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Post-release movements of leatherback turtles captured by the Peruvian small-scale driftnet fishery: insights from satellite telemetry

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ABSTRACT: The subpopulation of leatherback turtles *Dermochelys coriacea* in the eastern Pacific Ocean is classified as Critically Endangered due to multiple anthropogenic threats, the most urgent of which remains mortality at sea from fisheries interactions. Here we used satellite telemetry to assess the post-capture movements of leatherbacks in foraging grounds off Peru and attempt to evaluate post-release mortality. The 16 turtles tracked were bycatch from small-scale driftnet fishing vessels from the Peruvian ports of San Jose, Salaverry, and Parachique between 2014 and 2018. Sampled individuals included juveniles, subadults, and adults (curved carapace length range: 100.0 to 150.0 cm). Post-release overlap with driftnet fishing grounds was low and, upon release, all but one leatherback tracked for >30 d (n = 10) moved offshore beyond the continental shelf. From the subset of 6 tags with dive data, turtles spent 39.1 ± 11.8% of their time (range: 27.5 to 55.9%) within 10 m of the surface. Turtles spent significantly more time conducting shallow dives compared to deep dives during the day and night, carried out significantly more shallow dives compared to deep dives during the day and night, and carried out significantly more shallow dives during the day compared to night. Of the 16 tracks, biofouling (n = 3) and turtle injury or death (n = 3) were identified as the possible cause of tag cessation. Study results can inform ongoing population modeling and bycatch mitigation initiatives and efforts to predict and prevent bycatch interactions and mortality of this population.

KEY WORDS: Bycatch · Marine turtles · Small-scale fisheries · Gillnets · Telemetry

1. INTRODUCTION

The subpopulation of leatherback turtles *Dermochelys coriacea* in the eastern Pacific Ocean is classified as Critically Endangered by the IUCN Red List due to multiple anthropogenic threats, the most urgent of which remains mortality at sea resulting from fisheries interactions (Spotila et al. 2000, Wallace et al. 2013a,b). Small-scale fisheries in Peru have been identified as having high levels of incidental catch (i.e. bycatch) and mortality of leatherbacks (Alfaro-Shigueto et al. 2007, 2011, Quiñones et al. 2021). These massive fishing fleets, which total ca. 18 000 vessels (Castillo et al. 2018), largely operate in the coastal and pelagic waters within Peru's exclusive economic zone (EEZ) (Alfaro-Shigueto et al. 2010, Estrella Arellano & Swartzman 2010). Available evidence indicates that these fleets primarily interact with juvenile and sub-adult-sized leatherbacks as well as adults (de Paz et al. 2006, Alfaro-Shigueto et al. 2011, Quiñones et al. 2021).

Satellite telemetry studies of leatherbacks in the eastern Pacific Ocean have been undertaken with adult females from nesting beaches in Costa Rica and

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Mexico (e.g. Morreale et al. 1996, Eckert & Sarti 1997, Shillinger et al. 2008, Bailey et al. 2012a, Schick et al. 2013). First noted by Morreale et al. (1996), upon departing the nesting beaches, these highly migratory turtles primarily head along a 'migratory corridor' for the southeastern Pacific Ocean (SEP) to putative foraging grounds, but these routes take them far offshore of the Pacific coast of South America (Shillinger et al. 2008, Bailey et al. 2012b). Fishery bycatch data indicate that leatherback turtles occupy nearshore waters and can consist of smaller size-class individuals (Quiñones et al. 2021). It appears, therefore, that the nearshore waters of Peru may also be an important foraging area, with leatherback presence shown to be correlated with the abundance of their gelatinous zooplankton prey (Quiñones et al. 2021). Saba et al. (2008) suggested that the highly productive Peruvian Coastal Upwelling should be a common destination for foraging leatherbacks but that they form a minority of the remaining eastern Pacific population due to high mortality rates in coastal gillnet fisheries. This assertion appears to have been borne out by more recent modeling efforts combining telemetry, fishery, and environmental data, which shows a strong, year-round coastal distribution of leatherbacks that strongly overlaps with small-scale fishing effort (Degenford et al. 2021, Lopez et al. 2022, Liang et al. 2023).

