SATELLITE TRACKING OF GALAPAGOS PETREL *PTERODROMA PHAEOPYGIA* REVEALS DISTRIBUTION AND MOVEMENTS DURING CHICK REARING

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ABSTRACT

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We tracked 19 adult Galapagos Petrels *Pterodroma phaeopygia* during the chick-rearing seasons in 2009 and 2010 (Santa Cruz Island [n = 16] and Floreana Island [n = 3]) in the Galápagos Islands, Ecuador. Eight petrels performed 27 complete foraging trips lasting 0.6 to 18.8 days. Short trips (3.2 ± 2.1 days; 785 km; max displacement 671 km) and long trips (10.8 ± 3.9 days; 2,856 km; max displacement 1,034 km) resulted in concentrated use of waters off southern and western Isabela Island and within the Galápagos Marine Reserve (GMR). Less concentrated time extended farther southwest and eastward, in that case toward mainland Ecuador. Total distance covered among all completed trips, independent of duration, was strongly correlated with trip duration (R^2 = 0.92), indicating a strategy favoring active searching and foraging over commuting. Petrels ranged across Ecuador's exclusive economic zone (EEZ), as well as other countries' (Colombia, Costa Rica, Perú), and waters beyond; they spent 46%, 27%, and 34% of their time in the GMR during short, long, and apparent (incomplete) trips, respectively. However, overlap with EEZs or marine protected areas (MPAs) does not necessarily confer protection, because commercial tuna fishing, including legal fishing historically permitted inside the GMR, occurs within these waters. Including all complete and incomplete trips, petrels spent 37% of their time in high-seas waters without formal protection, outside both MPAs and EEZs. While some hot spots overlapped Galápagos MPAs, the far-ranging nature of chick-provisioning petrels underscores the importance for this species of also having coordinated, multinational protection of the high seas.

Key words: foraging, Galápagos Marine Reserve, Galapagos Petrel, Hermandad Marine Reserve, Humboldt squid fisheries, marine protected areas, movement ecology, satellite telemetry, seabird

INTRODUCTION

The Critically Endangered Galapagos Petrel *Pterodroma phaeopygia* (IUCN Red List; Birdlife International, 2018; Cruz & Cruz, 1996), endemic to the Galápagos archipelago, Ecuador, nests exclusively in the highlands of five islands—Santa Cruz, Floreana, San Cristóbal, Isabela, and Santiago—where it is threatened by introduced predators and habitat degradation. Gadfly petrels, including the Galapagos Petrel, are far-ranging seabirds that forage broadly, mostly in pelagic waters, in search of food (Pinaud & Weimerskirch, 2007; Ventura et al., 2020). Important foraging opportunities occur when tuna and other predatory fishes and cetaceans drive petrel prey (Imber et al., 1992) to the surface (Ashmole & Ashmole, 1967; Au & Pitman, 1986; Maxwell & Morgan, 2013; Spear et al., 2007). Although stocks of skipjack *Katsuwonus pelamis* and yellowfin tuna *Thunnus albacares* in the eastern tropical Pacific (ETP) have been heavily exploited in recent decades, with extraction at historically high levels (Food and Agriculture Organization [FAO], 2024), present day skipjack stocks are considered healthy (Bi et al., 2024). At the same time, range-wide efforts are underway to understand and rebuild yellowfin tuna stocks (Muñoz-Abril et al., 2022). Nonetheless, excessive harvest of tuna and depleted stocks can potentially reduce prey availability and increase foraging effort among seabirds like petrels and terns that depend on prey driven to the surface by tuna.

Despite many previous studies informing biology and ecology of the Galapagos Petrel, there remains limited understanding of at-sea movements. Seabird distributions in the ETP have been documented through extensive ship-based surveys (Joyce, 2016; Pitman, 1986; Spear et al., 1995, 2007). These surveys effectively mapped the ranges of "Dark-rumped Petrels" (*P. phaeopygia* and Hawaiian Petrel *P. sandwichensis*) within the ETP (Joyce, 2016; Pitman, 1986; Spear et al., 1995, 2007). Ship-based records, however, could not differentiate birds of undetermined age, breeding status, and natal colony.

Whereas conservation strategies have focused primarily on terrestrial threats, a better understanding of the petrels' at-sea distribution can help quantify the extent to which petrels overlap with marine zones with differing jurisdictional responsibilities for ecosystem management and conservation (Beal et al., 2012; Marra et al., 2011). At the largest scale, tuna fishing in the ETP surrounding the Galápagos Islands is regulated and managed by the Inter-American Tropical Tuna Commission (IATTC) and is legally permitted in South American exclusive economic zones (EEZs). Overlap between petrels and designated marine zones may inform potential conflicts between seabird foraging and both legal and illegal fishing activity and help identify entities with authority to manage both. At a more local scale, existing marine protected areas (MPAs) may provide meaningful protection. Although these reserves, including the Galápagos Marine Reserve (GMR), prohibit industrial longline and purse-seine fishing, certain forms of tuna fishing have historically been permitted (Castrejón & Defeo, 2025), meaning that overlap with MPA boundaries, alone, does not necessarily indicate full protection for petrels. Marine zoning within the national reserves (allowable fishing vs. no-take zones) is complex, and reconfigurations of management areas within the large bounding areas are in process, in part using best available science (Castrejón & Defeo, 2025; Castrejón et al., 2024).

This study leverages satellite telemetry to track Galapagos Petrels during the chick-rearing period, marking the first application of this method to better understand and quantify the species' ranging behavior. Here, we focus specifically on chick-provisioning adults to provide insights into breeding-season ranging patterns at sea. Our primary goal was to determine the degree to which Galapagos Petrels used multinational waters (EEZs and the high seas), the GMR, and the recently formed Hermandad Marine Reserve (HMR). The reserves prohibit industrial longline and purse-seine fishing, but allowances for other local tuna fisheries remain—although under discussion (Castrejón & Defeo, 2025)—meaning protection for petrels is incomplete. We also sought to identify key foraging areas that can be evaluated in the future to help identify and address additional potential threats at sea. Importantly, these new results complement ongoing research in the Galápagos highlighting multispecies interactions with fisheries (Awkerman et al., 2006; Castrejón & Defeo, 2024, 2025; Montecalvo et al., 2023), the risks posed by plastic pollution to seabird populations in the region (Clark et al., 2023), efficacy of spatial overlaps with MPAs (Gilmour et al., 2025), and international jurisdictional responsibilities associated with EEZs and the high seas (Beal et al., 2021).

