tagging on body mass growth had an observed effect size of $\eta^2 = 0.001$, indicating a very small effect with insufficient power (~ 6%), while tagging on P10 growth had an even smaller effect size of $\eta^2 < 0.001$, corresponding to the lower limit of the power curve (~ 5%). Only subtle impacts of tagging may have gone undetected as my study did not have sufficient power for very small effects ($\eta^2 < 0.02$).

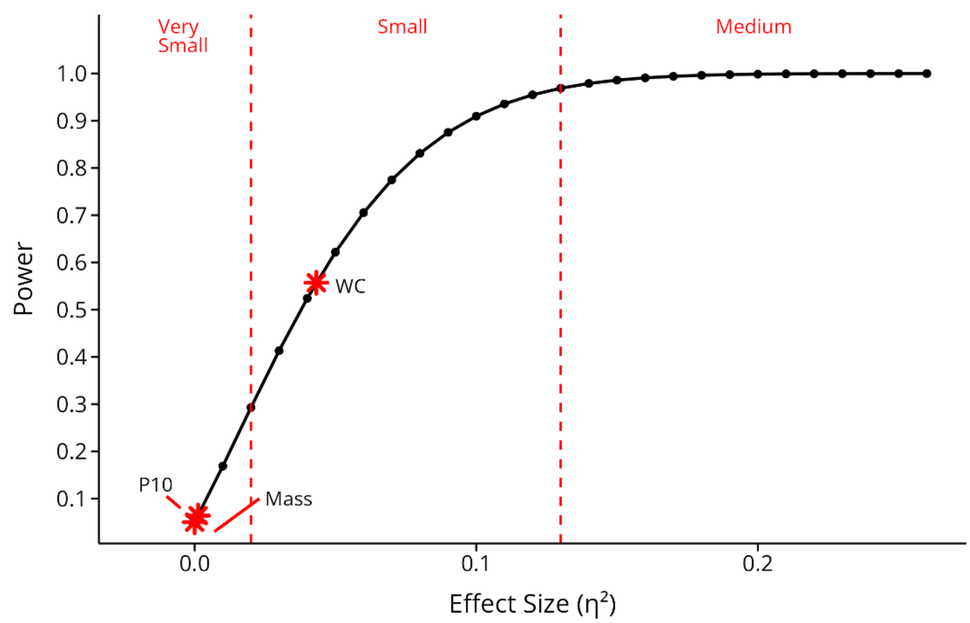


Figure 3. Power of the three ANOVA tests assessing the effects of tag deployment on chick growth rates, based on a sample size of 100 chicks (46 in 2022 and 56 in 2023). Red stars indicate the observed effect size of tagging on growth rates of body mass, wing chord (WC), and tenth primary (P10). Thresholds for effect sizes are based on Cohen (1992): Very Small ($\eta^2 < 0.02$); Small ($0.02 \leq \eta^2 < 0.13$); Medium ($0.13 \leq \eta^2 < 0.26$).

2.4.2 Effect of hatch date on chick growth

In 2022, the median MHD was 5 August (IQR: 31 July – 7 August), whereas in 2023, hatch dates were concentrated on August 7 (IQR: August 7 – August 7). Despite the reduced variability in hatch dates in 2023, chicks hatched significantly later compared to 2022 (Mann-Whitney, $U = 795$, $p < 0.001$). This difference in MHD between years may be attributed to differences in HDI, as there was a systematic difference in HDI between years (Mann-Whitney, $U = 1794$, $p < 0.001$). MHD and HDI were significantly correlated in both years (Spearman's rank, 2023: $\rho = 0.653$, n = 54, $p < 0.001$; 2022: $\rho = -0.745$, n = 46, $p < 0.001$). While I expected larger HDI values to correlate with later MHD, this pattern was not observed in 2022. HDI showed more variability in 2022 (IQR: 7 – 8 days), while in 2023, it was consistently around 7 days (IQR: 7 – 7 days).

However, I found no significant difference in MHD between the tagged and non-tagged groups in either 2023 (Mann-Whitney, $U = 376.5$, $p = 0.75$) or 2022 (Mann-Whitney, $U = 276.5$, $p = 0.78$). Similarly, there was no significant difference in HDI between the two groups in 2023 (Mann-Whitney, $U = 349.5$, $p = 0.79$) or 2022 (Mann-Whitney, $U = 270$, $p = 0.90$). Furthermore, MHD and HDI did not significantly explain interannual variation in growth rates of mass, wing chord, or P10 across both years (Table 4).

Table 4. Summary of general linear models explaining the effects of median hatch date (MHD) and hatch date interval (HDI) on the variation in growth rates of three measured biometrics in Wedge-tailed Shearwater chicks. Treatment is tagged or non-tagged.

Metric	Year	Predictor	Slope	*t*-value	*p*	R^2	Adj R^2
Mass	2022	Treatment	0.329	1.091	0.282		
		MHD	-0.053	-1.841	0.073	0.106	0.041
		HDI	0.024	0.294	0.770		
	2023	Treatment	-0.300	-1.068	0.291		
		MHD	0.053	1.235	0.223	0.066	0.009
		HDI	-0.600	-1.289	0.203		
Wing chord	2022	Treatment	-0.081	-1.244	0.221		
		MHD	0.005	0.808	0.423	0.076	0.010
		HDI	0.019	1.044	0.302		
	2023	Treatment	-0.013	-0.254	0.800		
		MHD	0.012	1.537	0.131	0.057	< 0.001
		HDI	-0.047	-0.538	0.593		
P10	2022	Treatment	0.006	0.069	0.945		
		MHD	-0.004	-0.491	0.626	0.014	< 0.001
		HDI	0.012	0.558	0.580		
	2023	Treatment	0.022	0.388	0.699		
		MHD	< 0.001	-0.100	0.921	0.006	< 0.001
		HDI	-0.022	-0.228	0.820		

2.5 Discussion

Geolocator deployment did not adversely affect the ability of Wedge-tailed Shearwaters to provision chicks over both study years, even when accounting for hatching phenology. Return rates further indicated no difference in the survival and skipping in the subsequent breeding season between tagged and non-tagged adults. The power analysis indicated that if device effects existed, negative impacts on growth and return rates would be subtle. These findings indicate that over-wintering (six months to one year) deployment of geolocators, attached via leg bands and weighing less than 1% of body mass, does not negatively impact the survival and breeding success of Wedge-tailed Shearwaters.

Despite their monomorphism, males and females segregate at sea during foraging trips, leading to a higher rate of chick provisioning by males (Peck and Congdon, 2006). I did not find sex-specific device effects on adult return rates or chick growth rates. However, I observed an interactive effect of year and sex on chick mass gain during the El Niño year; rates of mass gain in chicks raised by tagged males was lower than those raised by tagged females in 2023. The foraging behavior of males may make them more susceptible to device effects, potentially reduce their provisioning ability under challenging oceanographic conditions. Similar sex-specific device effects have been documented in other seabirds. Ackerman et al., (2004) found reduced fledging success in male Cassin's Auklets (*Ptychoramphus aleuticus*) tagged with VHF transmitters compared to females, and Schacter and Jones, (2017) found reduced fledging success in male Parakeet Auklets (*Aethia psittacula*) tagged with geolocators. Male-biased parental care may contribute to sex-specific vulnerability to device deployment.

Because chicks hatched later in 2023, I expected greater wing chord growth rates to compensate for the shorter development period. However, I observed lower wing chord growth rates across both groups in 2023, despite no significant differences in peak wing chord length and the age at which chicks reached their peak wing length between years. I suggest wing chord is a more sensitive biometric of growth in response to interannual oceanographic variability compared to body mass, which can be highly variable in Procellariiform seabirds due to irregular feeding patterns. Thus, wing chord could be a more reliable metric for detecting potential device effects and interannual variation, particularly when frequent mass measurements are not feasible.

Growth rates of P10 varied the least across comparison groups and years, despite slower wing chord growth during the El Niño year. This result indicates a degree of developmental plasticity in Wedge-tailed Shearwater chick growth under food-limited conditions. Preferential feather growth enables chicks to achieve flight and fledge by the end of the rearing season—a requirement for survival. Differential growth in response to food scarcity has been observed in Caspian Terns (*Hydroprogne caspia*) and Atlantic Puffins (*Fratercula arctica*), where feather growth is maintained over other structural growth parameters, such as wing length and tarsus, under reduced food availability (Øyan and Anker-Nilssen, 1996; Lyons and Roby, 2011).

The 2022 chick-provisioning season occurred during the cool phase (MEI range: -1.8 to -1.3) of the El Niño Southern Oscillation (ENSO), while the 2023 season experienced contrasting conditions during the warm ENSO phase (MEI range: 0.5 to 1.1; Figure 4). I observed a negative mean effect on mass gain in chicks raised by tagged adults compared to non-tagged adults during the 2023 El Niño, evidenced by the significant interaction of tagging and year. Although the effect of year was not statistically significant, it raises the possibility that a device effect on chick mass gain could become detectable during years with stronger ENSO events (larger MEI positive values). Positive MEI values during the chick-provisioning period (August to November) in 2023 indicated that the central Pacific experienced a weak to moderate warm phase. These ENSO conditions appeared to impact all chicks, as they attained lower peak masses despite continued feeding at older ages during the warm El Niño year. Previous studies have suggested that the impacts from device deployment might become more pronounced during years with unfavorable conditions (Igual et al., 2005; Chivers et al., 2016). However, the threshold of challenging environmental conditions required to produce a significant negative device effect on Wedge-tailed Shearwater chick growth and adult survival remains unclear.

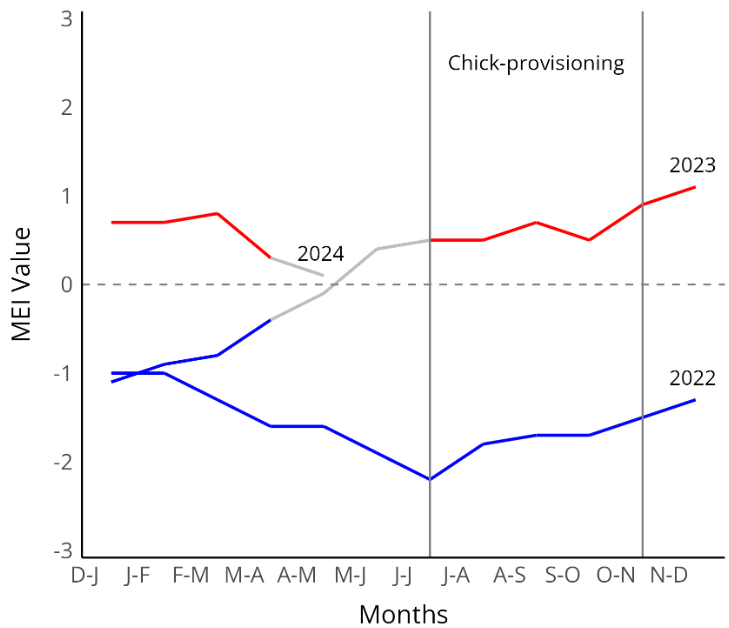


Figure 4. Multivariate El Niño Southern Oscillation Index (MEI) across the study years. Warm (red), cold (blue), and neutral (grey) periods are based on a threshold of +/- 0.5 ºC. Values were downloaded directly from the NOAA Physical Sciences Laboratory (https://psl.noaa.gov/enso/mei/).

Wedge-tailed Shearwaters may be able to offset some of the pressures from unfavorable environmental conditions, thereby reducing any potential additive impacts from device deployment. This population can forage far from breeding colonies (up to 500 km) and can dive deep (down to 10 m) to access prey (Felis et al., 2019), providing some capacity to buffer the effects of warm water anomalies and its associated effects on prey availability. Additionally, Wedge-tailed Shearwaters feed with subsurface predators, especially Skipjack Tuna (*Katsuwonus pelamis,* locally known as Aku) around Hawai'i and in the tropical North Pacific (King, 1974; Hebshi et al., 2008). This foraging association enhances prey accessibility (Au and Pitman, 1986; Ballance and Pitman, 1999), and may allow Wedge-tailed Shearwaters to mitigate the effects of warm ENSO years, especially if tuna become more abundant within their foraging range. Consequently, chick-provisioning during the breeding season may be more influenced by how El Niño events affect the abundance and distribution of Aku. The adaptive foraging strategies of Wedge-tailed Shearwaters may explain why I did not observe year-to-year variation in the growth rates of chicks raised by tagged parents compared to non-tagged parents.

While my study did not detect significant effects of geolocator deployment on chick growth rates in either year, it is possible that device effects were transferred to the non-tagged partner. Since only one parent in each pair was tagged, the partner may have compensated for any reduction in provisioning effort. This compensatory behavior, observed in other seabird species (e.g. Paredes et al., 2005; Navarro and González-Solís, 2007), could account for why chicks fledged at similar rates to those raised by non-tagged parents. However, any potential impacts on either the tagged parent or its partner may have been mitigated over the non-breeding season, as there was no difference in return rates in the following season and recapture success in both tagged and non-tagged birds with cumulative survey effort.