More fine-scale foraging and movement information have been derived from telemetry studies of leatherback turtles in multiple ocean basins, including the northern Pacific (Benson et al. 2011), Gulf of Mexico (Evans et al. 2021), and northern Atlantic foraging grounds (James et al. 2005a, Dodge et al. 2014), and the Caribbean (Eckert 2002, 2006, Fossette et al. 2010), south Atlantic (Witt et al. 2011, Garzon et al. 2023), and eastern Pacific nesting habitats (Eckert & Sarti 1997, Shillinger et al. 2008, Bailey et al. 2012a). Such information has helped detail numerous behavioral characteristics, such as time spent at or near the ocean surface, dive depths and dive durations, displacements and travel speeds, foraging behaviors, relationships with environmental parameters, and overlap with fisheries and national boundaries, among others. In some cases, it has also been possible to investigate the causes of the cessation of telemetry data (Hamelin & James 2018, Hart et al. 2021, Hays et al. 2021). Potential reasons include tag failure due to battery exhaustion or biofouling, antenna damage, tag loss, entanglement in lost or abandoned fishing gear, or animal death or recapture (Hays et al. 2007). This information is valuable in informing our understanding of leatherback behavior and how that relates to the anthropogenic risk factors faced by the species. These data can also underpin the development of conservation goals and initiatives to recover the species (e.g. Arlidge et al. 2020, Griffiths et al. 2020, The Laúd OPO Network 2020) and reduce fishery interactions (Howell et al. 2015, Hoover et al. 2019, Barbour et al. 2023). For example, information on post-release mortality can help in estimating age-class survival probabilities from bycatch interactions, information that is important for population modeling and setting bycatch mortality reduction targets (Swimmer & Gilman 2012, The Laúd OPO Network 2020). Moreover, as diving animals, it is essential to document how leatherbacks use the water column, for conservation and for a more complete understanding of behavior (Schick et al. 2013).

While useful, these types of information are still more available for adult female leatherbacks given the relative ease of tag attachments from nesting beaches compared to finding and tagging animals at sea. However, data on males and females from multiple size classes are needed for more robust modeling and to better understand leatherback behavior and habitat use (Dodge et al. 2014). The coastal waters of the SEP are one region where such telemetry data is lacking. Given this paucity of data and the known high rates of bycatch and mortality of leatherbacks of multiple size classes in nearshore waters in the SEP, we aimed to better understand the post-capture movements of leatherbacks in this region. More specifically, we assessed leatherback horizontal and vertical movements and distribution within territorial and international waters in relation to the small-scale gillnet fishing area and, to the extent possible, assessed post-release mortality.

2. MATERIALS AND METHODS

2.1. Study area and data collection

The turtles in this study were bycatch from small-scale driftnet fishing vessels. Instances of bycatch were reported by fishers as part of the ProDelphinus bycatch monitoring program. This comprises a network of onboard and shore-based observers in the study ports of San Jose (6.758° S, 79.975° W), Salaverry (8.233° S, 78.983° W), and Parachique (5.7667° S, 80.8667° W) between the years 2014 and 2018 (see Table 2, Fig. 1). Gillnets used in this fishery were made of multifilament twine and were composed of multiple net panes that measured ca. 56 m long by 11 m high, with a stretched mesh of 24 cm. These fisheries are highly opportunistic but target catch consists primarily of elasmobranchs, including multiple species of sharks (e.g. smooth hammerheads *Sphyrna zygaena*, smoothhounds *Mustelus* spp., blue sharks *Prionace glauca*, eagle rays *Myliobatis* spp.), dolphinfish *Coryphaena hippurus*, tunas *Thunnus* spp., and other Osteichthyes (For more fishery-related information see also Alfaro-Shigueto et al. 2010, Mangel et al. 2010, Bielli et al. 2020).

2.2. Morphometric data and transmitter attachment

Only leatherbacks incidentally caught during a vessel's last fishing set were candidates for tag attachment to avoid interfering with normal fishing operations, as these sets are typically nearer to the home port and allow for prompt return to the port. Animals were lifted aboard the fishing vessel where they were disentangled and kept in shaded conditions, with seawater regularly applied to the body. All procedures and releases occurred from the vessel. Prior to tag attachment, measurements of curved carapace length (CCL) to the nearest 0.1 cm were taken with a flexible measuring tape and each animal was assessed to confirm that it had no visible injuries. Additionally, we applied passive integrated transponder (PIT) tags (Avid Identification Systems) to the front shoulder muscles and Inconel style 681IC tags (National Band and Tag) to the rear flippers for future identification if encountered. Turtles were released within 15 min of tag attachment, and time from capture to release averaged 9 h. Tagged turtles ranged in size from 100.0 to 150.0 cm CCL and, following Quiñones et al. (2021), were classified into 3 groups: juveniles (<123 cm CCL), subadults (>123 and <144.4 cm CCL), and adults (>144.5 cm CCL).