Understanding the spatial distribution of seabirds like the Galapagos Petrel is increasingly important because marine ecosystems face mounting pressures from direct human activities (e.g., industrial fishing) and atmospheric loading of greenhouse gases that contribute in part to stochastic variability in marine climate and ecosystem function (Dias et al., 2019; Gilmour et al., 2025). This research is particularly timely considering recent global efforts to expand and effectively manage large MPAs (Sala et al., 2021). Our study also complements ship-based surveys, which log birds of unknown provenance, by providing more fine-scale, individual-based telemetry quantifying how chick-provisioning adults from known colonies use at-sea habitats.

STUDY AREA AND METHODS

Study sites and marine protected areas

During 2009 and 2010, we studied petrels at two breeding colonies: Media Luna Crater on Santa Cruz Island (00.650°S, 090.342°W) and Cerro Pajas on Floreana Island (01.295°S, 090.456°W) within the Galápagos Islands, Ecuador (Fig. 1). This study was permitted by the Galápagos National Park Authority, which manages both colony sites and conducts annual predator control and vegetation management.

In 1998, Ecuador created the Galápagos Marine Reserve (GMR) about 1,000 km west of Ecuador's coast (Fig. 1). The large (138,000 km^2) reserve was established to protect waters within 40 nautical miles (74 km) of the Galápagos Islands from large-scale industrial fisheries. In 2022, to better protect key migratory routes used by marine wildlife and to further limit the extent of impactful illegal fishing, reserve waters were expanded through creation of the Hermandad Marine Reserve (HMR). The latter added ~60,000 km^2 northwest of the archipelago, extending beyond the original 40-nautical-miles boundary of the GMR, to close part of the high-seas gap toward Costa Rica (Acuerdo Ministerial No. MAATE-2022-039, 2022). The combined contiguous MPA constitutes a total protected area of 202,819 km^2, making it one of the largest zones of its kind in the world (Fig. 1). Legal tuna fisheries operating within the GMR increased after 1998, when electrification of the islands allowed freezers to be used to support an increasing residential and tourist economy (Castrejón & Defeo, 2024). Although much smaller in scale (total catch) compared with larger external fisheries that operated before the GMR, it is unknown whether increasing local tuna harvests may indirectly affect petrels by reducing prey availability to the birds.

Satellite telemetry

To determine active burrows with chicks, we monitored Galapagos Petrel nests for breeding activity three weeks prior to satellite tag deployments. We captured adult, chick-provisioning petrels by hand or by a small net bag covering the burrow entrance and outfitted with a one-way flap door. In that way, we prevented the exiting bird from returning to its inaccessible nesting chamber. We deployed platform transmitter terminals (PTTs; Solar 12 g PTT; Microwave Telemetry, Inc.; Columbia, Maryland, USA) on 19 adult petrels: 12 in August through November 2009 (Santa Cruz Island) and seven in August through September 2010 (four on Santa Cruz Island, three on Floreana Island). Each PTT weighed approximately 2.9% of the median adult petrel mass (410 g; Brooke, 2004). We attached PTTs using the suture-tape-glue method following MacLeod et al. (2008) and Raine et al. (2020). Specifically, we placed a 1-cm-wide strip of cloth tape (Tesa 4655, Charlotte, North Carolina, USA) sticky-side up under approximately four contour interscapular feathers and wrapped this over itself. This created a tape tab to glue (LOCTITE 422, Henkel Corporation, Bridgewater, New Jersey, USA) to the base of the PTT. The base of the PTT was secured to skin using four subcutaneous surgical sutures (2-0 monofilament polydioxanone synthetic absorbable suture; Mono-Dox; CP Medical, Inc.; Portland, Oregon, USA). The absorbable sutures used in this study minimize the expected maximum attachment duration (~45 days) compared with non-absorbable polypropylene sutures (> 100 days) used in other studies (Adams et al., 2012; Adams, 2013–2014; Felis et al., 2019). We attempted to remove PTTs and sutures by recapturing birds (n = 9) at their burrows after they completed trips at sea and before the end of the chick-rearing period; we observed no external effects among birds when PTTs were removed. For the remaining birds that were not recaptured (n = 10), we assumed that tags were lost at sea after absorbable suture attachments failed, consistent with other tracking studies of petrels and shearwaters using similar Microwave Telemetry, Inc. solar PTTs (Felis et al., 2019; Raine et al., 2020). All procedures followed ethical guidelines for animal care and were approved by the Galápagos National Park and corresponding institutional review boards (permit PNG No. PC-16-08).

Data collection and filtering

We retrieved location data from the Argos satellite system (CLS America), which provided a set of locations with associated location classes (LC 3, 2, 1, 0, A, B, and Z). We evaluated all available locations for each tracked individual and applied a filtering process to remove inaccurate points. Specifically, locations were excluded