My study examined geolocator device effects within the context of interannual variation and sex-specific differences in foraging behavior, allowing me to better evaluate potential biases on the resulting tracking data. Yet, it is likely that not all seabird species respond equally to the combined pressures of device deployment and challenging environmental conditions. The tags I used are small (<1% of body mass), and Wedge-tailed Shearwaters, being mostly surface feeders with low wing-loading, primarily glide with occasional flapping (Spear and Ainley, 2008). In contrast, seabirds with deep-diving habits and high wing-loading might experience greater drag, potentially impacting their overall fitness. This comparison underscores the importance of experimental studies, as the impacts of tagging can vary based on species, tag type, and even the year of study. Despite the challenges posed by site accessibility and logistical constraints, assessing device effects remains essential to refine biologging methodologies for each specific study system. Given the results of several device effect studies that revealed behavioral impacts, researchers should interpret tracking results in the context of the original research question. Ultimately, the insights gained through biologging can justify potential trade-offs, because they enhance our understanding of human impacts on wildlife and inform more effective conservation strategies. While balancing these trade-offs may not be straightforward, experimental assessments of device effects can improve the efficacy and ethical standards of biologging research in the future. This ongoing vigilance is particularly critical as biologging expands to smaller species, and researchers try novel attachment methods with the goal of lengthening the duration of tag deployments. Finally, potential device effects should be interpreted within the context of sex-based differences (e.g., morphometrics, incubation, ranging behavior, migration) and interannual variability in ocean conditions (e.g., prey availability, diving effort, wind speeds).

2.6 References

Ackerman, J. T., Adams, J., Takekawa, J. Y., Carter, H. R., Whitworth, D. L., Newman, S. H., et al. (2004). Effects of radiotransmitters on the reproductive performance of Cassin's auklets. *Wildl. Soc. Bull.* 32, 1229–1241. doi: 10.2193/0091-7648(2004)032[1229:EOROTR]2.0.CO;2

Adams, J., Scott, D., McKechnie, S., Blackwell, G., Shaffer, S. A., and Moller, H. (2009). Effects of geolocation archival tags on reproduction and adult body mass of sooty shearwaters (*Puffinus griseus*). *N. Z. J. Zool.* 36, 355–366. doi: 10.1080/03014220909510160

Au, D. W. K., and Pitman, R. L. (1986). Seabird Interactions with Dolphins and Tuna in the Eastern Tropical Pacific. *The Condor* 88, 304–317. doi: 10.2307/1368877

Ballance, L. T., and Pitman, R. L. (1999). Foraging ecology of tropical seabirds. *Adams NJ Slotow RH Eds Proc 22 Int Ornithol Congr Durb.*, 2057–2071.

Barron, D. G., Brawn, J. D., and Weatherhead, P. J. (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods Ecol. Evol.* 1, 180–187. doi: 10.1111/j.2041-210X.2010.00013.x

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., et al. (2018). A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods Ecol. Evol.* 9, 946–955. doi: 10.1111/2041-210X.12934

Bull, L. S., Bell, B. D., and Pledger, S. (2005). Patterns of Size Variation in the Shearwater Genus *Puffinus*. *Mar. Ornithol.* 33, 27–39.

Bulus, M. (2023). pwrss: Statistical Power and Sample Size Calculation Tools. R package version 0.3.1. https://CRAN.R-project.org/package=pwrss.

Burger, A. E., and Shaffer, S. A. (2008). Application of Tracking and Data-logging Technology in Research and Conservation of Seabirds. *The Auk* 125, 253–264. doi: 10.1525/auk.2008.1408

Casper, R. M. (2009). Guidelines for the instrumentation of wild birds and mammals. *Anim. Behav.* 78, 1477–1483. doi: 10.1016/j.anbehav.2009.09.023

Catry, T., Ramos, J., Le Corre, M., and Phillips, R. (2009). Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Mar. Ecol. Prog. Ser.* 391, 231–242. doi: 10.3354/meps07717

Chivers, L. S., Hatch, S. A., and Elliott, K. H. (2016). Accelerometry reveals an impact of short-term tagging on seabird activity budgets. *The Condor* 118, 159–168. doi: 10.1650/CONDOR-15-66.1

Clewley, G. D., Cook, A. S. C. P., Davies, J. G., Humphreys, E. M., O'Hanlon, N. J., Weston, E., et al. (2021). Acute impacts from Teflon harnesses used to fit biologging devices to Black-legged Kittiwakes *Rissa tridactyla*. *Ringing Migr.* 36, 69–77. doi: 10.1080/03078698.2022.2151065

Cohen, J. (1992). Statistical Power Analysis. *Curr. Dir. Psychol. Sci.* 1, 98–101. doi: https://doi.org/10.1111/1467-8721.ep10768783

Costantini, D., and Møller, A. P. (2013). A meta-analysis of the effects of geolocator application on birds. *Curr. Zool.* 59, 697–706. doi: 10.1093/czoolo/59.6.697

Creelman, E., and Storey, A. E. (1991). Sex Differences in Reproductive Behavior of Atlantic Puffins. *The Condor* 93, 390–398. doi: 10.2307/1368955

Elliott, K., McFarlane-Tranquilla, L., Burke, C., Hedd, A., Montevecchi, W., and Anderson, W. (2012). Year-long deployments of small geolocators increase corticosterone levels in murres. *Mar. Ecol. Prog. Ser.* 466, 1–7. doi: 10.3354/meps09975

Fayet, A. L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K. E., Fifield, D., et al. (2017). Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird. *Curr. Biol.* 27, 3871-3878.e3. doi: 10.1016/j.cub.2017.11.009

Felis, J. J., Czapanskiy, M. F., and Adams, J. (2019). At-Sea Ranging Behavior of Seabirds Breeding in the Main Hawaiian Islands: Bio-logger Data Release (ver. 2.0, May 2020). doi: 10.5066/P9NTEXM6

Geen, G. R., Robinson, R. A., and Baillie, S. R. (2019). Effects of tracking devices on individual birds – a review of the evidence. *J. Avian Biol.* 50, 1–13. doi: 10.1111/jav.01823

Gillies, N., Fayet, A. L., Padget, O., Syposz, M., Wynn, J., Bond, S., et al. (2020). Short-term behavioural impact contrasts with long-term fitness consequences of biologging in a long-lived seabird. *Sci. Rep.* 10, 15056. doi: 10.1038/s41598-020-72199-w

Hatch, S. A. (1990). Incubation rhythm in the Fulmar *Fulmarus glacialis:* annual variation and sex roles. *Ibis* 132, 515–524. doi: 10.1111/j.1474-919X.1990.tb00275.x

Hebshi, A., Duffy, D., and Hyrenbach, K. (2008). Associations between seabirds and subsurface predators around Oahu, Hawaii. *Aquat. Biol.* 19, 89–98. doi: 10.3354/ab00098

Heggøy, O., Christensen-Dalsgaard, S., Ranke, P., Chastel, O., and Bech, C. (2015). GPS-loggers influence behaviour and physiology in the black-legged kittiwake Rissa tridactyla. *Mar. Ecol. Prog. Ser.* 521, 237–248. doi: 10.3354/meps11140

Huin, N., and Prince, P. A. (2000). Chick growth in albatrosses: curve fitting with a twist. *J. Avian Biol.* 31, 418–425. doi: 10.1034/j.1600-048X.2000.310318.x

Hyrenbach, K. D. (2011). Tale of Two Years: Monitoring Wedge-tailed Shearwaters at Freeman Seabird Preserve in Black Point, O'ahu. *'Elepaio* 71, 17–20.

Hyrenbach, K. D., Gleichman, J. S., and Karnovsky, N. J. (2014). Diving Behavior of Wedge-tailed Shearwaters Rearing Chicks on Lehua Islet. *'Elepaio* 74, 1–3.

Igual, J. M., Forero, M. G., Tavecchia, G., González-Solis, J., Martínez-Abraín, A., Hobson, K. A., et al. (2005). Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). *Mar. Biol.* 146, 619–624. doi: 10.1007/s00227-004-1461-0

Khan, M. K., and McLean, D. J. (2024). Durga: an R package for effect size estimation and visualization. *J. Evol. Biol.* 37, 986–993. doi: 10.1093/jeb/voae073

King, W. B. (1974). Pelagic studies of seabirds in the central and eastern Pacific Ocean. *Smithson. Contrib. Zool.*, 1–277. doi: 10.5479/si.00810282.158

Lyons, D. E., and Roby, D. D. (2011). Validating growth and development of a seabird as an indicator of food availability: captive-reared Caspian Tern chicks fed ad libitum and restricted diets: Tern Chick Growth and Food Availability. *J. Field Ornithol.* 82, 88–100. doi: 10.1111/j.1557-9263.2010.00311.x

McDuie, F., and Congdon, B. (2016). Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas. *Mar. Ecol. Prog. Ser.* 550, 219–234. doi: 10.3354/meps11713

Monaghan, P., Nager, R. G., and Houston, D. C. (1998). The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. *Proc. R. Soc. Lond. B Biol. Sci.* 265, 1731–1735. doi: 10.1098/rspb.1998.0495

Navarro, J., and González-Solís, J. (2007). Experimental increase of flying costs in a pelagic seabird: effects on foraging strategies, nutritional state and chick condition. *Oecologia* 151, 150–160. doi: 10.1007/s00442-006-0559-0

Øyan, H. S., and Anker-Nilssen, T. (1996). Allocation of Growth in Food-Stressed Atlantic Puffin Chicks. *The Auk* 113, 830–841. doi: 10.2307/4088861

Paredes, R., Jones, I. L., and Boness, D. J. (2005). Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Anim. Behav.* 69, 197–208. doi: 10.1016/j.anbehav.2003.12.029

Paton, P. W. C., Loring, P. H., Cormons, G. D., Meyer, K. D., Williams, S., and Welch, L. J. (2020). Fate of Common (*Sterna hirundo*) and Roseate Terns (*S. dougallii*) with Satellite Transmitters Attached with Backpack Harnesses. *Waterbirds* 43. doi: 10.1675/063.043.0315

Peck, D. R., and Congdon, B. C. (2006). Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Puffinus pacificus*. *J. Avian Biol.* 37, 245–251. doi: 10.1111/j.2006.0908-8857.03558.x

Peck, D. R., Smithers, B. V., Krockenberger, A. K., and Congdon, B. C. (2004). Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Mar. Ecol. Prog. Ser.* 281, 259–266. doi: 10.3354/meps281259

Pettit, T. N., Byrd, G. V., Whittow, G. C., and Seki, M. P. (1984). Growth of the Wedge-Tailed Shearwater in the Hawaiian Islands. *The Auk* 101, 103–109.

Phillips, R. A., Xavier, J. C., and Croxall, J. P. (2003). Effects of Satellite Transmitters on Albatrosses and Petrels. *The Auk* 120, 1082–1090. doi: https://doi.org/10.2307/4090279

Schacter, C. R., and Jones, I. L. (2017). Effects of Geolocation Tracking Devices on Behavior, Reproductive Success, and Return Rate of *Aethia* Auklets: An Evaluation of Tag Mass Guidelines. *Wilson J. Ornithol.* 129, 459–468. doi: 10.1676/16-084.1

Schroeder, I., Sydeman, W., Sarkar, N., Thompson, S., Bograd, S., and Schwing, F. (2009). Winter pre-conditioning of seabird phenology in the California Current. *Mar. Ecol. Prog. Ser.* 393, 211–223. doi: 10.3354/meps08103

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., et al. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biol. Lett.* 11, 20150671. doi: 10.1098/rsbl.2015.0671

Spear, L. B., and Ainley, D. G. (2008). Flight speed of seabirds in relation to wind speed and direction. *Ibis* 139, 234–251. doi: 10.1111/j.1474-919X.1997.tb04621.x

Sun, A., Whelan, S., Hatch, S., and Elliott, K. (2020). Tags below three percent of body mass increase nest abandonment by rhinoceros auklets, but handling impacts decline as breeding progresses. *Mar. Ecol. Prog. Ser.* 643, 173–181. doi: 10.3354/meps13341

Sydeman, W., and Bograd, S. (2009). Marine ecosystems, climate and phenology: introduction. *Mar. Ecol. Prog. Ser.* 393, 185–188. doi: 10.3354/meps08382

Vandenabeele, S. P., Shepard, E. L., Grogan, A., and Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar. Biol.* 159, 1–14. doi: 10.1007/s00227-011-1784-6

Whittow, G. C. (2020). Wedge-tailed Shearwater *(Ardenna pacifica)*. version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: https://doi.org/10.2173/bow.wetshe.01

Wilson, R. P., and McMahon, C. R. (2006). Measuring Devices on Wild Animals: What Constitutes Acceptable Practice? *Front. Ecol. Environ.* 4, 147–154. doi: https://doi.org/10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2

CHAPTER 3

Post-breeding migration and distribution of Wedge-tailed Shearwaters from O‘ahu during El Niño and La Niña years

3.1 Abstract

Following protection of breeding sites, Wedge-tailed Shearwater (*Ardenna pacifica*) colonies in the Hawaiian Islands are growing, yet little is known about their post-breeding dispersal. Using light-level geolocators, I estimated the non-breeding distribution, timing of migration, and activity patterns of 48 adults during La Niña (2022–23) and El Niño (2023–24) years. Shearwaters consistently migrated eastward to core areas off Central America in the eastern tropical Pacific (ETP), with no sex-specific differences. Repeated interannual distribution, despite ENSO variability, posits a reliance on surface-feeding tuna–key foraging associates in the ETP. During the El Niño year, colony departures were delayed by one week due to an extended chick provisioning period, though the timing of return to the colony for the subsequent breeding season remained consistent. In core non-breeding areas, shearwaters foraged primarily during the day, with foraging activity spread over a broader area during the El Niño year, possibly due to interannual shifts in tuna distribution. These results demonstrate the importance of Central American coastal and pelagic waters for overwintering Wedge-tailed Shearwaters and align with previous at-sea surveys. With most non-breeding time spent within international Exclusive Economic Zones, our findings highlight that coordinated multinational conservation measures, including bycatch mitigation and sustainable tuna fisheries, are essential for supporting this species throughout its life cycle.