Wildlife Computers SPOT or SPLASH10 platform transmitter terminals (PTTs) were used. All tags were either shipped with a clear anti-fouling coating or had a black-colored antifouling coating applied upon receipt of the tags. Following Dodge et al. (2014), PTTs were attached to the carapace via direct attachment through the dorsal ridge using a plastic-coated metal cable. To minimize time aboard the vessel, as soon as the tag attachment procedure was performed, the turtles were released several kilometers offshore, typically near the port of capture.

2.3. Data analysis

All PTTs had an 'always-on' configuration. ARGOS data were managed and downloaded using the STAT (Satellite Tracking and Analysis Tool; Coyne & Godley 2005) and Wildlife Computers web portals. Raw ARGOS locations (n = 8439) were filtered using STAT to exclude poor quality (Z location class) and successive locations that exceeded a maximum rate of travel of 10 km h^{-1}. A Douglas Argos Filter Algorithm (Douglas et al. 2012) was then applied in Movebank (Wikelski et al. 2021) to derive the best daily location from the filtered Argos data (n = 793). Speed of travel (km per day) between filtered daily locations was calculated based on the distance in km between consecutive latitude and longitude positions divided by the time difference in days between those 2 locations. Bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO Compilation Group 2023). Data were imported into ArcGIS Pro v.2.9.1 for visualization and to extract depth data for data points.

Six of the PTTs had additional sensors allowing for tracking of the following variables: (1) time-at-depth (TAD), (2) time-at-temperature, (3) maximum depth, and (4) daily percent time spent above the programmed 10 m depth threshold based upon pre-programmed bins (Table 1). Dive data were accumulated into four 6 h time bins (00:00–05:59, 06:00–11:59, 12:00–17:59, 18:00–23:59 h). A dive was defined as a submergence of more than 2 m.

To assess turtle vulnerability to fishery interactions, using ArcGIS Pro v.2.9.1, we created minimum convex polygons (MCPs) of the fishing zones of the small-scale driftnet fisheries operating from the ports of San Jose and Salaverry monitored through the ProDelphinus bycatch monitoring program. MCPs specify

Table 1. Platform transmitter terminal data bin settings according to each parameter. Bin data was accumulated in 6 h time intervals (00:00–5:59, 06:00–11:59, 12:00–17:59, 18:00–23:59 h)

Depth bin (m)	Duration bin (min)	Time-at-depth bin (min)
2–10	1.1–2	0–2
10.1–15	2.1–3	2.1–5
15.1–20	3.1–4	5.1–10
20.1–25	4.1–5	10.1–15
25.1–50	5.1–10	15.1–20
50.1–100	10.1–15	20.1–25
100.1–150	15.1–20	25.1–50
150.1–200	20.1–25	50.1–100
200.1–250	25.1–30	100.1–150
250.1–350	30.1–40	150.1–200
350.1–500	40.1–50	200.1–250
500.1–800	50.1–60	250.1–500
>800	>60	>500

the smallest polygon area that encloses all the points being studied such that no internal angle exceeds 180° (Powell 2000). These MCPs were derived from onboard observer monitoring of fishing sets from 2014 to 2018 and consisted of 1725 and 1542 sets from San Jose and Salaverry, respectively. Using handheld GPS units (Garmin eTrex 10), onboard observers recorded the latitude and longitude at the start of net setting.