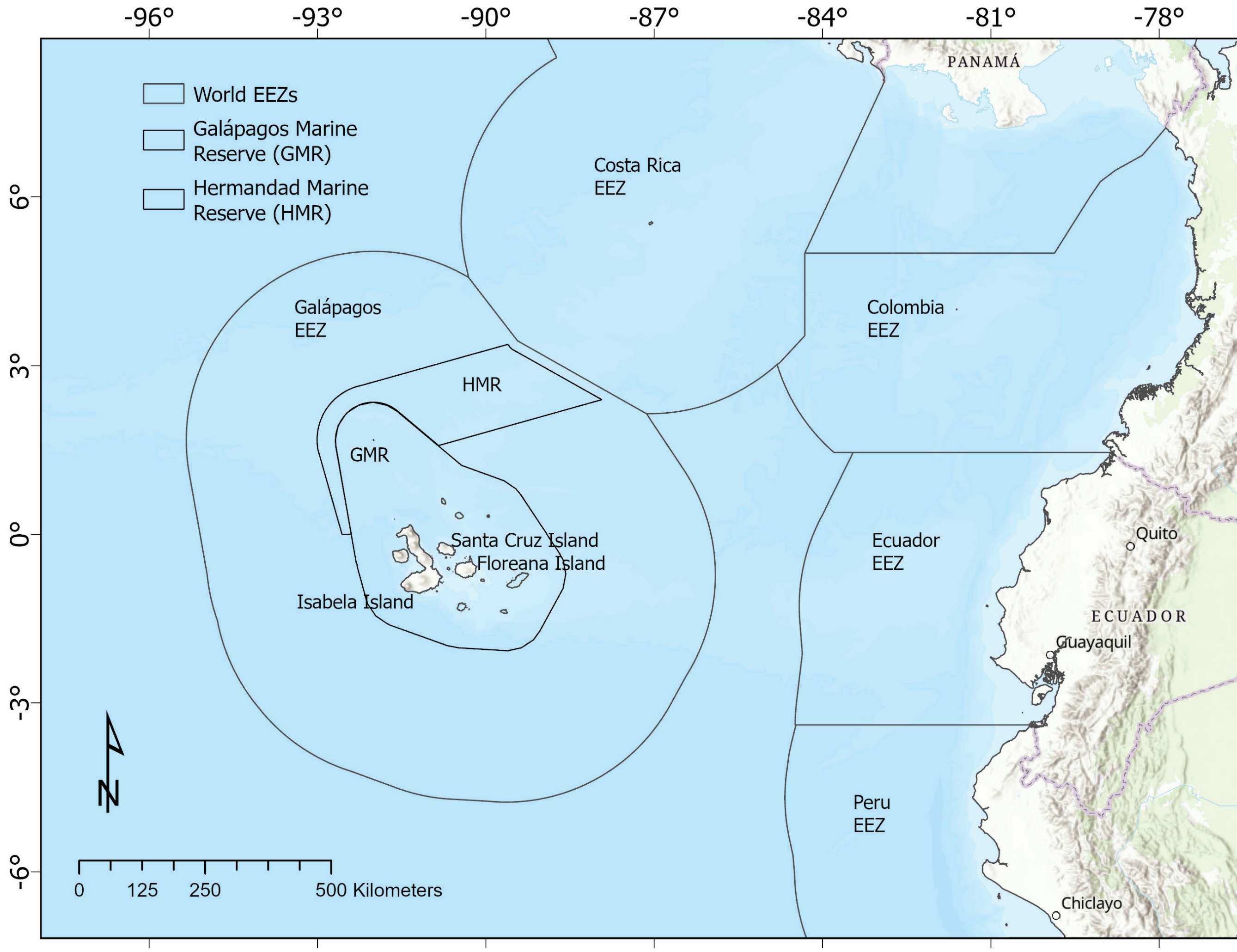

Fig. 1. Galápagos Islands study area in the eastern tropical Pacific Ocean showing locations of study colonies on Santa Cruz and Floreana Islands. Boundaries indicate the Galápagos Marine Reserve (GMR), Hermandad Marine Reserve (HMR), and various exclusive economic zones (EEZs). Basemap service layer credits: Esri, TomTom, Garmin, FAO, NOAA, USGS

when estimated travel speed between two consecutive points exceeded 100 km/h, a threshold slightly greater than the maximum ground speed estimated for a Desertas Petrel *P. deserta* flying with strong, quartering tail winds (~80 km/h; Ventura et al., 2020) and a value greater than the mean +1 standard error allometric prediction for ground speed among large gadfly petrels flying with a 10-m/s tailwind (71 km/h; see Table 2 in Spear & Ainley, 1997). Additionally, we removed locations over land, except near colony deployment sites. To account for errors in the Argos location data and provide the most accurate representation of bird movements, we used a continuous-time state-space model (SSM) implemented in the R statistical software environment (Version 4.5.1) using the package "aniMotum" (Jonsen et al., 2023). The SSM combined a movement process model with a measurement error model to estimate the true locations of the birds by considering the uncertainty in the raw Argos data. Only sequential locations with a time gap < 24 hr were included in the SSM analysis to ensure robust path reconstruction. We applied the SSM to interpolate locations every 2 hr along continuous tracks for each foraging trip. These filtering steps ensured only high-quality location data were retained for tracks and provided a uniform time spacing for locations for quantification of time spent per area (MPAs, EEZs, and the high seas).

Foraging trips and trip types

We defined complete foraging trips as those in which an individual left the colony for > 12 hr before returning. Trips with fewer than six high-quality location points and all locations along tracklines of petrels that did not show a start and end at their colony (e.g., cases where trip segments ended at sea without returning to the colony) were deemed "incomplete"; these were mapped but excluded from trip-specific analysis. Using data for departure and arrival times at the colony and based on the median value for complete trip durations (7.1 days), we classified three trip types. Complete short trips were < 7.1 days; complete long trips were ≥ 7.1 days. For each complete trip, we calculated (1) total distance traveled as the cumulative distance traveled (km) over the entire trip; (2) the maximum straight-line distance (km) from the colony; (3) trip duration (total time [days] spent away from the colony); and (4) travel speed (km/day), calculated as the slope of the linear regression of duration (days) vs. cumulative distance (km) traveled per complete trip. The third set of trips, based on visual examination and considering starting and ending locations near the Galápagos Islands, was classified as an "apparent" trip type. The apparent trips were those in which absolute departure or arrival at the colony could not be confirmed, thus preventing us from computing accurate duration and distance traveled and from classifying them as either short or long type.

International exclusive economic zones and marine protected area use

To quantify petrel use of EEZs and the international high seas, we overlaid short, long, and apparent tracks with polygon boundaries (Flanders Marine Institute, 2024) in ArcGIS Pro (Version 3.3.2; Esri, 2024) and calculated the percentage of total time spent by petrels during the three trip types. Ecuador's EEZ is composed of two discrete areas separated by the high seas: (1) a 200-nautical-mile (370 km) boundary surrounding the Galápagos Islands, containing the MPAs, and (2) the zone 200 nautical miles out to sea from mainland Ecuador. Similarly, to quantify petrels' use of broad MPAs, we overlaid tracks with the boundaries of the GMR and HMR (United Nations Environment Programme World Conservation Monitoring Centre [UNEP-WCMC], 2025a, 2025b) and calculated the percentage of total time spent in these reserves according to trip type.

Heat maps of area use

Using the predicted locations from the SSM, we created heat maps to visualize the spatiotemporal intensity of petrel area use. We used the kernel density tool in ArcGIS Pro 3.3.2—with default parameters based on the spatial extent of petrel locations for each trip type, following the quartic kernel function described in Silverman (1986)—to highlight and compare areas most intensively used by individuals during each of the three trip types. These maps were used to identify trip-type-specific important at-sea habitat areas and to compare the overlap of most intensively used areas with the EEZs and existing MPAs.