3.2 Introduction

Migration is a critical component of seabird ecology, largely driven by seasonal fluctuations in prey availability across marine environments (Polovina et al., 2001; Péron et al., 2010; Hromádková et al., 2020). After breeding, many seabirds migrate in response to declining food resources, a behavior especially common in temperate and subpolar species, which often undertake extensive, sometimes trans-equatorial migrations to oceanographic features with seasonally elevated primary productivity (Guilford et al., 2009; Felis et al., 2019a; Clay and Brooke, 2024). In contrast, tropical oceans are generally less productive and lack strong seasonal patterns, leading tropical seabirds to range widely and rely more on opportunistic foraging associations (Weimerskirch, 2007). Many species depend on subsurface predators, like tunas and marine mammals, to drive prey to the surface (Ballance and Pitman, 1999). Despite the aseasonal nature of tropical oceans, many tropical seabirds still disperse widely after breeding, though the drivers of these movements are less well understood (e.g., Pinet et al., 2011; Priddel et al., 2014; Dias et al., 2015; Franklin et al., 2022b). Considerable knowledge gaps remain about at-sea distributions and migratory routes of many tropical seabird species, especially in the vast equatorial Pacific where research has been limited (Mott and Clarke, 2018; Bernard et al., 2021).

Wedge-tailed Shearwater (*Ardenna pacifica*), a species widely distributed across the subtropical and tropical Pacific and Indian Oceans, engages in a post-breeding dispersal away from nesting grounds, despite foraging year-round in oligotrophic waters (Whittow, 2020). The Hawaiian population represents the species' northernmost range, with more than 87,000 breeding pairs estimated on the Main Hawaiian Islands (King, 1974; Pyle and Pyle, 2017). Despite their abundance, limited information exists about their post-breeding movements from colonies in the Hawaiian Archipelago. During the breeding season, individuals from the Main Hawaiian Islands alternate between intraday (< 1 d), short (1-4 d), and long (> 4 d) foraging trips, ranging up to 500 km from their breeding colonies (Felis et al., 2019b). However, they are rarely observed around the archipelago during the non-breeding season from December to February (Whittow, 2020). While numerous at-sea records span the Pacific, linking individuals sighted during surveys to specific breeding colonies is challenging (e.g., Jenkins, 1979; Au and Pitman, 1986; Ballance et al., 2002; Duffy and Frazier, 2014; Young and Zook, 2016). To date, no Hawaiian Wedge-tailed Shearwaters have been tracked during the post-breeding period (December – April).

Biologging studies have revealed that Wedge-tailed Shearwaters from the south Pacific and Indian Oceans often remain within or migrate to equatorial regions after breeding. For example, individuals from the tropical Indian Ocean (4°−20° S) migrated longitudinally between 5°N and 10°S (Catry et al., 2009; Surman et al., 2018), while birds from south Pacific colonies (21.6°−23.3° S) moved northward, settling between 5°−20° N (McDuie and Congdon, 2016; Weimerskirch et al., 2020). Colony-specific differences in timing of migration have also been observed. For example, Wedge-tailed Shearwaters from New Caledonia began their outward and return migrations one week earlier than birds from Heron Island (eastern Australia), located 1,400 km to the west (McDuie and Congdon, 2016; Weimerskirch et al., 2020). These differences in migratory patterns among colonies, likely influenced by local environmental conditions (e.g., weather, ocean productivity, seasonality) and colony-specific traits (e.g., breeding phenology, colony size, or inter-colony overlap). Such differences make it challenging to generalize findings across studies at different colonies. Located in the central Pacific at the northern extent of the species’ range, Wedge-tailed Shearwaters from Hawai‘i likely disperse southward towards equatorial regions. However, they may move southwest to the wintering areas used by colonies from New Caledonia and Heron Island during the austral summer, or southeast to the eastern tropical Pacific (ETP), where this species has been consistently sighted during vessel surveys year-round (Ballance et al., 2002).

In addition to regional differences in winter distributions, migratory behavior is further influenced by both extrinsic factors, such as distribution and abundance of prey, and intrinsic factors, such as sex and age (Müller et al., 2014; Yamamoto et al., 2014; Whelan et al., 2020; Franklin et al., 2022a). Shifts in oceanographic conditions that impact prey availability (Baduini et al., 2001; Montevecchi, 2007), can potentially cause seabirds to adjust their migratory destinations or timing. Because Wedge-tailed Shearwaters decreased their provisioning rates and delivered smaller meal sizes to chicks during periods of elevated sea surface temperatures (Peck et al., 2004), they may be sensitive to interannual changes in ocean climate. Although Wedge-tailed Shearwaters are sexually monomorphic (Bull et al., 2005), when chick-provisioning they exhibited sex-specific foraging behaviors, with females undertaking longer duration foraging trips and covering larger ranges compared to males (Peck and Congdon, 2006; Catry et al., 2009). Understanding the influence of environmental drivers and individual characteristics is essential for accurately describing seabird distributions and for modeling seabird responses to environmental change.

Here, I used light-level geolocators to study the post-breeding migration of Wedge-tailed Shearwaters from Oʻahu during La Niña (2022–23) and El Niño (2023–24) years. These contrasting El Niño Southern Oscillation (ENSO) phases provided a natural experiment to assess how interannual oceanographic conditions associated with climate variability influence post-breeding distribution and phenology of this tropical species. My objectives were to describe the post-breeding timing of migration, distribution, and activity patterns, while investigating potential sex-based differences in these behaviors. This research seeks to expand the understanding of tropical seabird migration and offer insights into how oceanographic variability may influence dispersal and migratory patterns.

3.3 Methods

3.3.1 Study Site

The study was conducted at the Freeman Seabird Preserve (21°15.36' N, 157°47.51' W), a one-acre colony on the south shore of O‘ahu, Hawai‘i. Wedge-tailed Shearwaters nest here from March to November in natural rock crevices, burrows, and in artificial rock and brick structures and ceramic nest modules, which facilitate easy capture of shearwaters by hand through the burrow entrance. Egg-laying begins in early June, chicks hatch by late July and early August, and fledge by mid-November. Since the preserve’s restoration in 2009, the growing colony has been monitored annually, supporting at least 450 breeding pairs during the study period.

3.3.2 Data Collection

I deployed MK4093 light-level geolocators (1.5 g, L × W × D: 15 mm × 10 mm × 6 mm, Lotek Wireless Inc.) on chick-provisioning adults: 25 in 2023 and 30 in 2024; combined this represents about 5% of adults in this colony. Geolocators were attached to a metal incoloy band on the right tarsus with a single nylon cable tie. Unbanded individuals were given a new metal band for identification. The total attachment weight was 2.6 g, accounting for < 1 % of adult body mass (mean mass ± SD: 393 ± 30.7 g; n = 113; Whittow, 2020). Only one adult per breeding pair was tagged each year, with different individuals selected per deployment. Breeding status was confirmed by capturing adults in burrows with their chicks. To reduce the risk of nest abandonment, all tagging was conducted during the brooding period shortly after chicks hatched.

The geolocators recorded light intensity every minute, storing the highest value every five minutes. Saltwater immersion was tested every three seconds, with the total number of positive (wet) counts saved every ten minutes, resulting in values from zero (always dry) to 200 (always wet). I calibrated geolocators in an area without shading at the breeding colony for 2 weeks before deployment and again after recovery. Geolocators deployed in 2022 were calibrated only after recovery.

I recovered geolocators when adults returned to the colony the following breeding season (April 2023 and April 2024), prior to their pre-laying exodus. The data covered periods from August 2022 to April 2023 and from August 2023 to April 2024, respectively. One bird tagged in August 2022 was opportunistically recaptured in August 2023, resulting in a year-long track for that individual.

To determine sex, I collected a drop of blood from the foot webbing vein during recaptures. Blood samples were preserved on Flinders Technology Associate (FTA) cards, and sex determination was conducted by the Pacific Center for Molecular Biodiversity using molecular techniques.

3.3.3 Data processing

Daily locations were estimated from raw light-level data using methods outlined by Lisovski et al., 2020. I used ‘preprocessLight’ from the R package TwGeos to identify sunrise and sunset times (Lisovski et al., 2016), using a light-intensity threshold of 10 lux. For each geolocator, I manually reviewed light curves to flag unrealistic twilight times caused by weather effects or shading due to bird behavior. When necessary, I adjusted these twilight times based on sunrise and sunset times from previous and following days, resulting in the adjustment of 0.03% of twilights in both years combined. Twilight events that could not be reasonably adjusted, such as those impacted by colony attendance before geolocator recovery, were deleted, resulting in the removal of < 0.01% of twilights.

I used the SGAT package, which estimates initial locations and then refines them through Markov Chain Monte Carlo (MCMC) simulations (Sumner et al., 2009). To improve location accuracy, I incorporated a spatial probability mask, a flight speed model, and a twilight error distribution as priors. Because the deployed geolocators did not have the capability to record sea-surface temperatures, I could not include this parameter. Zenith angles were defined for each tag individually based on calibration periods, with values ranging from 95.3° to 96.0° for the 2022 deployment and 95.6° to 96.3° for the 2023 deployment (calibration periods were pooled for the 2023 tags). When estimating initial paths, I applied tolerance values between 0.1 and 0.18 to interpolate latitude during periods when the sine of the solar declination was lower than the tolerance value, typically around the equinoxes. I used a spatial probability mask of the Pacific Ocean to reduce the probability of a location being estimated over land, based on the assumption that Wedge-tailed Shearwaters do not cross continents during the non-breeding season. Flight speeds were modeled with a gamma distribution (shape: 2.0, scale: 0.1) based on similar Procellariform species (Franklin et al., 2022b; Clay and Brooke, 2024). The twilight error model, also gamma-distributed, was based on each tag's calibration period. MCMC simulations involved an initial burn-in of 1,000 iterations, followed by three runs of 300 samples each, and a final run of 1,000 iterations to derive the location estimates (Lisovski et al., 2020). I then used the median tracks for all subsequent analyses.

I focused on three annual post-breeding stages: outward migration, non-breeding, and return migration. I define non-breeding as the time spent in the 50% utilization distribution, lasting from late December to March. Wedge-tailed Shearwaters began their return migration between March 3 and March 31 (except for one individual, which left on April 11). Due to the spring equinox's effect on latitude estimates, I conservatively filtered locations up to one month before the equinox by using minimum and maximum February latitudes, which removed 12.0% of non-breeding locations for 2022 deployments and 11.1% for 2023. Because the return migration coincided with the equinox period, I could not use this method to filter locations in the month following the equinox due to movement during migration. As a result, I removed 2–4 weeks of data post-equinox, leaving full tracks for five birds in 2022 and fifteen in 2023.

Immersion data were processed via the Actave web tool (Mattern et al., 2015), summarizing the time (in hours) the geolocators spent wet or dry across night, dawn, day, and dusk periods. Actave assigns activity type based on thresholds of wet and dry: flight or colony attendance indicated by summing the 10-min intervals with a value of 0 (dry), uninterrupted sitting on the sea by summing the 10-min intervals with a value of 200 (wet), and foraging behavior indicated by intermediate values of 1–199. Following McKnight et al., (2011) and Cherel et al., (2016), I believe intermittent wet and dry periods reflect take-offs and landings on the sea surface and are reasonably indicative of foraging behavior (Dean et al., 2013). Day periods were defined from local nautical (when the sun's center is 12° below the horizon) sunrise to sunset and night periods from local nautical sunset to sunrise.

I delineated migration start and end dates using processed locations, immersion data, and raw light-level records. Outward migration began on the last day a bird remained within 500 km of the colony, based on the maximum foraging range during chick provisioning (Felis et al., 2019b). When location data were unreliable, behavioral indicators, such as increased dry time during the day or wet time at night, signaled colony departure. The end of the outward migration was identified by an increase in wet time over a single day, indicating arrival at the non-breeding site. For birds making stopovers (defined here as clusters of stationary locations exceeding a week), the end of migration was marked as the arrival in the next cluster of locations, confirmed by an increase in wet time. One bird from the 2022 deployment used multiple non-breeding sites, and its migration end date was defined by the first day in a location cluster, verified by increased wet time.

Return migration began with an increase in dry time over a single day, ending on the first day the bird returned to the colony. This return was identified by extended dry and dark periods exceeding 20 hours or recapture at the colony.

3.3.4 Spatial analysis

To characterize the non-breeding areas used by the tagged birds, I generated kernel utilization distributions (UDs) for each individual using the adehabitatHR package (Calenge, 2006), with a grid cell size of 50 × 50 km. I used 186 km as the smoothing parameter (h) to ensure comparability with geolocator-derived Wedge-tailed Shearwater distributions in different regions (Catry et al., 2009; McDuie and Congdon, 2016; Weimerskirch et al., 2020). Consistent with standard practices in biologging studies, I used 50% UDs as the core use area, indicating where birds spend 50% of their time, and the 95% UD as the general use area (Ford and Krumme, 1979; Soanes et al., 2013). I visualized spatial usage intensity across years by mapping the number of individuals based on their 95% UDs and creating a gridded raster (cell size 186 × 186 km) showing location and individual densities. To assess the representativeness of each year's sample of tracks in capturing colony-level space use, I used the 'RepAssess' function in the track2KBA package (Beal et al., 2021), which is based on iterative subsampling detailed in Lascelles et al., (2016).

For each year, I quantified the degree of spatial aggregation of bird locations using Green's index of dispersion (Gx):

$$Gx = \frac{\left(\frac{S^2}{\bar{x}}\right) - 1}{\sum x - 1}$$

where S^2 is the variance of the number of birds and locations, $\bar{x}$ is the mean of the number of birds and locations, and Σx is the sum of the number of birds and locations. Gx ranges from 1 (maximum aggregation) to a small negative number equal to $-1 \times (\sum x - 1)^{-1}$ (uniform distribution), with a value of 0 indicating a random distribution (variance equal to the mean) (Green, 1966; Hyrenbach et al., 2006; Michael et al., 2016).