We also analyzed the telemetry data to estimate post-release mortality or otherwise attempt to determine the cause of signal cessation. Three possible causes for tag 'failure' were assessed: (1) low battery voltage, (2) biofouling of the tag, and (3) injury or death of the turtle. Battery voltage data are communicated by the tag at each transmission, with consistently low values below the normal range of 3.1 to 3.5 V indicative of battery exhaustion. These values are given in the 'status.csv' file of each PTT. Following Hart et al. (2021), we plotted these voltage values to determine if they dropped and remained below 3.1 V. Tag biofouling was assessed by monitoring PTT maximum and minimum wet—dry state values from the 'status.csv' data files for each PTT. A decline in the dry state daily value from its maximum value of 255 indicates that the tag is becoming biofouled due to growth over or around the saltwater switch (Wildlife Computers 2019). Injury or death was assessed by looking for evidence of an animal remaining at the ocean surface for an extended period (evident from relatively continuous data transmission from the tag and suggestive of an animal floating dead or unable to dive) or from direct observation data (e.g. tag recovery).

The number of days within maritime political boundaries was also calculated based on the Flanders Maritime Institute maritime boundaries geodatabase version 11 (FMI 2019). Time was calculated based on entry and exit times from specific polygons. For gap periods, a polygon was assigned when it could be reasonably determined (i.e. when no other borders were nearby given the time gap). Some gap days could not be assigned in cases where the appropriate boundary could not be determined (2 tags, 46 track days).

A subset of 6 tags (DC2, DC3, DC4, DC8, DC14, DC15) also recorded 14 predetermined binned summaries of TAD (%), maximum dive depth (m), and dive duration (min) within a 24 h period (Table 1). To investigate differences in depth use (TAD and maximum dive depth) in relation to the potential threat of surface set nets that extend to approximately 10 m depth and are set at night, dive data were assigned as either day (06:00–17:59 h) or night (18:00–05:59 h), and either shallow (top 10 m of water column) or deep (depths greater than 10 m). These categories were then combined to create 'day—shallow', 'day—deep', 'night—shallow', and 'night—deep' groups. A Kruskal-Wallis (KW) test was used to test differences between groups, with differences identified post hoc using Dunn's all-pairs comparisons. Statistical analyses were conducted with R software v.4.3.0 (R Core Team 2023), with a significance level of $\alpha = 0.05$. Unless otherwise specified, descriptive statistics are given as mean ± SD (range, sample size).

3. RESULTS

3.1. Leatherback turtle bycatch

Individuals sampled comprised 75% juveniles (n = 12), 12.5% subadults (n = 2), and 12.5% adults (n = 2) (CCL: 120.1 ± 15.0 cm, 100.0–150.0 cm) (Table 2). The adult-sized animals consisted of one female and one male (identified by its diagnostic long tail). The bycatch of leatherbacks reported per year (average per year: 3.2 ± 1.1) and by ports was variable, with the majority caught by vessels departing from San Jose (n = 13) and in 2016 (n = 7) (Table 2). Leatherback bycatch largely occurred year-round, with peak catch rates occurring in September (monthly average per year: 0.6 ± 0.4, n = 3). There were no bycatch reports in August and December. The precise location of capture is known for 13 of the 16 turtles (Table 2, Fig. 1). The average distance from the point of capture of the turtle to its release location was 54.5 ± 32.5 km (10–140 km, n = 13). All capture locations were over the continental shelf (n = 10) or continental slope (n = 3), in the small-scale driftnet fishing ground, and averaged 26.4 ± 23.5 km from shore and ranged from 300 m to 82.2 km from the coast (Table 2, Fig. 1). Water depths at the capture locations ranged from 3 to 3168 m (Table 2).

3.2. Horizontal movements

We used 15 PTTs in this study because one leatherback turtle (DC10) stranded 4 d after the tagging. The tag was recovered and later fitted to another leatherback (DC14). The track durations for all tags ranged from 3 to 297 d (n = 16; Table 2).

Individual leatherbacks tracked for more than 30 transmitting days (46–297 d, n = 10 d) were considered for horizontal movements analysis. These individual tracks were deemed long enough to suggest any hab-

Table 2. Summary of bycatch events of *Dermochelys coriacea* (n = 16) in the small-scale gillnet fishery in northern Peru between 2014 and 2018. CCL: curved carapace length. Size classes: J: juvenile; S: sub-adult; A: adult. Platform transmitter terminal (PTT) models: 1: SPLASH10-F-294; 2: SPOT-310; 3: SPOT-317; 4: SPLASH10-F-295. Capture ports: 1: San Jose; 2: Parachique; 3: Salaverry. Tag cessation categories: UnID: unidentified cause; biofoul: resulting from biofouling; injury: evidence the turtle was injured or died; bycatch: possible recapture as bycatch. PTTs in **bold** collected dive data