RESULTS

Foraging range, speed, duration, and time spent in marine zones

We recorded a total of 52 foraging trips from 19 Galapagos Petrels during the chick-rearing periods in 2009 and 2010 (Table 1). Provisioning Galapagos Petrels nesting on Santa Cruz and Floreana Islands utilized a foraging area encompassing approximately 1.4 million km², bounded by 81°E to 102°E and 2°N to 10°S. We classified 27 trips (eight individuals) as "complete", with uninterrupted data to quantify total trip duration, total distance traveled, and maximum displacement from the colony (Table 1). Among complete trips, six petrels completed 18 short trips, and five petrels completed nine long trips (Table 1, Fig. 2). We classified an additional 10 trips (nine individuals) as "apparent" (Table 1, Fig. 2). The remaining 15 trips were "incomplete" (Table 1, Fig. 2).

Eight petrels with 27 complete foraging trips exhibited trips lasting 0.6 to 18.8 days. Short trips lasted 3.2 ± 2.1 days, covering a cumulative distance of 784.9 ± 602.6 km (maximum distance from colony = 670.6 km); long trips lasted 10.8 ± 3.9 days, covering a cumulative distance of 2,855.5 ± 664.9 km (maximum distance

TABLE 1
Summary of Galapagos Petrel satellite tracking during the chick-rearing seasons 2009 and 2010

Petrel ID	Island	Start date	End date	Tracking duration (days)	No. of trips (short, long, apparent, incomplete)
41646a	Santa Cruz	25 August 2009	5 September 2009	10.9	(0, 0, 0, 1)
41646b	Santa Cruz	25 September 2009	4 October 2009	9.2	(0, 0, 0, 1)
41680a	Santa Cruz	24 August 2009	5 September 2009	11.9	(0, 0, 1, 2)
41680b	Santa Cruz	24 September 2009	4 November 2009	40.8	(0, 0, 0, 1)
68019a	Santa Cruz	24 August 2009	8 September 2009	14.8	(0, 0, 0, 1)
68021a	Santa Cruz	24 August 2009	8 September 2009	15.0	(2, 0, 1, 0)
68021b	Santa Cruz	13 August 2010	22 September 2010	40.3	(0, 0, 0, 1)
68022a	Santa Cruz	24 August 2009	9 September 2009	15.7	(0, 0, 1, 0)
94659a	Santa Cruz	4 September 2009	16 September 2009	12.1	(0, 0, 1, 0)
94659b	Santa Cruz	25 August 2010	5 October 2010	40.7	(0, 4, 0, 1)
94660a	Santa Cruz	20 September 2009	19 October 2009	28.8	(0, 0, 0, 1)
94661a	Santa Cruz	19 September 2009	8 October 2009	18.6	(1, 1, 0, 1)
94661b	Santa Cruz	25 August 2010	7 September 2010	13.0	(0, 0, 1, 0)
94662a	Santa Cruz	24 September 2009	26 October 2009	32.3	(0, 1, 1, 1)
94663a	Santa Cruz	20 September 2009	8 October 2009	17.7	(0, 0, 1, 0)
94663b	Santa Cruz	25 August 2010	2 October 2010	38.7	(2, 1, 2, 1)
41646c	Floreana	12 August 2010	14 September 2010	33.3	(2, 2, 0, 1)
68019b	Floreana	13 August 2010	18 September 2010	36.5	(9, 0, 0, 1)
68022b	Floreana	13 August 2010	24 September 2010	41.6	(2, 0, 1, 1)