I generated yearly 50% UDs separately for males and females. I quantified the degree of overlap in core use areas between sexes using 'kerneloverlap' in the adehabitatHR package, with the Bhattacharyya's affinity (BA) index ranging from no overlap (0) to complete overlap (1) (Fieberg and Kochanny, 2005).

To determine the proportion of time spent within Exclusive Economic Zones (EEZs) during the non-breeding period, I intersected bird locations with EEZ polygons for each year (Flanders Marine Institute, 2024), and calculated the proportion as the number of locations within EEZs divided by the total number of locations. I used the R package terra for all spatial data manipulation and analysis (Hijmans, 2024). All locations were projected in the Albers Equal Area Conic projection, centered on the centroid of non-breeding locations. Unless stated otherwise, all values are presented as the mean ± SD, and data processing and analysis were completed using R version 4.3.2.

3.4 Results

I recovered 52 of 55 (95%) geolocators deployed across the two years of the study, and 48 of the 52 (92%) recovered geolocators successfully recorded light-level data that could be processed into tracks (Table 1). I found no adverse impacts of geolocator deployment on chick-provisioning behavior, breeding success, or adult return rates (refer to Chapter 2 for details).

Table 1. Summary of geolocators deployed and recovered by year of deployment and sex of adults. Unknown sex is due to the inability to sample blood.

				Sex		
Year	Deployed	Recovered	Tracks	F	M	Unknown
2022	25	24	22	8	13	1
2023	30	28	26	11	15	0

3.4.1 Migratory timing and non-breeding distribution

Wedge-tailed Shearwaters began their outward migration from the breeding colony between mid-November and early December in both years, returning the following season between mid-March and early April (Figure 1). The earliest return date was 12 March in 2024, and the latest was 23 April in 2023. Of 48 tracked birds, 47 successfully fledged a chick. Despite nest failure during early chick rearing in late August 2022, the single failed breeder (male) departed the colony on 6 November, similar to the timing of other tagged birds.

During the El Niño winter of 2023–24, departure from the breeding colony was delayed by one week compared to the previous La Niña year (Mann-Whitney, $U = 178.5$, $p = 0.03$), with a median departure date of 13 November in 2022 compared to 20 November in 2023. Despite this delay, return timing to the colony the following breeding season did not significantly differ between years (Mann-Whitney, $U = 327$, $p = 0.40$), with median return dates of 19 March in 2023 and 15 March in 2024. Additionally, the return migration was more synchronous among individuals compared to the outward migration (Levene's test, $F_{1,94} = 19.14$, $p < 0.001$), likely due to the absence of stopovers during the journey back to the colony. In 2022–23, the outward migration lasted 22.4 ± 8.0 days, while the return migration was significantly shorter at 13.5 ± 1.7 days (Paired t-test, $t_{21} = 5.02$, $p < 0.001$). A similar pattern was observed in 2023–24, with outward migration lasting 20.1 ± 6.0 days, and the return migration 12.8 ± 3.7 days (Paired t-test, $t_{25} = 6.75$, $p < 0.001$).

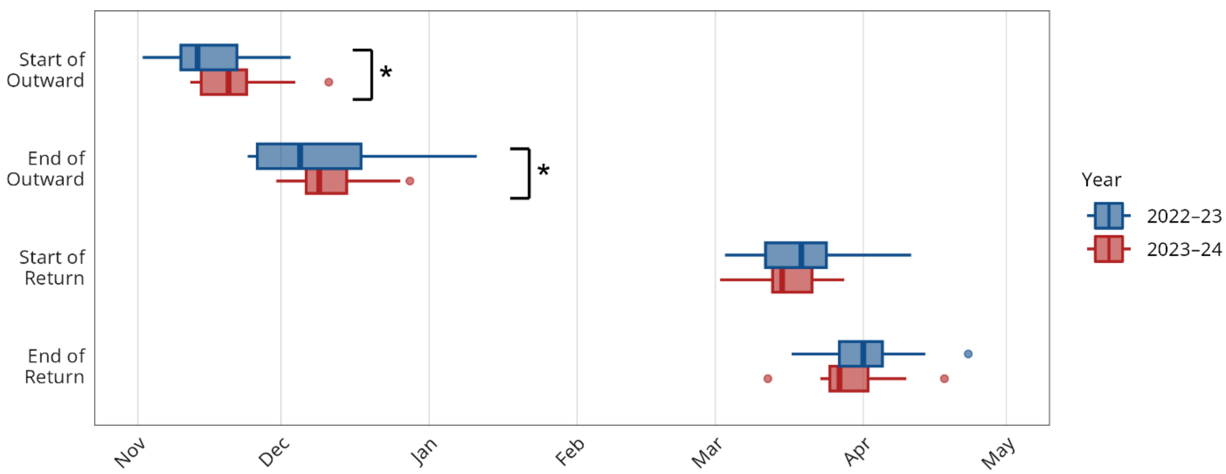


Figure 1. Estimated migration start and end dates for Wedge-tailed Shearwaters tagged with geolocators, comparing outward (eastward movement to non-breeding areas) and return (westward movement to the breeding colony in Hawai‘i) migrations across two years. Blue represents the La Niña year, and red represents the El Niño year. The end of the outward migration indicates arrival at a non-breeding residency site, while the end of the return migration marks the first night back at the colony. Asterisks denote significant differences in dates between years (*$p < 0.05$).

Across both years, Wedge-tailed Shearwaters consistently migrated eastward to the ETP (Figure 2). Migration routes were similar for the outward and return migration and consistent between years, with birds dispersing longitudinally between approximately 10°N and 20°N. The great circle distance between the colony and the farthest 50% UD centroid was 8,179 km in the winter of 2023–24. Each year, a few individuals made a single stopover between Hawaiʻi and Central America, spending 10.7 ± 3.7 days before continuing to their non-breeding sites (Table 2). These stopovers occurred only during the outward migration.

Table 2. Summary of stopovers made by male and female Wedge-tailed Shearwaters during the outward migration. Year indicates the deployment year.

ID	Sex	Year	Number of Stopovers	Date	Duration (days)
961	M	2022	1	16 Dec – 26 Dec	10
962	M	2022	1	16 Nov – 4 Dec	18
977	M	2022	1	17 Dec – 30 Dec	13
1032	F	2023	1	12 Dec – 20 Dec	8
1057	F	2023	1	5 Dec – 13 Dec	10
1063	F	2023	1	15 Dec – 25 Dec	8
1069	M	2023	1	17 Dec – 25 Dec	8

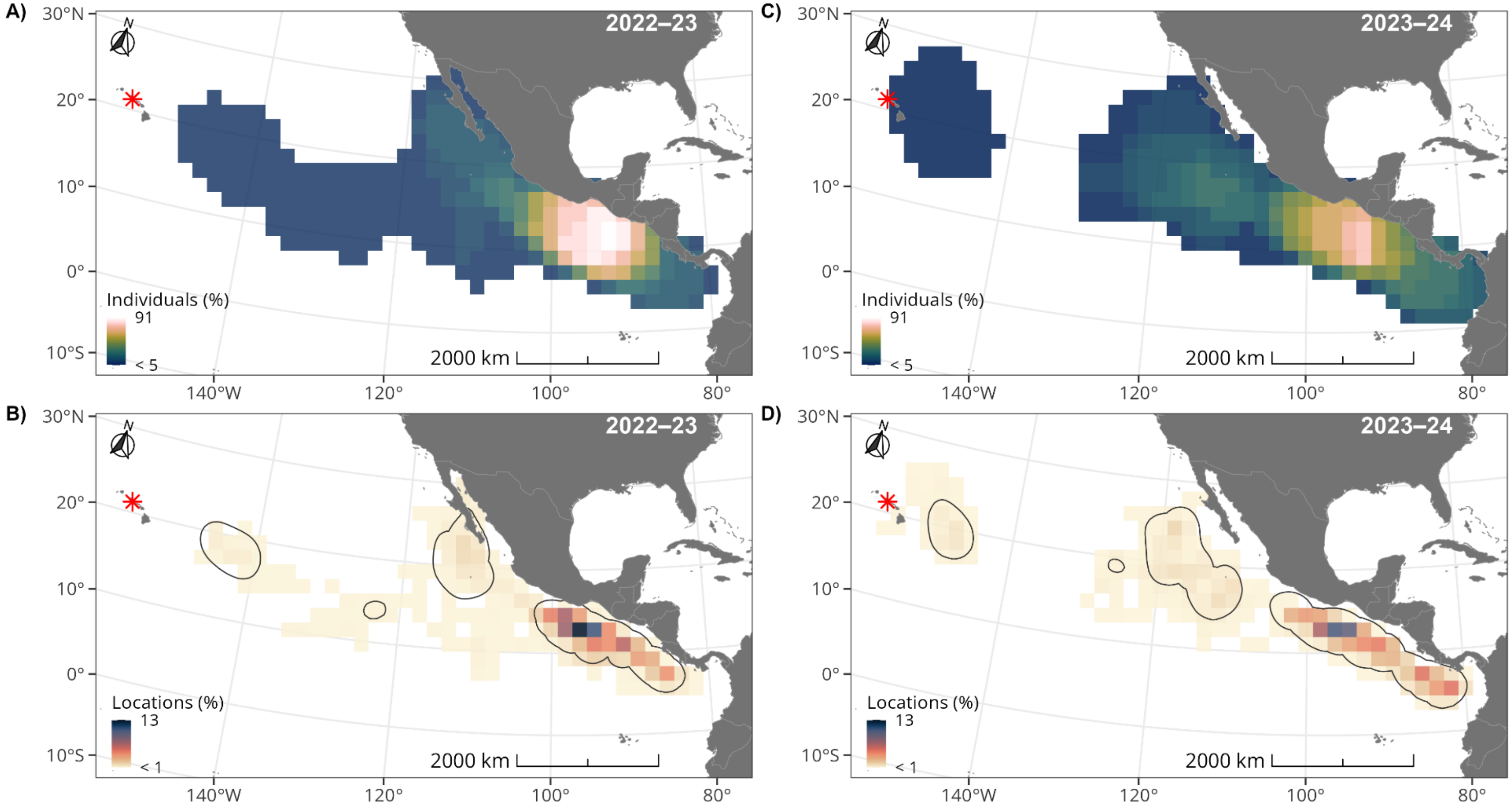


Figure 2. Non-breeding distribution of Wedge-tailed Shearwaters during the 2022–23 (n = 22) and 2023–24 (n = 26) winter periods, estimated using light-level geolocation. Panels (A) and (C) represent the percentage of the total number of individuals, while panels (B) and (D) show the percentage of total locations, all binned into 186 × 186 km grid cells using the Albers Equal Area Conic Projection. Black polygons indicate 50% UDs for each individual and then subsequently pooled together. The red star marks the breeding colony on O‘ahu, Hawai‘i.

Most shearwaters (46 of 48, 96%) settled at a single non-breeding site located from Baja California, Mexico to Panama, between 5°–20° N and 80°–120° W. Individuals remained at these sites for 96.5 ± 10.5 days before initiating their westward return migration to Hawaiʻi. During the 2023–24 winter, one individual dispersed a short distance, remaining within 1,200 km east of Hawaiʻi. Another individual during the 2022–23 winter moved between multiple locations throughout the non-breeding period, eventually settling off Baja California, Mexico about 70 days after departing the colony.

Most individuals concentrated in a primary core area off southwestern Mexico and Guatemala, roughly between 10°–15° N and 90°–95° W. This core area was used by 91% of individuals in the 2022–23 winter and by 77% in the 2023–24 winter. A secondary core area near the Revillagigedo Islands (about 18–19° N) off Baja California, Mexico, was used to a lesser extent, with 14% of individuals occupying this area in 2022–23 and 27% in 2023–24.

Core areas were concentrated along the Central American continent and overlapped with eight national EEZs: Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Clipperton Island (France). Over the two years, birds spent 77% and 75% of their non-breeding time within an EEZ, respectively. Additionally, the core UDs were highly representative of the population-level distribution for both deployment years. The estimated representativeness of the core areas used by individuals during the 2022–23 and 2023–24 non-breeding periods were 95.4% and 92.4%, respectively (Supplementary Figure 1).

3.4.2 Interannual and sex-related differences

Wedge-tailed Shearwaters showed considerable overlap in grid cell usage during the non-breeding period across both years (Figure 3). Although the mean number of locations per cell, adjusted for sample size differences, was not significantly correlated with the cell's coefficient of variation (Spearman's rank, ρ = -0.12, p = 0.29), several grid cells were consistently occupied across both years, indicating site fidelity during the non-breeding season. In contrast, a few peripheral grid cells showed greater variability between years, reflected by a higher coefficient of variation. This result demonstrates that these areas were used more in one year than the other. Birds were widely dispersed in both years (Gx: +0.006 in 2022 and +0.003 in 2023). The distribution of bird locations was consistently neither strongly aggregated nor uniform across years (Gx: +0.05 in 2022 and +0.04 in 2023).

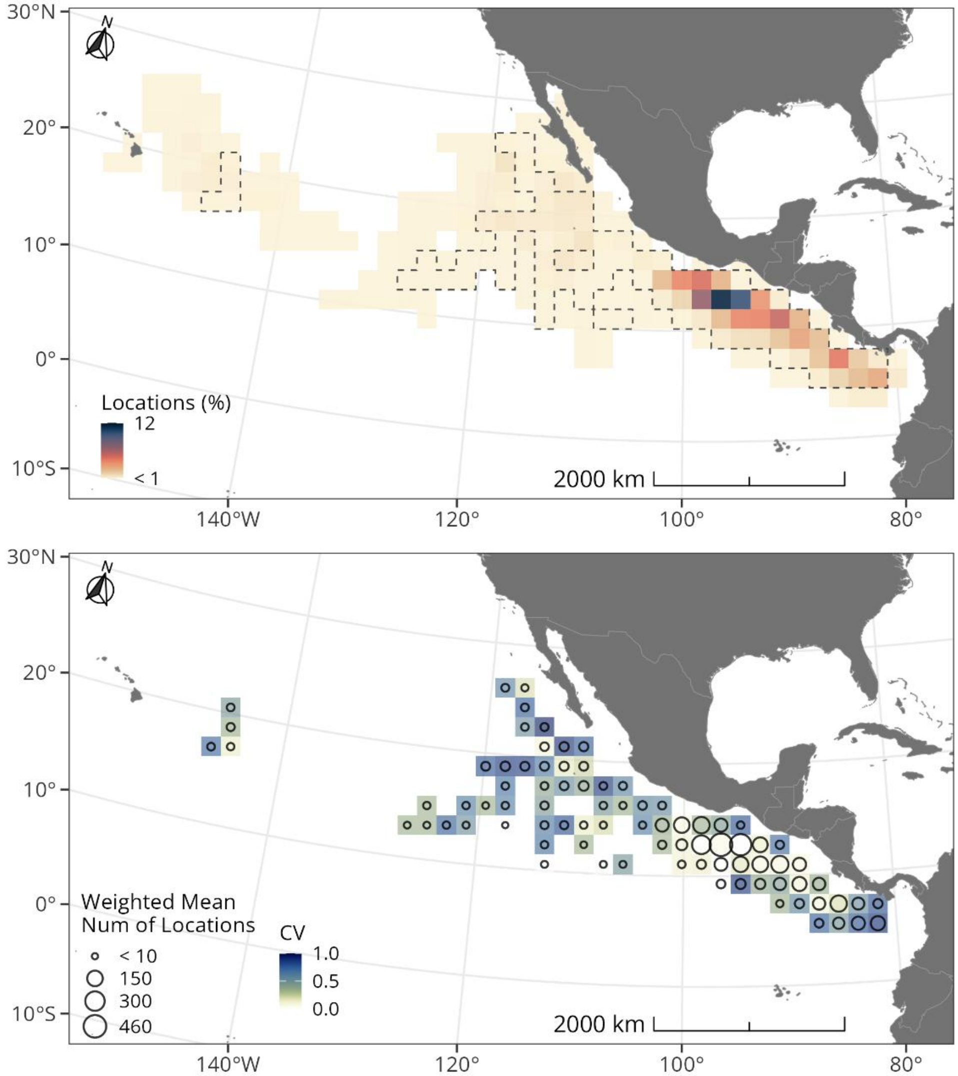


Figure 3. Grid cells represent areas used by Wedge-tailed Shearwaters during the 2022–23 and 2023–24 non-breeding periods. The top panel shows the percentage of total locations across both years, with the dashed lines outlining the grid cells used in both periods. The bottom panel focuses on multi-year cells only, where circle sizes represent the mean number of locations per cell, weighted by sample size to account for differences each year. The color scale indicates the coefficient of variation, highlighting variability in spatial use across years. Grid cells are 186 × 186 km.

Comparing core use areas between sexes indicated a high degree of spatial overlap between males and females in both years, with BA values of 0.89 in 2022–23 and 0.86 in 2023–24 (Figure 4). Additionally, individual core UD areas of males and females did not differ in either year (2022: Mann-Whitney, $U = 48$, $p = 0.80$; 2023: $U = 70$, $p = 0.53$). There were also no significant sex-based differences in the duration of either the outward migration (U = 307.5, p = 0.37) or the return migration (U = 258, p = 0.87). Similarly, the starting dates of outward migration (U = 264, p = 0.97) and return migration (U = 329.5, p = 0.17) were consistent between males and females.

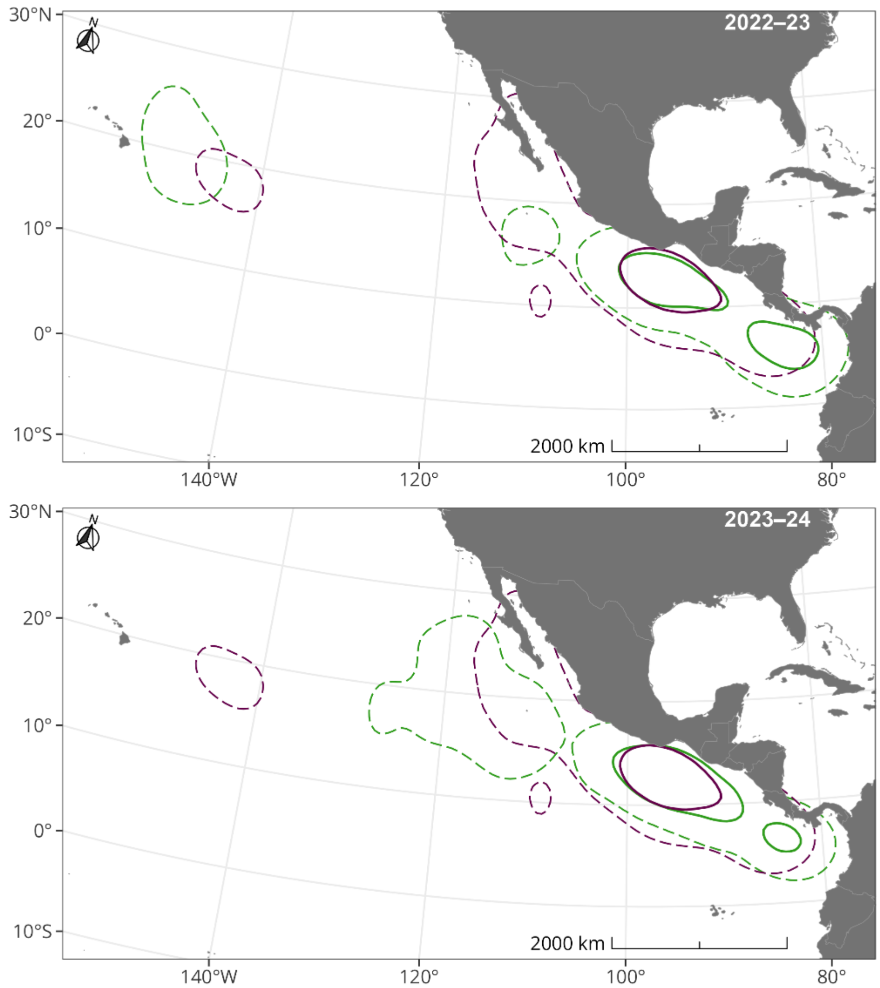


Figure 4. Core (50%) and general use (95%) utilization distributions (UDs) of non-breeding male (green) and female (purple) Wedge-tailed Shearwaters. Solid and dashed lines indicate core and general use areas, respectively.

3.4.3 Activity patterns

Wedge-tailed Shearwaters varied their at-sea activity throughout the migration and the non-breeding period. At the start of migration, daily time spent on the water gradually increased during both day and night (Figure 5). Across both years, there was no evidence of sex-based differences in the amount of time spent on the water. Overall, males and females collectively spent approximately 28% of the day and 45% of the night on the water (Table 3). As they departed on their return migration, time on the water steadily decreased for both day and night, eventually reaching levels similar to those observed during the chick-provisioning period at the breeding colony (15% of the day wet and 9% of the night wet).

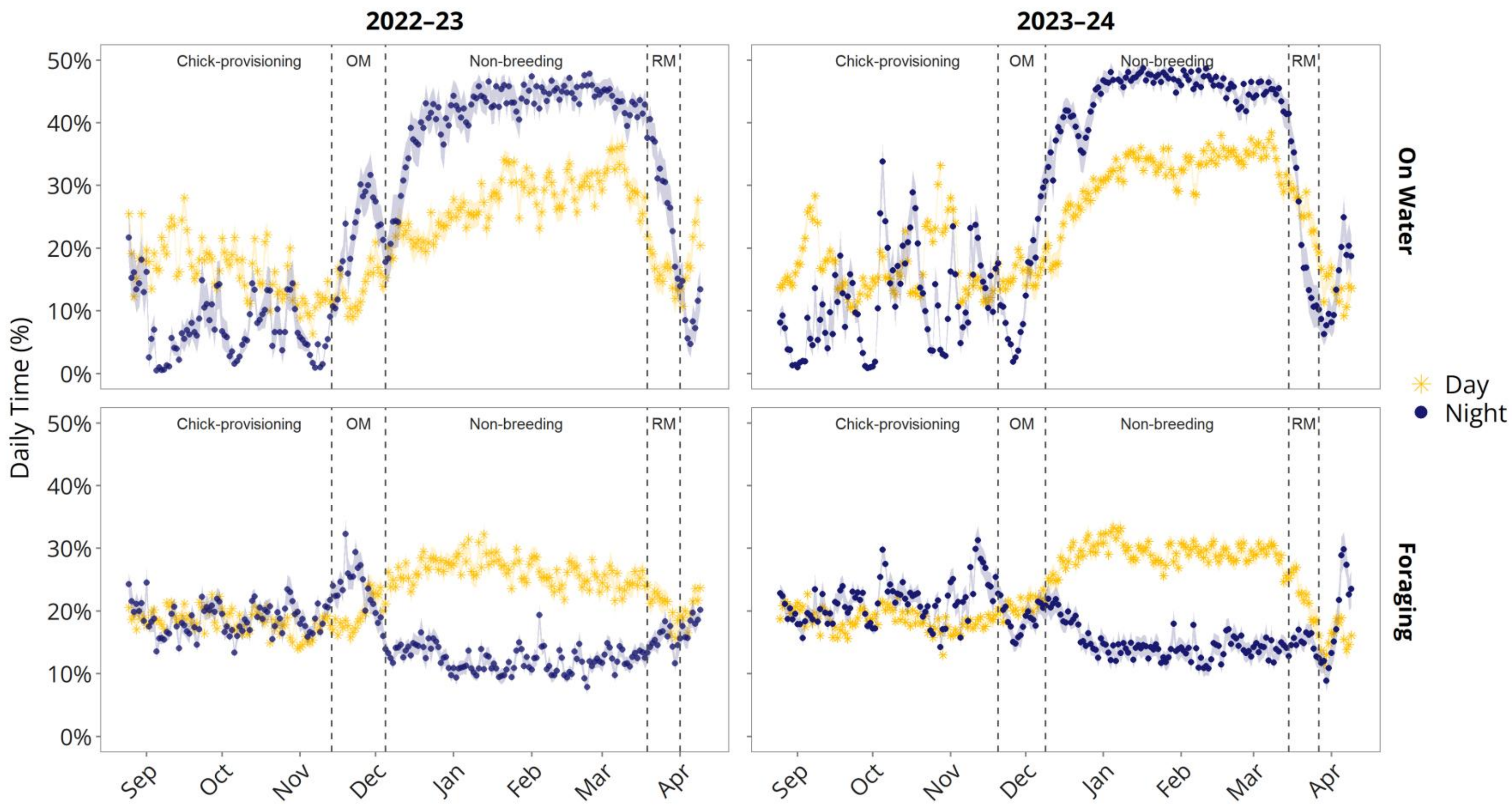


Figure 5. Daily mean (± SE) percentage of time spent by Wedge-tailed Shearwaters on the water (top row) and foraging (bottom row) during the day (yellow stars) and night (blue dots) for two non-breeding periods: 2022–23 (left column) and 2023–24 (right column). Grey vertical lines delineate the median start and end dates of each life stage. OM is outward migration and RM is return migration.

Table 3. Daily proportion (%) of time spent on the water (mean ± SD) for Wedge-tailed Shearwaters during migration and the non-breeding period. Number in parantheses indicates sample size.

		Outward Migration		Non-breeding		Return Migration	
Sex	Year	Day	Night	Day	Night	Day	Night
M (13)	2022–23	12.4 ± 8.3	17.5 ± 14.3	26.2 ± 9.1	44.6 ± 9.5	15.5 ± 9.1	28.1 ± 15.5
F (8)	2022–23	11.3 ± 8.1	16.7 ± 13.6	25.1 ± 9.8	42.3 ± 11.9	13.3 ± 8.6	28.1 ± 15.4
M (15)	2023–24	14.0 ± 8.8	14.4 ± 13.4	29.8 ± 8.0	44.7 ± 9.6	20.8 ± 10.0	21.6 ± 16.6
F (11)	2023–24	12.2 ± 8.3	12.6 ± 12.7	30.6 ± 7.8	46.1 ± 7.3	20.4 ± 10.0	18.9 ± 15.8
Both (22*)	2022–23	12.1 ± 8.2	16.8 ± 14.0	25.9 ± 9.4	43.8 ± 10.4	14.7 ± 9.0	27.7 ± 15.5
Both (26)	2023–24	13.2 ± 8.7	13.6 ± 8.7	30.1 ± 8.0	45.3 ± 8.7	20.6 ± 10.0	20.4 ± 16.3
Both (48)	Both	12.7 ± 8.5	15.2 ± 13.6	28.1 ± 9.0	44.6 ± 9.6	17.8 ± 10.0	23.8 ± 16.3

* Includes one individual of unknown sex

Throughout the tagging period, Wedge-tailed Shearwaters consistently spent about 35–40% of their daily time foraging. In non-breeding areas, foraging activity primarily occurred during daylight, in contrast to the more balanced day and night foraging when provisioning chicks at the breeding colony (Figure 5). Daylight foraging was concentrated offshore of Central America (Figure 6). Although the overall amount of daylight foraging was similar across years, it was distributed over a broader area during the 2023–24 El Niño winter.