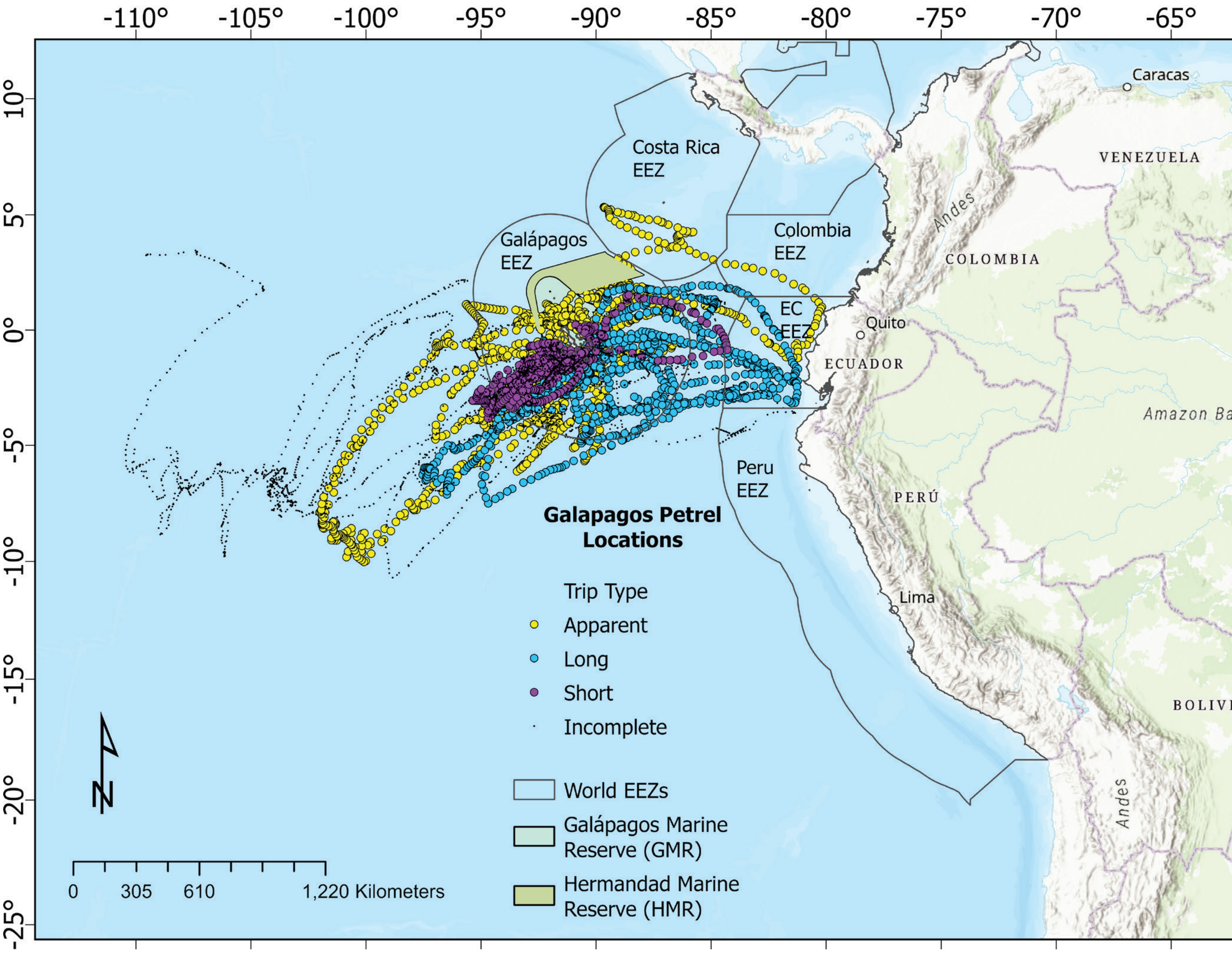

Fig. 2. Locations of Galapagos Petrels (every 2 hr, filtered and interpolated) showing three trip types: short (purple dots), long (blue dots), and apparent (yellow dots). Locations from incomplete trips are indicated by smaller black dots. Boundaries indicate the Galápagos Marine Reserve (GMR), Hermandad Marine Reserve (HMR), and various exclusive economic zones (EEZs). Basemap service layer credits: Esri, TomTom, Garmin, FAO, NOAA, USGS

from colony = 1,034.0 km). Among both complete trip types (short and long), total cumulative distance was highly correlated with trip duration (R^2 = 0.92, slope = 246 km/d; Fig. 3). Short trips resulted in concentrated time spent off the southern coast of Isabela Island and within the GMR, with little time spent in other areas (Fig. 4A). During long trips, petrels also spent concentrated time within the GMR, to the west of Isabela Island and within the waters surrounding the southern-most Galápagos Islands (Fig. 4B). However, long trips involved more far-ranging time at sea within mainland Ecuador's EEZ and toward the southwest, beyond the Galápagos territorial EEZ (Fig. 4B). "Apparent" trips resembled a combination of short and long trip area use (Fig. 2) and revealed similar hot spot use to both short and long trips. Overall, however, these were more widely dispersed and included slightly more concentrated area use within the GMR to the north of Isabella Island and toward the southwest, within the Galápagos EEZ (Fig. 4C).

Petrels spent time in four international EEZ territories: those of Ecuador (Galápagos and Ecuadorian mainland zones, together), Costa Rica, Columbia, and Perú. Eighty three percent (83%) of short trips occurred within Ecuador's EEZ, with 17% extending farther to sea. Long trips were spent in two EEZs—Ecuador's (76%) and Colombia's (1%)—and 23% were within the high seas. Petrels with apparent trips spent time in three EEZ territories—Ecuador's (71%), Costa Rica's (4%), and Colombia's (1%)—and 24% of apparent trips were within the high seas. Only one petrel (41646b) spent time in the northern-most part of Perú's EEZ (< 4 days; Fig. 2). During short, long, and apparent trips, petrels spent 46%, 27%, and 34% of their time in the GMR, respectively; only four petrels from Santa Cruz Island used the HMR during apparent and incomplete track segments (< 1% of the total time among petrels at sea). Including "incomplete" trips, petrels spent 37% of their time ranging throughout high-seas waters, with no formal protections outside MPAs and EEZs.

DISCUSSION

Galapagos Petrels provisioning chicks on Santa Cruz and Floreana Islands undertook foraging trips throughout a large area of the ETP, consistent with previous descriptions of their at-sea range as determined by at-sea surveys from ships. The total area used by tracked birds provisioning chicks, however, included < 20% of their

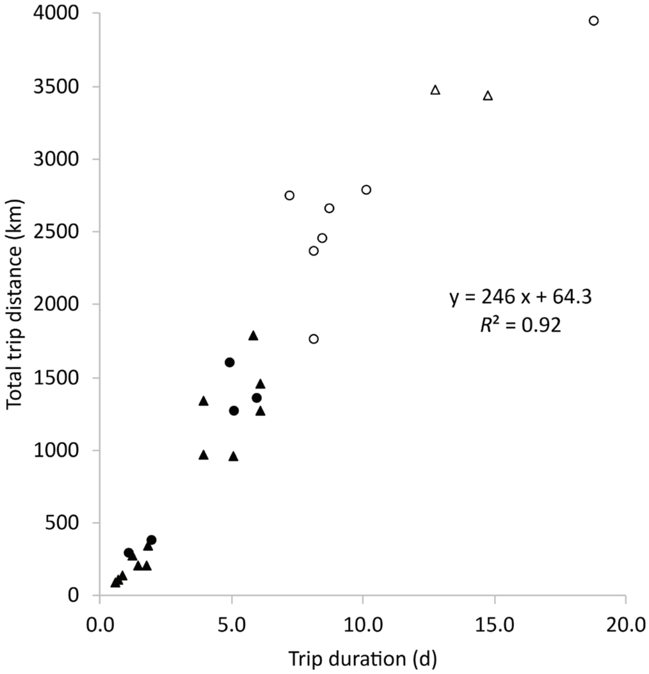

Fig. 3. Linear relationship between complete trip duration and total distance covered for petrels from Santa Cruz (circles) and Floreana (triangles) Islands. Short trips (< 7.1 days, filled symbols), long trips (≥ 7.1 days, hollow symbols).