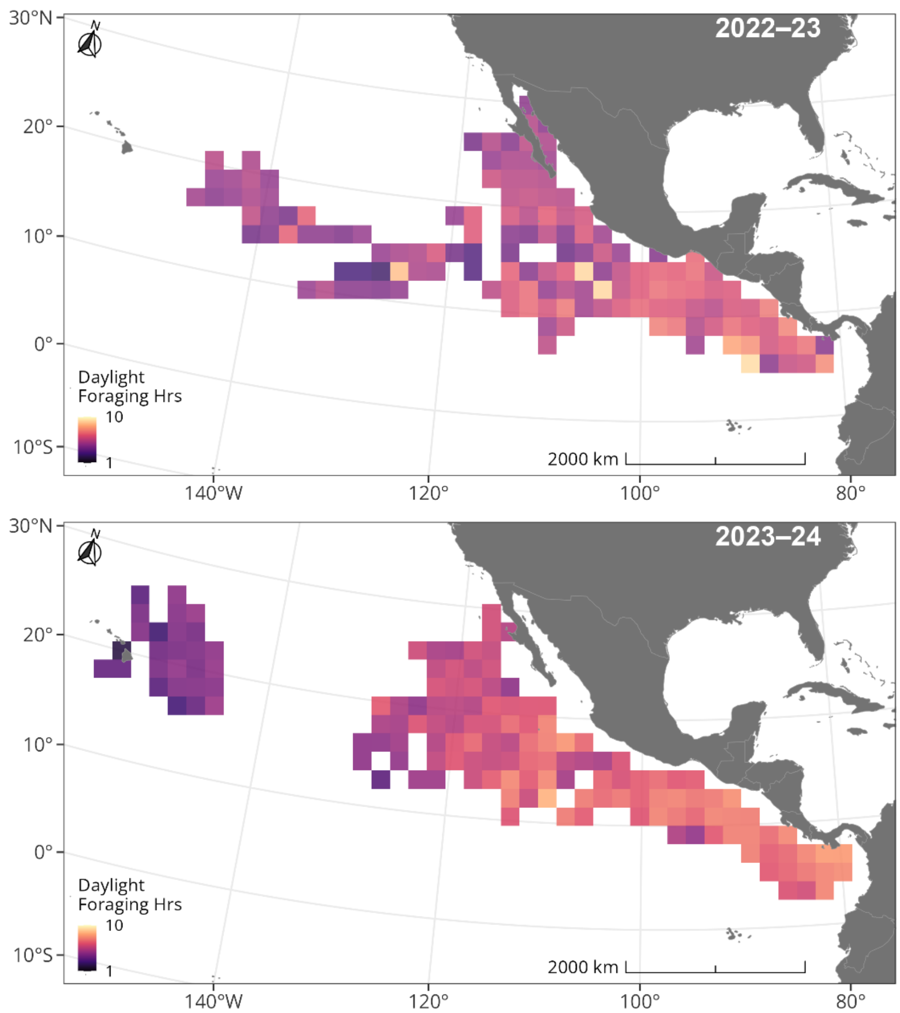


Figure 6. Spatial distribution of daylight foraging activity of Wedge-tailed Shearwaters during the two non-breeding periods of 2022–23 (top) and 2023–24 (bottom). Colors represent the mean daily hours spent foraging during daylight. Daylight foraging is primarily concentrated in the eastern Pacific, offshore of Central America. Grid cells are 186 × 186 km.

3.5 Discussion

My study provides new insights into the post-breeding dispersal of Wedge-tailed Shearwaters from a Main Hawaiian Island colony. I observed a consistent eastward migration and spatial distribution across years, regardless of interannual ENSO variability or sex differences. Although Wedge-tailed Shearwaters are known to undertake trans-equatorial migrations in the South Pacific, individuals from Oʻahu had migration patterns more similar to those in the Indian Ocean. Like shearwaters from Aride Island and Western Australia in the Indian Ocean, these birds migrated longitudinally towards equatorial regions, primarily settling just north of the equator. My findings are consistent with migration patterns of tropical seabirds, which generally undertake shorter post-breeding migrations and largely remain within tropical waters (e.g., Pinet et al., 2011; Jaeger et al., 2017). I also documented one individual that remained near Hawaiʻi after breeding, indicating a mix of rare short- and more common long-distance migration strategies within this colony. This variability in dispersal distances within a colony has also been observed in Indian Ocean Wedge-tailed Shearwaters and other tropical seabirds (Catry et al., 2009; Zajková et al., 2017; Correia et al., 2024).

Aside from the short-dispersal individual, all shearwaters used non-breeding sites in the ETP, with most concentrating in areas off southwestern Mexico and Guatemala. The secondary core area near Baja California indicates that Wedge-tailed Shearwaters from Hawaiʻi join birds dispersing from colonies on the Revillagigedo Islands, which share a similar breeding phenology with Hawaiian shearwaters but are predominantly dark morph (Whittow, 2020). Since light morph Wedge-tailed Shearwaters are predominant in the Hawaiian population (Whittow, 2020), researchers conducting at-sea surveys in the ETP suggested that light-morph individuals are likely non-breeding migrants from Hawaiʻi (Howell and Engel, 1993; Young and Zook, 2016;

Marín, 2024). Thus, distributions patterns identified through light-level geolocation are consistent with previous observations from vessel-based surveys.

The repeated interannual use of a primary core area implies that ENSO conditions during the study period (2022–24) did not affect their overall non-breeding distribution, with variability limited to peripheral areas. This core area generally aligns with the North Equatorial Countercurrent (NECC) and its associated thermocline ridge, both of which shift seasonally and vary with ENSO phases and are typically located between 5° and 10°N (Reilly, 1990; Fiedler et al., 1991; Ballance et al., 2006). Consistent with our findings, at-sea surveys have documented high densities of predominantly light-morph birds in the NECC (King, 1974). During El Niño years, when the thermocline deepens, shearwater abundance along the NECC remains stable (Ribic et al., 1992). In contrast, population estimates are lower during La Niña years, when a shallower and weaker thermocline may reduce the abundance of tuna that forage at the thermocline (Spear et al., 2001; Ballance et al., 2002).

In the ETP, Wedge-tailed Shearwaters locate prey by joining multispecies feeding assemblages of tunas, dolphins, and other tropical seabirds (Au and Pitman, 1986). In these assemblages, they rely on surface-feeding Yellowfin Tuna (*Thunnus albacares*) and Skipjack Tuna (*Katsuwonus pelamis*) to increase foraging success. Therefore, ENSO effects on Wedge-tailed Shearwater distribution are likely mediated by the ENSO influence on the abundance and distribution of surface-feeding tuna.

Adult Yellowfin and Skipjack Tuna are most abundant in or just below the thermocline along the northern boundary of the NECC (Blackburn and Williams, 1975; Brill et al., 1999). This aggregation may explain the shearwaters' consistent use of non-breeding sites within the NECC, where surface-feeding tuna forage along a well-defined thermocline (Green, 1967; Spear et al., 2001). During the El Niño year, daytime foraging activity of Wedge-tailed Shearwaters was spread out over a broader area, potentially as a response to increased tuna presence near the surface due to a strengthened thermocline. Diurnal foraging by Wedge-tailed Shearwaters may improve their chances of visually locating conspicuous dolphin schools and, subsequently, tuna.

While overall movement patterns remained consistent across years, ENSO conditions appeared to affect the timing of migration. Outward migration was delayed during the El Niño year due to an extended chick provisioning period at the breeding colony in 2023. Chicks were provisioned to an older age compared to 2022 (see Chapter 2, section 2.4.1), though they reached lower peak masses. These results demonstrate that ENSO conditions impacted shearwaters during the breeding season, possibly by altering prey abundance or availability and prompting adults to compensate by feeding chicks for a longer period.

The stopovers birds took during the outward migration are unlikely related to a flightless molt, as Wedge-tailed Shearwaters molt their primary feathers progressively throughout the non-breeding period (King, 1974). While the precise timing of their primary molt is unknown, 23% of the shearwaters I recaptured in April, just before the pre-laying exodus, had a shorter tenth primary than the ninth, indicating the tenth primary was still growing as they returned to the colony. This observation agrees with the March and April specimens reported by King (1974). As a result, I suggest that Wedge-tailed Shearwaters molt one or a few primaries at a time. Since stopovers occurred around similar dates among individuals each year, they are more likely associated with foraging hotspots or periods of low wind rather than molt. Additionally, I did not observe a peak in time spent on the water (> 50% of the day) which is often associated with energy-intensive molting (Cherel et al., 2016; Clay and Brooke, 2024). Our findings further support the hypothesis that Wedge-tailed Shearwaters do not undergo a flightless molt.

While sex-specific differences in chick-provisioning behavior have been observed in Wedge-tailed Shearwaters (Peck and Congdon, 2006; Catry et al., 2009), I found no evidence of sexual segregation during the post-breeding dispersal. Because the size of core areas, timing, and duration of migration were similar between males and females, both sexes may have similar ecological requirements during the non-breeding period. This lack of segregation may also indicate minimal intersexual competition in these habitats, likely due to resource abundance.

Although only one failed breeder was tagged, this individual remained near the breeding colony for over two months after its nest failure, a pattern that contrasts with other Procellariforms where failed breeders typically depart earlier than successful breeders (e.g., Yamamoto et al., 2014; Dias et al., 2015; Delord et al., 2019; Rayner et al., 2023). I propose that food resource availability may be more favorable around the Main Hawaiian Islands than in the ETP during fall (September – October), and that Wedge-tailed Shearwaters time their migration to match the seasonal increase in winter-time tuna densities in the ETP.

3.6 References

Au, D. W. K., and Pitman, R. L. (1986). Seabird Interactions with Dolphins and Tuna in the Eastern Tropical Pacific. *The Condor* 88, 304–317. doi: 10.2307/1368877

Baduini, C. L., Hyrenbach, K. D., Coyle, K. O., Pinchuk, A., Mendenhall, V., and Hunt, G. L. (2001). Mass mortality of short-tailed shearwaters in the south-eastern Bering Sea during summer 1997. *Fish. Oceanogr.* 10, 117–130. doi: 10.1046/j.1365-2419.2001.00156.x

Ballance, L. T., and Pitman, R. L. (1999). Foraging ecology of tropical seabirds. *Adams NJ Slotow RH Eds Proc 22 Int Ornithol Congr Durb.*, 2057–2071.

Ballance, L. T., Pitman, R. L., and Fiedler, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Prog. Oceanogr.* 69, 360–390. doi: 10.1016/j.pocean.2006.03.013

Ballance, L. T., Pitman, R. L., Spear, L. B., and Fiedler, P. C. (2002). Investigations Into Temporal Patterns in Distribution, Abundance, and Habitat Relationships Within Seabird Communities of the Eastern Tropical Pacific. Southwest Fisheries Center, Administrative Report No. LJ-02-17. La Jolla, CA. 79 p.

Beal, M., Oppel, S., Handley, J., Pearmain, E. J., Morera-Pujol, V., Carneiro, A. P. B., et al. (2021). track2KBA: An R package for identifying important sites for biodiversity from tracking data. *Methods Ecol. Evol.* 12, 2372–2378. doi: 10.1111/2041-210X.13713

Bernard, A., Rodrigues, A. S. L., Cazalis, V., and Grémillet, D. (2021). Toward a global strategy for seabird tracking. *Conserv. Lett.* 14, e12804. doi: 10.1111/conl.12804

Blackburn, M., and Williams, F. (1975). Distribution and ecology of skipjack tuna, *Katsuwonus pelamis*, in an offshore area of the eastern tropical Pacific Ocean. *Fish. Bull.* 73, 382–411. doi: 10.1111/j.1095-8649.1974.tb01338.x.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Mar. Biol.* 133, 395–408. doi: 10.1007/s002270050478

Bull, L. S., Bell, B. D., and Pledger, S. (2005). Patterns of Size Variation in the Shearwater Genus *Puffinus*. *Mar. Ornithol.* 33, 27–39.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519. doi: 10.1016/j.ecolmodel.2006.03.017

Carle, R. D., Felis, J. J., Vega, R., Beck, J., Adams, J., López, V., et al. (2019). Overlap of Pink-footed Shearwaters and central Chilean purse-seine fisheries: Implications for bycatch risk. *The Condor* 121, duz026. doi: 10.1093/condor/duz026

Catry, T., Ramos, J., Le Corre, M., and Phillips, R. (2009). Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Mar. Ecol. Prog. Ser.* 391, 231–242. doi: 10.3354/meps07717

Cherel, Y., Quillfeldt, P., Delord, K., and Weimerskirch, H. (2016). Combination of At-Sea Activity, Geolocation and Feather Stable Isotopes Documents Where and When Seabirds Molt. *Front. Ecol. Evol.* 4. doi: 10.3389/fevo.2016.00003

Clay, T. A., and Brooke, M. D. L. (2024). Trans-equatorial migration links oceanic frontal habitats across the Pacific Ocean: year-round movements and foraging activity of a small gadfly petrel. *Mar. Biol.* 171, 60. doi: 10.1007/s00227-023-04373-3

Correia, E., Granadeiro, J. P., Diop, N., Wambar, F., Hernandez-Rios, A., and Catry, T. (2024). High variability in the migratory behaviour of a tropical seabird. *Mar. Biol.* 171, 212. doi: 10.1007/s00227-024-04538-8

Cortés, V., Arcos, J., and González-Solís, J. (2017). Seabirds and demersal longliners in the northwestern Mediterranean: factors driving their interactions and bycatch rates. *Mar. Ecol. Prog. Ser.* 565, 1–16. doi: 10.3354/meps12026

Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., et al. (2013). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *J. R. Soc. Interface* 10, 20120570. doi: 10.1098/rsif.2012.0570