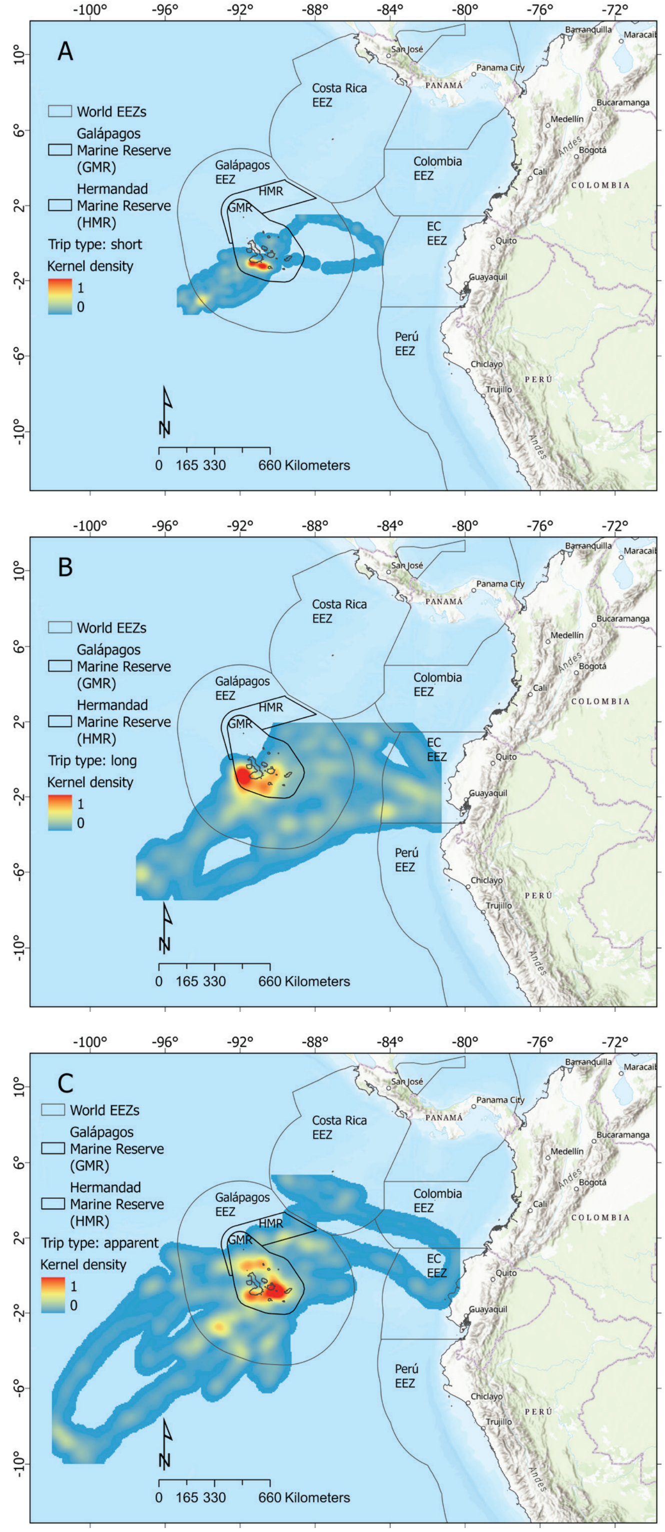

Fig. 4. Heat maps of Galapagos Petrel location kernel densities for chick-rearing adults during short (A), long (B), and apparent (C) trip types. Boundaries indicate the Galápagos Marine Reserve (GMR), Hermandad Marine Reserve (HMR), and various exclusive economic zones (EEZs). Basemap service layer credits: Esri, TomTom, Garmin, FAO, NOAA, USGS

previously described range at sea in the ETP (~7.8 million km^2; Joyce, 2016). During ship surveys (Pitman, 1986; Spear et al., 1995; Joyce, 2016), the subtle difference in plumage that can be used to discriminate between the two sister species of "Dark-rumped Petrel"—Hawaiian Petrel and Galapagos Petrel (Force et al., 2007; Pyle et al., 2011)—prohibited identification to species (Spear et al., 1995). Therefore, these authors differentiated among species after surveys based on the distinct gap in at-sea sightings now known to exist: Hawaiian Petrels west of 130°W and Galapagos Petrels east of 130°W (Joyce, 2016; see summary in Howell & Zufelt, 2019). Considering this information, our results from a small sample of tracked individuals from the two colonies were consistent with the patterns exhibited in extensive ship surveys and revealed that the distribution of central-place-foraging, chick-feeding birds was more constrained than the species' full range, which also included subadults and non-breeders.

The use of solar PTTs to track petrels near the equator surrounding the Galápagos was made difficult in 2009 through 2010 by persistent cloud cover and precipitation associated with the climate condition known locally as the garúa season. The solar PTTs in this study were small and relatively lightweight; insufficient solar charging at sea contributed to extended gaps in sequent locations, making it difficult in some cases to accurately confirm individual trip starting and ending times. As a result, we could not confirm "apparent" trips to be complete and, therefore, treated these separately. However, apparent trips were consistent with the patterns in foraging range and at-sea area use revealed by petrels on complete short and long trips. The high correlation of trip duration with total distance covered (R^2 = 0.92; Fig. 3) during complete foraging trips indicates low variability in traveling speeds among individuals, reflecting a strategy that favors searching compared with one involving rapid, directed transit to a known, distant foraging area (i.e., similar regression with duration and maximum distance had a much lower R^2 = 0.52, not shown). Although we discriminated between short and long trip types based on a median duration of 7.1 days, the scatter plot describing distance covered includes the full range of trip durations (Fig. 3) and indicates a distinct short-trip mode (< 3 days and < 400 km). However, the cluster of shortest trips (< 2 days) consisted of only two petrels from Floreana (41646c and 68019b; Table 1) and one petrel from Santa Cruz (68021a; Table 1).

Among gadfly petrels, there is variation in the short versus long trip pattern. Sometimes referred to as a dual foraging strategy, this pattern has been documented more broadly among Procellariiformes. First described in Blue Petrels *Halobaena caerulea* (Chaurand & Weimerskirch, 1994) and Snowy Albatross *Diomedea exulans* (Weimerskirch et al., 1993), the dual foraging strategy appears to maximize fresh food delivery rates to chicks (short trips) while minimizing intraspecific competition within the colony "foraging halo". However, provisioning adults need long trips to replenish their own depleted resources (Baduini & Hyrenbach, 2003; Charaund & Wiemerskirch, 1994; Phillips et al., 2023; Weimerskirch & Cherel, 1998) and to distill and deliver energy-dense stomach oil to compensate for the chick's relatively prolonged fast during extended parental absences during the provisioning period (Simons & Whittow, 1984; Warham et al., 1976). Other gadfly petrels also exhibit this strategy while raising their chicks (see Halpin et al., 2022; Pinet et al., 2012; Ventura et al., 2020). The pronounced cluster among the shortest trips by Galapagos Petrels (0.6 to 1.9 days; Fig. 3) was consistent with short trips described for the Black-winged Petrel *P. nigripennis*, White-necked Petrel *P. cervicalis* (Halpin et al., 2022), and Desertas Petrel (Ventura et al., 2020). Another cluster of trip durations (3.9 to 6.1 days; Fig. 3) was more dispersed and could represent a medium duration strategy. Although our study could not conclusively determine whether Galapagos Petrels employed the dual foraging trip strategy, the patterns were consistent with those of other species, indicating that a dual foraging framework may also apply to *P. phaeopygia*.