Delord, K., Barbraud, C., Pinaud, D., Ruault, S., Patrick, S. C., and Weimerskirch, H. (2019). Individual consistency in the non-breeding behavior of a long-distance migrant seabird, the Grey Petrel *Procellaria cinerea*. *Mar. Ornithol.* 47, 93–103. doi: 10.5038/2074-1235.47.1.1298

Dias, M. P., Alho, M., Granadeiro, J. P., and Catry, P. (2015). Wanderer of the deepest seas: migratory behaviour and distribution of the highly pelagic Bulwer's petrel. *J. Ornithol.* 156, 955–962. doi: 10.1007/s10336-015-1210-9

Duffy, D. C., and Frazier, J. G. (2014). A census of Tehuantepec and Papagayo eddies in the northeastern tropical Pacific. *Geophys. Res. Lett.* 32, 2005GL024324. doi: 10.1029/2005GL024324

Felis, J., Adams, J., Hodum, P., Carle, R., and Colodro, V. (2019a). Eastern Pacific migration strategies of pink-footed shearwaters *Ardenna creatopus*: implications for fisheries interactions and international conservation. *Endanger. Species Res.* 39, 269–282. doi: 10.3354/esr00969

Felis, J. J., Czapanskiy, M. F., and Adams, J. (2019b). At-Sea Ranging Behavior of Seabirds Breeding in the Main Hawaiian Islands: Bio-logger Data Release (ver. 2.0, May 2020). doi: 10.5066/P9NTEXM6

Fieberg, J., and Kochanny, C. O. (2005). Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *J. Wildl. Manag.* 69, 1346–1359. doi: 10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Fiedler, P. C., Philbrick, V., and Chavez, F. P. (1991). Oceanic upwelling and productivity in the eastern tropical Pacific. *Limnol. Oceanogr.* 36, 1834–1850. doi: 10.4319/lo.1991.36.8.1834

Flanders Marine Institute (2024). Union of the ESRI Country shapefile and the Exclusive Economic Zones (version 4). Available at: https://www.marineregions.org/

Ford, R. G., and Krumme, D. W. (1979). The Analysis of Space use Patterns. *J. Theroetical Biol.* 76, 125–155. doi: 10.1016/0022-5193(79)90366-7

Franklin, K. A., Nicoll, M. A. C., Butler, S. J., Norris, K., Ratcliffe, N., Nakagawa, S., et al. (2022a). Individual repeatability of avian migration phenology: A systematic review and meta-analysis. *J. Anim. Ecol.* 91, 1416–1430. doi: 10.1111/1365-2656.13697

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., et al. (2022b). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.* 10, 13. doi: 10.1186/s40462-022-00311-y

García-Barón, I., Authier, M., Caballero, A., Vázquez, J. A., Santos, M. B., Murcia, J. L., et al. (2019). Modelling the spatial abundance of a migratory predator: A call for transboundary marine protected areas. *Divers. Distrib.* 25, 346–360. doi: 10.1111/ddi.12877

Gilman, E., Chaloupka, M., Ishizaki, A., Carnes, M., Naholowaa, H., Brady, C., et al. (2021). Tori lines mitigate seabird bycatch in a pelagic longline fishery. *Rev. Fish Biol. Fish.* 31, 653–666. doi: 10.1007/s11160-021-09659-7

Green, R. E. (1967). Relationship of the Thermocline to Success of Purse Seining for Tuna. *Trans. Am. Fish. Soc.* 96, 126–130. doi: 10.1577/1548-8659(1967)96[126:ROTTTS]2.0.CO;2

Green, R. H. (1966). Measurement of non-randomness in spatial distributions. *Popul. Ecol.* 8, 1–7. doi: 10.1007/BF02524740

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., et al. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proc. R. Soc. B Biol. Sci.* 276, 1215–1223. doi: 10.1098/rspb.2008.1577

Hijmans, R. (2024). _terra: Spatial Data Analysis_. R package version 1.7-78. Available at: <https://CRAN.R-project.org/package=terra>.

Howell, S. N. G., and Engel, S. J. (1993). Seabird Observations off Western Mexico. *West. Birds* 24, 167–181.

Hromádková, T., Pavel, V., Flousek, J., and Briedis, M. (2020). Seasonally specific responses to wind patterns and ocean productivity facilitate the longest animal migration on Earth. *Mar. Ecol. Prog. Ser.* 638, 1–12. doi: 10.3354/meps13274

Hyrenbach, K. D., Keiper, C., Allen, S. G., Ainley, D. G., and Anderson, D. J. (2006). Use of marine sanctuaries by far-ranging predators: commuting flights to the California Current System by breeding Hawaiian albatrosses. *Fish. Oceanogr.* 15, 95–103. doi: 10.1111/j.1365-2419.2005.00350.x

IATTC (2024). Status of the Tuna and Billfish Stocks in 2022. La Jolla, CA: Inter-American Tropical Tuna Commission.

Jaeger, A., Feare, C. J., Summers, R. W., Lebarbenchon, C., Larose, C. S., and Le Corre, M. (2017). Geolocation Reveals Year-Round at-Sea Distribution and Activity of a Superabundant Tropical Seabird, the Sooty Tern *Onychoprion fuscatus*. *Front. Mar. Sci.* 4, 394. doi: 10.3389/fmars.2017.00394

Jenkins, J. A. F. (1979). Observations on the Wedge-tailed shearwater *(Puffinus pacificus)* in the South West Pacific. *Notornis* 26, 331–348.

King, W. B. (1974). Pelagic studies of seabirds in the central and eastern Pacific Ocean. *Smithson. Contrib. Zool.*, 1–277. doi: 10.5479/si.00810282.158

Lascelles, B. G., Taylor, P. R., Miller, M. G. R., Dias, M. P., Oppel, S., Torres, L., et al. (2016). Applying global criteria to tracking data to define important areas for marine conservation. *Divers. Distrib.* 22, 422–431. doi: 10.1111/ddi.12411

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., et al. (2020). Light-level geolocator analyses: A user's guide. *J. Anim. Ecol.* 89, 221–236. doi: 10.1111/1365-2656.13036

Lisovski, S., Wotherspoon, S., and Sumner, M. (2016). TwGeos: basic data processing for light-level geolocation archival tags. R package version 0.1.2. Available at: https://github.com/slisovski/TwGeos

Marín, M. (2024). Status and occurrence of Wedge-tailed Shearwater *Ardenna pacifica* in waters of the northwestern coast of South America. *Mar. Ornithol.* 52, 81–84. doi: 10.4319/mo.2021.49.1.071

Mattern, T., Masello, J. F., Ellenberg, U., and Quillfeldt, P. (2015). Actave.net – a web-based tool for the analysis of seabird activity patterns from saltwater immersion geolocators. *Methods Ecol. Evol.* 6, 859–864. doi: 10.1111/2041-210X.12398

McDuie, F., and Congdon, B. (2016). Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas. *Mar. Ecol. Prog. Ser.* 550, 219–234. doi: 10.3354/meps11713

McKnight, A., Irons, D., Allyn, A., Sullivan, K., and Suryan, R. (2011). Winter dispersal and activity patterns of post-breeding black-legged kittiwakes *Rissa tridactyla* from Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 442, 241–253. doi: 10.3354/meps09373

Medrano, F., Hernández-Montoya, J., Saldanha, S., Bedolla-Guzmán, Y., and González-Solís, J. (2024). Contrasting migratory ecology of two threatened and allochronic storm-petrels breeding in the Mexican Pacific. *Endanger. Species Res.* 54, 331–339. doi: 10.3354/esr01344

Michael, P. E., Jahncke, J., and Hyrenbach, K. D. (2016). Placing Local Aggregations in a Larger-Scale Context: Hierarchical Modeling of Black-Footed Albatross Dispersion. *PLOS ONE* 11, e0153783. doi: 10.1371/journal.pone.0153783

Montevecchi, W. (2007). Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. *Mar. Ecol. Prog. Ser.* 352, 213–220. doi: 10.3354/meps07075

Mott, R., and Clarke, R. H. (2018). Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu - Austral Ornithol.* 118, 235–246. doi: 10.1080/01584197.2017.1416957

Müller, M. S., Massa, B., Phillips, R. A., and Dell'omo, G. (2014). Individual consistency and sex differences in migration strategies of Scopoli's shearwaters *Calonectris diomedea* despite year differences. *Curr. Zool.* 60, 631–641. doi: 10.1093/czoolo/60.5.631

Peck, D. R., and Congdon, B. C. (2006). Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Puffinus pacificus*. *J. Avian Biol.* 37, 245–251. doi: 10.1111/j.2006.0908-8857.03558.x

Peck, D. R., Smithers, B. V., Krockenberger, A. K., and Congdon, B. C. (2004). Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Mar. Ecol. Prog. Ser.* 281, 259–266. doi: 10.3354/meps281259

Péron, C., Delord, K., Phillips, R., Charbonnier, Y., Marteau, C., Louzao, M., et al. (2010). Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. *Mar. Ecol. Prog. Ser.* 416, 267–284. doi: 10.3354/meps08785

Pike, E. P., MacCarthy, J. M. C., Hameed, S. O., Harasta, N., Grorud-Colvert, K., Sullivan-Stack, J., et al. (2024). Ocean protection quality is lagging behind quantity: Applying a scientific framework to assess real marine protected area progress against the 30 by 30 target. *Conserv. Lett.* 17, e13020. doi: 10.1111/conl.13020

Pinet, P., Jaquemet, S., Pinaud, D., Weimerskirch, H., Phillips, R., and Le Corre, M. (2011). Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. *Mar. Ecol. Prog. Ser.* 423, 291–302. doi: 10.3354/meps08971

Polovina, J. J., Howell, E., Kobayashi, D. R., and Seki, M. P. (2001). The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Prog. Oceanogr.* 49, 469–483. doi: 10.1016/S0079-6611(01)00036-2

Priddel, D., Carlile, N., Portelli, D., Kim, Y., O'Neill, L., Bretagnolle, V., et al. (2014). Pelagic distribution of Gould's Petrel (*Pterodroma leucoptera*): linking shipboard and onshore observations with remote-tracking data. *Emu - Austral Ornithol.* 114, 360–370. doi: 10.1071/MU14021

Pyle, R. L., and Pyle, P. (2017). The Birds of the Hawaiian Islands: Occurrence, History, Distribution, and Status. *BP Bish. Mus. Honol. HI USA*. Available at: http://hbs.bishopmuseum.org/birds/rlp-monograph/

Rayner, M. J., Gaskin, C. P., and Taylor, G. A. (2023). Seasonal movements, foraging activity, and breeding biology of black-winged petrel (*Pterodroma nigripennis*) from three New Zealand colonies. *Notornis* 70, 111–123.

Regular, P., Montevecchi, W., Hedd, A., Robertson, G., and Wilhelm, S. (2013). Canadian fishery closures provide a large-scale test of the impact of gillnet bycatch on seabird populations. *Biol. Lett.* 9, 20130088. doi: 10.1098/rsbl.2013.0088

Reilly, S. (1990). Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66, 1–11. doi: 10.3354/meps066001

Ribic, C., Ainley, D., and Spear, L. (1992). Effects of El Niño and La Niña on seabird assemblages in the Equatorial Pacific. *Mar. Ecol. Prog. Ser.* 80, 109–124. doi: 10.3354/meps080109

Sato, N., Katsumata, N., Yokota, K., Uehara, T., Fusejima, I., and Minami, H. (2016). Tori-lines with weighted branch lines reduce seabird bycatch in eastern South Pacific longline fishery. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 26, 95–107. doi: 10.1002/aqc.2492

Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Sumner, M. D., and Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *J. Appl. Ecol.* 50, 671–679. doi: 10.1111/1365-2664.12069

Spear, L., Ballance, L., and Ainley, D. (2001). Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Mar. Ecol. Prog. Ser.* 219, 275–289. doi: 10.3354/meps219275

Sumner, M. D., Wotherspoon, S. J., and Hindell, M. A. (2009). Bayesian Estimation of Animal Movement from Archival and Satellite Tags. *PLoS ONE* 4, e7324. doi: 10.1371/journal.pone.0007324

Surman, C. A., Nicholson, L. W., and Phillips, R. A. (2018). Distribution and patterns of migration of a tropical seabird community in the Eastern Indian Ocean. *J. Ornithol.* 159, 867–877. doi: 10.1007/s10336-018-1556-x

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Res. Part II* 54, 211–223. doi: 10.1016/j.dsr2.2006.11.013

Weimerskirch, H., de Grissac, S., Ravache, A., Prudor, A., Corbeau, A., Congdon, B., et al. (2020). At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. *Mar. Ecol. Prog. Ser.* 633, 225–238. doi: 10.3354/meps13171

Whelan, S., Hatch, S. A., Irons, D. B., McKnight, A., and Elliott, K. H. (2020). Increased summer food supply decreases non-breeding movement in black-legged kittiwakes. *Biol. Lett.* 16, 20190725. doi: 10.1098/rsbl.2019.0725

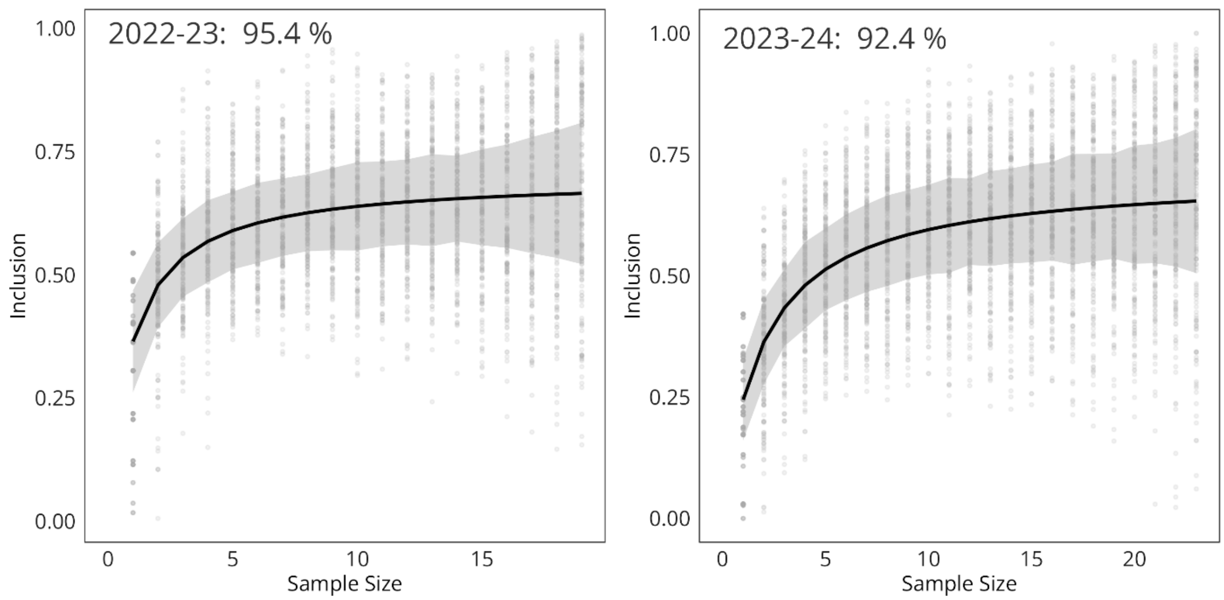
Whittow, G. C. (2020). Wedge-tailed Shearwater *(Ardenna pacifica)*. version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: https://doi.org/10.2173/bow.wetshe.01

Yamamoto, T., Takahashi, A., Sato, K., Oka, N., Yamamoto, M., and Trathan, P. N. (2014). Individual consistency in migratory behaviour of a pelagic seabird. *Behaviour* 151, 683–701. doi: 10.1163/1568539X-00003163

Young, B. E. Y., and Zook, J. R. (2016). Observation frequency and seasonality of marine birds off the Pacific coast of Costa Rica. *Rev. Biol. Trop.* 64, 235. doi: 10.15517/rbt.v64i1.23453

Zajková, Z., Militão, T., and González-Solís, J. (2017). Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. *Mar. Ecol. Prog. Ser.* 579, 169–183. doi: 10.3354/meps12269

Supplementary Figure



Supplementary Figure 1. Estimated sample representativeness for population-level space use across two deployment years, 2022–23 and 2023–24. The inclusion rate was calculated by sub-sampling individual tracks from sample sizes ranging from n = 1 to 19 for 2022–23 and from n = 1 to 23 for 2023–24 and represents the proportion of out-sample locations that fall within the 50% UD of sub-sampled tracks. The analysis was conducted using the 'repAssess' function from the track2KBA package, with 200 bootstrap iterations. Shaded areas represent the SD of inclusion rates for the 200 iterations, while the solid black lines indicate a fitted nonlinear least squares regression line, i.e., where the line asymptotes is the sample size where population-level space use is not likely to change (Beal et al., 2021). Percentage of representativeness is calculated as the inclusion rate of the sample size at the asymptote divided by the estimated asymptote.

CHAPTER 4

Conclusion

4.1 Management Implications and Recommendations

Research on seabird migration has largely focused on species in higher latitudes (Mott and Clarke, 2018; Bernard et al., 2021), often based on the assumption that many tropical species are non-migratory due to the aseasonal nature of tropical marine environments. Yet, an increasing number of studies illustrate the high variability in migratory behaviors of tropical seabirds (Catry et al., 2009; Paiva et al., 2016; Correia et al., 2024). These studies emphasize the timeliness and growing importance of studying migration in tropical species, offering insights into their ecology and improving conservation efforts.

My thesis highlights the importance of the coastal and pelagic waters off Central America for non-breeding Wedge-tailed Shearwaters from Oʻahu. Unlike many migratory seabirds that spend most of their non-breeding period in the high seas (e.g., Clay and Brooke, 2024; Medrano et al., 2024), Wedge-tailed Shearwaters spend over 75% of this period within a national Exclusive Economic Zone (EEZ). Non-breeding distributions overlapped with eight national EEZs in the ETP: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, El Salvador, Panama, and Clipperton Island (France) (Figure 1). These findings show there is potential for conservation measures within EEZs, where management actions can be more readily implemented.

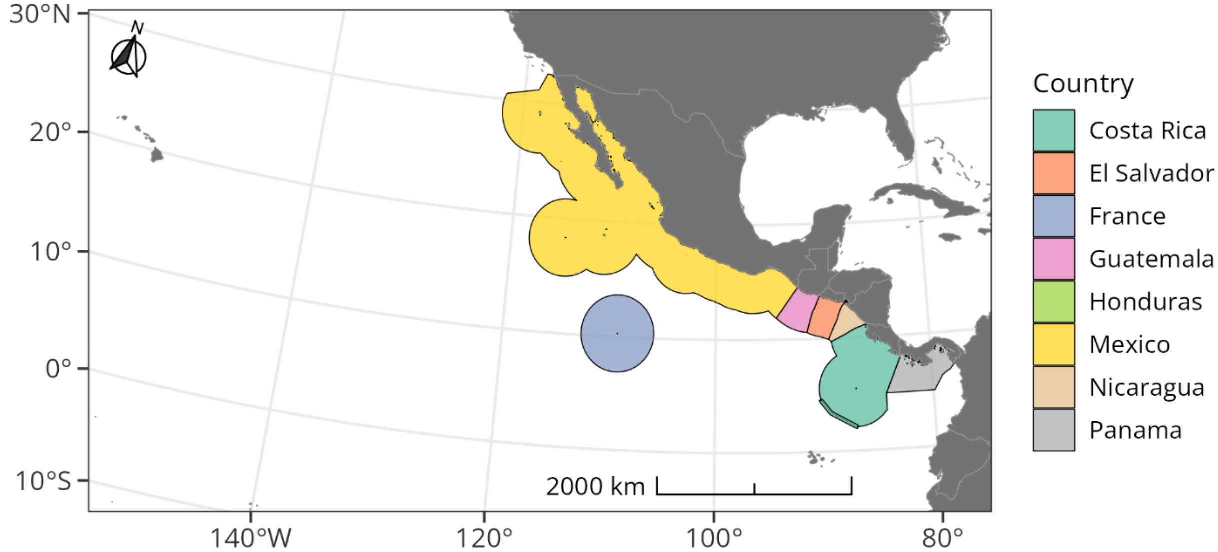


Figure 1. Map of Exclusive Economic Zones (EEZs) in the eastern tropical Pacific. Highlighted EEZs include those of Costa Rica, El Salvador, France (Clipperton Island), Guatemala, Honduras, Mexico, Nicaragua, and Panama. Honduras was included due to its jurisdiction within the Gulf of Fonseca.

International collaboration is essential for protecting large oceanic areas, including marine protected areas (MPA) that are transboundary (García-Barón et al., 2019). While the eastern tropical Pacific (ETP) includes two fully protected MPAs, the Revillagigedo National Park and the Cordillera de Coiba, the primary core area used by Wedge-tailed Shearwaters overlaps with the Pacifico Mexicano Profundo, an MPA that allows high-impact activities, including industrial fishing (Pike et al., 2024). The southeastern extent of the Wedge-tailed Shearwater non-breeding distribution overlaps with the Eastern Tropical Pacific Marine Corridor (CMAR), a regional initiative involving Costa Rica, Panama, Colombia, and Ecuador, which aims to conserve and sustainably manage biodiversity and marine resources (Enright et al., 2021). Collaborative efforts like CMAR are important for protecting this marine corridor used by sharks, sea turtles, marine mammals, and seabirds. Enhanced protection in this region would benefit Hawaiian Wedge-tailed Shearwaters, which are also regularly sighted as far south as the northwestern coast of South America (Marín, 2024).

The conservation of Wedge-tailed Shearwaters also depends on maintaining healthy tuna populations, as these seabirds rely on tuna aggregations to access prey. Stock status indicators show that fishing mortality for both Yellowfin and Skipjack Tuna has reached the highest levels since 2000, largely driven by a rise in fishing effort (IATTC, 2024). I suggest this dependency on tuna results in spatial overlap with tuna fisheries, heightening the risk of bycatch (Cortés et al., 2017; Carle et al., 2019). Mitigation measures, such as gear modifications and seasonal fishing closures, could reduce these risks (Regular et al., 2013; Sato et al., 2016; Gilman et al., 2021). Future research should prioritize quantifying this overlap between shearwaters and tuna fisheries to identify high-risk areas and guide bycatch reduction strategies in the ETP.

4.1.1 Conclusion

Wedge-tailed Shearwaters are among the many tropical seabirds that use the ETP both as residents (e.g., sabbatical non-breeders, juveniles) and as seasonal migrants (Ballance et al., 2002). My thesis provides a foundation for a comprehensive risk assessment, to inform management actions throughout the species' life cycle. Multinational collaboration will be indispensable for ensuring the long-term conservation of Hawaiian Wedge-tailed Shearwaters in the ETP. Initiatives like CMAR demonstrate the potential of regional partnerships to address transboundary conservation challenges. By identifying the species present in this region and the potential threats they face, this research provides the foundation necessary to support the development of effective and actionable management strategies. Protecting Wedge-tailed

Shearwaters in the ETP not only benefits this species but also contributes to a broader goal of maintaining a healthy marine ecosystem in this biodiversity hotspot.

4.2 References

Ballance, L. T., Pitman, R. L., Spear, L. B., and Fiedler, P. C. (2002). Investigations Into Temporal Patterns in Distribution, Abundance, and Habitat Relationships Within Seabird Communities of the Eastern Tropical Pacific. Southwest Fisheries Center, Administrative Report No. LJ-02-17. La Jolla, CA. 79 p.

Bernard, A., Rodrigues, A. S. L., Cazalis, V., and Grémillet, D. (2021). Toward a global strategy for seabird tracking. *Conserv. Lett.* 14, e12804. doi: 10.1111/conl.12804

Carle, R. D., Felis, J. J., Vega, R., Beck, J., Adams, J., López, V., et al. (2019). Overlap of Pink-footed Shearwaters and central Chilean purse-seine fisheries: Implications for bycatch risk. *The Condor* 121, duz026. doi: 10.1093/condor/duz026

Catry, T., Ramos, J., Le Corre, M., and Phillips, R. (2009). Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. *Mar. Ecol. Prog. Ser.* 391, 231–242. doi: 10.3354/meps07717

Clay, T. A., and Brooke, M. D. L. (2024). Trans-equatorial migration links oceanic frontal habitats across the Pacific Ocean: year-round movements and foraging activity of a small gadfly petrel. *Mar. Biol.* 171, 60. doi: 10.1007/s00227-023-04373-3

Correia, E., Granadeiro, J. P., Diop, N., Wambar, F., Hernandez-Rios, A., and Catry, T. (2024). High variability in the migratory behaviour of a tropical seabird. *Mar. Biol.* 171, 212. doi: 10.1007/s00227-024-04538-8

Cortés, V., Arcos, J., and González-Solís, J. (2017). Seabirds and demersal longliners in the northwestern Mediterranean: factors driving their interactions and bycatch rates. *Mar. Ecol. Prog. Ser.* 565, 1–16. doi: 10.3354/meps12026

García-Barón, I., Authier, M., Caballero, A., Vázquez, J. A., Santos, M. B., Murcia, J. L., et al. (2019). Modelling the spatial abundance of a migratory predator: A call for transboundary marine protected areas. *Divers. Distrib.* 25, 346–360. doi: 10.1111/ddi.12877

Gilman, E., Chaloupka, M., Ishizaki, A., Carnes, M., Naholowaa, H., Brady, C., et al. (2021). Tori lines mitigate seabird bycatch in a pelagic longline fishery. *Rev. Fish Biol. Fish.* 31, 653–666. doi: 10.1007/s11160-021-09659-7

IATTC (2024). Status of the Tuna and Billfish Stocks in 2022. La Jolla, CA: Inter-American Tropical Tuna Commission.

Medrano, F., Hernández-Montoya, J., Saldanha, S., Bedolla-Guzmán, Y., and González-Solís, J. (2024). Contrasting migratory ecology of two threatened and allochronic storm-petrels breeding in the Mexican Pacific. *Endanger. Species Res.* 54, 331–339. doi: 10.3354/esr01344

Mott, R., and Clarke, R. H. (2018). Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu - Austral Ornithol.* 118, 235–246. doi: 10.1080/01584197.2017.1416957

Paiva, V. H., Fagundes, A. I., Romão, V., Gouveia, C., and Ramos, J. A. (2016). Population-Scale Foraging Segregation in an Apex Predator of the North Atlantic. *PLOS ONE* 11, e0151340. doi: 10.1371/journal.pone.0151340

Pike, E. P., MacCarthy, J. M. C., Hameed, S. O., Harasta, N., Grorud-Colvert, K., Sullivan-Stack, J., et al. (2024). Ocean protection quality is lagging behind quantity: Applying a scientific framework to assess real marine protected area progress against the 30 by 30 target. *Conserv. Lett.* 17, e13020. doi: 10.1111/conl.13020

Regular, P., Montevecchi, W., Hedd, A., Robertson, G., and Wilhelm, S. (2013). Canadian fishery closures provide a large-scale test of the impact of gillnet bycatch on seabird populations. *Biol. Lett.* 9, 20130088. doi: 10.1098/rsbl.2013.0088

Sato, N., Katsumata, N., Yokota, K., Uehara, T., Fusejima, I., and Minami, H. (2016). Tori-lines with weighted branch lines reduce seabird bycatch in eastern South Pacific longline fishery. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 26, 95–107. doi: 10.1002/aqc.2492