The Galapagos Petrel's annual breeding phenology varies among different island colonies. On Santa Cruz Island, hatching and chick provisioning begin in early August, whereas on Floreana, chick rearing begins during late February (Cruz & Cruz, 1990). Our tracking during August to September in both years would have included younger chicks at Santa Cruz compared with older chicks at Floreana. While our sample size was comparatively smaller at Floreana than Santa Cruz, this asynchrony in tracking during late- and early-chick stages, respectively, may contribute to variability in our overall observations. While individuals from Floreana did perform two long trips, most complete trips were short (< 7 days) and very short (< 2 days; Fig. 3), possibly indicating more frequent deliveries and reliance on fresh food sourced from closer foraging areas later in the chick rearing period among petrels at Floreana. This appears to contrast with the observation by Imber et al. (1992), who reported greatest feeding rates among younger chicks raised on Floreana, with the caveat that feeding rates later in the chick season may be underestimated. We suspect that there exists additional individual and intercolony variability in foraging distance and duration. More information about nest attendance among parent birds during the provisioning period (see Simons, 1985) and additional fine-scale tracking would help discern the predominant patterns and allow a more refined definition of functional trip types (i.e., short vs. long) in Galapagos Petrels.

The prevailing south to southeasterly winds around the Galápagos likely influenced the overall southwestward/northeastward foraging routes of Galapagos Petrels, allowing them to optimize flight efficiency with crossing winds (Adams & Flora, 2010; Spear & Ainley, 1997; Ventura et al., 2020). These routes also overlap with productive tuna grounds, particularly to the southwest of the archipelago and along the equatorial upwelling zone (Ballance et al., 1997). Although rarely seen foraging in association with tunas (e.g., yellowfin; Spear et al., 2007), Galapagos Petrels are believed to feed nocturnally (Imber et al., 1992) and exploit, to some degree, prey driven to the surface by subsurface predators such as tuna (Au & Pitman, 1986; Ballance et al., 1997; Spear et al., 2007). While this association indicates that tuna schools are perhaps an important facilitator of foraging opportunities during the day, petrels also likely forage opportunistically on prey unrelated to tuna schools and available near the surface at night (Imber et al., 1992). Therefore, wind patterns and tuna distributions, together, likely influence foraging routes, while allowing Galapagos Petrels some degree of foraging flexibility.

The relatively infrequent, more distant eastward trips toward the Ecuadorian coast (Fig. 2) are interesting in comparison with similar ranging strategies of Waved Albatross *Phoebastria irrorata* breeding in the Galápagos Islands. Eastward trips toward Ecuador among tagged petrels contrast with the ranging strategies of Waved Albatross that tend to embark on more southeastern journeys to target highly productive waters off northern Perú. Although Galapagos Petrels can travel similar distances from their colonies to Waved Albatross (approximately 1,300 to 1,500 km; Awkerman et al., 2014), the petrels' dynamic-soaring flight style relies more on crossing and quartering tailwinds (Adams & Flora, 2010; Spear et al., 1997; Ventura et al., 2020), whereas the heavier-bodied albatross are more adapted to flying into headwinds (Suryan et al., 2008). Under persistent southeasterly winds, the productive waters off Perú may be energetically less accessible or unavailable to provisioning Galapagos Petrels, which also forage more in association with generally less productive waters farther offshore. However, Spear and Ainley (2008) recorded infrequent sightings of "Dark-rumped Petrels" of unknown age and breeding status during November to January in oceanic waters bordering the outer edge of the Humboldt Current off Perú (3°S to 50°S, and to 370 km offshore) and it is possible these sightings consisted of non-breeding Galapagos Petrels (see Howell & Zufelt, 2019).

Based on at-sea surveys, Galapagos Petrels appeared to be more abundant during March through June than October through December and distributed broadly throughout the ETP (Joyce, 2016; Pitman, 1986; Spear et al., 1995; summarized in Howell & Zufelt, 2019). Within the ETP off South America, data from ship surveys indicated that Galapagos Petrels were associated with relatively lower sea-surface temperatures, greater sea-surface salinities, shallower thermoclines, increased wind speeds, and greater wave heights (Spear et al., 1995). Hayes and Baker (1989) conducted boat-based transects during June–July throughout the interior island waters of the archipelago and found relatively greater numbers of Galapagos Petrels especially between Isabela and Santa Cruz islands, although the authors did not report any behaviors. Spear et al. (1995) observed the greatest densities of Galapagos Petrels near the islands, as did Pitman (1986), with greatest densities at wind speeds between 35 and 45 km/h, and with a second increase in density ~1,300 km from the islands.

Our tracking coincided with the transition from near-neutral El Niño Southern Oscillation (ENSO) conditions during July 2009 to a strong La Niña phase for the remainder of the study period (JRA-3Q reanalysis; May 2010 through March 2012; Kosaka et al., 2024). This interannual variability may have affected the distribution of tracked petrels. During strong La Niña events, the topographically induced upwelling associated with a stronger and shallower Equatorial Counter Current expands and enriches the Galápagos Plume area of enriched surface chlorophyll concentration with especially pronounced elevated primary productivity off the southern and western coast of Isabela during July through September (Palacios, 2004; Palacios et al., 2006). We found this area to be important for petrels during all trip types (Fig. 4). It is also a known hot spot for numerous cetaceans (Palacios & Cantor, 2023) and part of a broader pattern in which seabird community structure and distributions in the eastern tropical Pacific are closely linked to productivity gradients that influence tuna-associated foraging (Ballance et al., 1997; Ribic et al., 1997). Under the right conditions, the Galápagos Plume area may serve as an important multi-predator foraging ground that includes resident breeding Galapagos Petrels.

Petrels from both Santa Cruz and Floreana Islands frequently ranged outside the boundaries of the GMR and HMR, with 37% of their time at sea spent in unprotected waters outside the international EEZs. While birds foraging from both colonies used the GMR, there was only limited use of the HMR by birds from Santa Cruz Island and no use by birds from Floreana Island.

The most important foraging areas among Galapagos Petrels, illustrated by mapping concentrated hot spots at sea, were partially contained within Ecuadorian EEZs and the GMR, where birds spent 72%–83% and 27%–46% of their time, respectively, depending on trip type (Fig. 4). However, birds also spent significant time beyond these MPA zones, both toward mainland Ecuador and > 1,000 km to the southwest within international high seas (37% of total time). Commercial tuna fishing (managed in part by IATTC) and other activities are legally permitted in South American EEZs, including Ecuador, and overlap with EEZs does not necessarily imply protection for petrels. Instead, these results highlight potential zones of overlap between chick-provisioning seabirds and fisheries, underscoring the need for informed regulation and multinational cooperation to ensure adequate protection (Beal et al., 2021).

Although this study included a larger sample of individuals from Santa Cruz Island, a more thorough evaluation of the ranging patterns among petrels from Floreana Island would provide much needed information useful for evaluating island-specific foraging behaviors. For example, the large degree of individual variation, small sample size at Floreana (e.g., only one of three petrels completed two long trips), and overall, relatively short tracking duration (25 ± 12 days) prevent robust interisland comparisons. More data including more complete trips, perhaps using GPS tracking data, would help to identify these patterns. Furthermore, similar to recent study of other gadfly petrels, additional tracking during non-breeding periods (Clay & Brooke, 2024; Ramos et al., 2017), perhaps including fledged chicks (Raine et al., 2023), would contribute toward a better understanding of non-breeding season and early life history stage habitat use at sea, respectively.

Conservation implications

Compared with previous delineations of the species' range at sea from vessel surveys, our tracking results identified a more constrained foraging area consisting of short and long trips. During short trips, adult chick-provisioning petrels concentrated their use of waters off southern and western Isabela Island and in the GMR. In contrast, during long trips, overall distribution was more diffuse, extending widely into the outer continental EEZ and high-seas waters. These distinctions are crucial for evaluating conservation strategies, because while enhanced protection of localized hot spots within the GMR (Castrejón et al., 2024) may predominately benefit chick-provisioning adults, international cooperation would be needed to mitigate risks during long-range foraging. Furthermore, petrel spatial data also offer a roadmap for quantifying MPA efficacy and can inform future improvements through data-driven spatial planning (Gilmour et al., 2025). Although current MPA boundaries may not fully contain the spatial needs of wide-ranging pelagic species like the Galapagos Petrel, marine reserves could be re-evaluated and expanded to cover important foraging grounds based on new and increasing ecological data (Castrejón et al., 2024).

Our results also indicate unresolved threats exist at sea, including overlap and exposure to interactions with international fishing fleets in the high seas (Montevecchi, 2023; Montecalvo et al., 2023; Seco Pon et al., 2015). For example, one of the world's largest and expanding fisheries, targeting Humboldt squid *Dosidicus gigas* (Seto et al., 2023), operates extensively within the east equatorial high seas, occasionally illegally within the Peruvian and Ecuadorian EEZs, and—at times—immediately within and adjacent to the southern boundary of the Galápagos (Ecuador) EEZ (Torchia, 2020; Torrico, 2021). Although direct evidence of Galapagos Petrels attending squid vessels or being taken as bycatch is lacking, the scale of these operations near the southern border of the Galápagos EEZ and overlapping with the petrels' ranging movements highlights a potential risk that warrants further investigation. Vessels in this multinational fishery are mostly foreign-registered and use multiple jigging lines to fish at night, aided by bright lights (Rodhouse et al., 2001). The fleet consists of hundreds to thousands of aggregated vessels that create a massive nocturnal light field (i.e., comparable with that of the city of Lima, Perú, population 10.3 million people). It is one of the brightest marine light sources in the world, clearly visible using space-based satellite sensors (Paulino et al., 2017; Waluda & Rodhouse, 2005; Waluda et al., 2006). Industrial vessels concentrate and form dense, persistent (e.g., 13 July to 13 August 2020) lighted areas at sea on the southwestern Galápagos EEZ boundary and within the petrels' moderately high-use areas (Fig. 4 heat maps; see Fig. 1 in Oceana, 2020). Although illegal squid fishing practices on the Galápagos EEZ boundary between 2020 and 2022 led to a US Coast Guard intervention at sea (Goodman, 2022) and US and Ecuadorian condemnation of certain fishing practices carried out by the Chinese distant-water fishing (DWF) squid fleet (Simmons & Saravia, 2023), the high-seas DWF operates extremely far from land. There is very little information about operational interactions with seabirds. Although the risk of seabird bycatch in similar lighted jigging fisheries off Argentina has been thought to be low (Reid et al., 2021), the massive scale of the lighted squid fisheries in the southeastern Pacific and lack of independent fisheries observations in this region preclude comprehensive evaluation of risks to far-ranging pelagic seabirds like Galapagos Petrels that are nocturnally active and among the group of seabirds most susceptible to the effects of artificial light pollution (Rodríguez et al., 2019). Light attraction and disorientation are well documented on land (Reed et al., 1985; Rodríguez et al., 2015; Troy et al., 2013) and at sea where seabirds interact with marine vessels (Ryan et al., 2021) and offshore oil platforms (Montevecchi, 2006; Ronconi et al., 2015). While the Humboldt squid fishery is economically important for Perú and Ecuador, it faces challenges from illegal, unreported, and unregulated fishing and fishing effort modulated by climate variability (Wen et al., 2024). Long-term conservation of endangered Galapagos Petrels, which may overlap at times with lighted squid fisheries, could be best achieved through strong regional cooperation (e.g., Ecuador and Perú), enhanced monitoring and enforcement, and science-based policies that can help ensure long-term population viability (Beal et al., 2021; Montecalvo et al., 2023; Rodríguez et al., 2019; Votier et al., 2023).

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AUTHOR CONTRIBUTIONS

CP: Conceptualization, methodology, investigation, data curation, analysis, writing—original draft preparation, final revision, validation, editorial reconciliation. SC: Investigation, writing—review & editing, analysis, data visualization. JA: Investigation, methodology, software resources, data visualization, writing—review & editing, final revision, validation, editorial reconciliation. MW: Conceptualization, funding acquisition, investigation, project administration, resources, supervision, draft revision.

AVAILABILITY OF SUPPORTING DATA

The dataset supporting the results of this study is accessible at the Movebank data repository: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study403960582.

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