Animal ID	PTT model	CCL (cm)	Size class	Deploy date (mm/dd/yy)	Capture port	Capture distance (km)		Catch Location depth (m)	Final voltage (V)	Track duration (d)	Displacement (km)	Minimum travel distance (km)	Displacement rate (km d^{-1})	Tag cessation cause
						To release	From coast							
DC1	1	114.5	J	01/19/14	1	46	2.97	83	3.31	5	184	185	42.4	UnID
DC2	**1**	**103.3**	**J**	**06/25/14**	1	**44**	**37.6**	**56**	**3.25**	**46**	**2588**	**2676**	**55**	**Biofoul**
DC3	**1**	**116.5**	**J**	**09/17/14**	1	**53**	**14.3**	**26**	**3.25**	**84**	**1239**	**1754**	**15.1**	**Injury**
DC4	**1**	**150.0**	**A ♀**	**09/17/14**	1	**28**	**0.3**	**3**	**3.12**	**108**	**518**	**3104**	**12.9**	**Bycatch**
DC5	2	112.6	J	09/19/15	2	57	16.2	354	3.44	53	1004	1267	18.2	UnID
DC6	2	122.3	J	11/18/15	3	–	–	–	3.46	297	7916	8937	26.3	Biofoul
DC7	1	144.6	A ♂	01/20/16	2	71	25.7	240	3.31	3	99	94	33.2	UnID
DC8	**1**	**110.8**	**J**	**02/10/16**	1	**–**	**–**	**–**	**3.25**	**145**	**1857**	**2420**	**16.6**	**Biofoul**
DC9	1	119.3	J	03/18/16	1	31	33.2	53	3.25	4	135	119	29.8	UnID
DC10	1	109.2	J	03/31/16	1	76	48.8	56	3.25	5	31	29	14.4	Injury
DC11	2	100.0	J	05/19/16	1	140	82.2	3168	3.46	18	323	452	18.7	UnID
DC12	3	120.1	J	06/12/16	1	10	8.6	2	3.34	70	2381	2680	35.1	UnID
DC13	3	121.6	J	10/15/16	1	66	17.9	30	3.42	50	1468	1612	28.1	UnID
DC14	**1**	**128.0**	**S**	**04/28/17**	1	**–**	**–**	**–**	**3.25**	**105**	**2281**	**2488**	**31.7**	**UnID**
DC15	**1**	**144.1**	**S**	**09/07/17**	1	**22**	**6.8**	**8**	**3.18**	**78**	**3756**	**4005**	**49.2**	**UnID**
DC16	4	104.6	J	02/11/18	1	65	48.1	70	3.25	4	126	137	31.1	UnID

itat preference and to reduce the impact of capture and handling stress on behavior. After their release, all but one leatherback (DC4) moved to oceanic waters and did not return to coastal waters (Fig. 2). Distances traveled ranged from 1691 to 10 555 km (3531.7 ± 811.6 km, n = 10; Table 2). Final displacements ranged from 518 to 7916 km (2500.8 ± 2113.9 km, n = 10; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n054p261_supp.pdf). The average calculated speed of travel between filtered daily locations was 35.7 ± 12.4 km d^{-1} (21.2–58.1 km d^{-1}, n = 10).

3.3. Overlap with fishing grounds and EEZs

These turtles spent a majority of their time in international waters (67.7%) but also moved within Peruvian, Ecuadorian, Colombian, and French Polynesian waters (Peru: 19.6 ± 20.0%, 3.4–73.6%; Ecuador: 9.1 ± 14.4%, 0–40.5%; Colombia: 3.3 ± 10.4%, 0–32.8%; French Polynesia: 0.3 ± 1.0%, 0–3.0%; international waters: 67.7 ± 30.0%, 16.4–93.6%; Table S1).

Overlap with the fishing grounds used by the San Jose- and Salaverry-based gillnet fisheries was relatively low, ranging from 2.4 to 14.9% of track days (7.3 ± 4.3%, n = 10; Fig. 1).

3.4. Dive data

Turtles spent 39.1 ± 11.8% of their time (27.5–55.9%) above the programmed 10 m depth threshold group by 24 daily 1 h time bins (Fig. 3A). Pooling the data from the 6 tags with dive data, over 24% of dives were less than 10 m deep, with another 24.9 and 14.6% of dives occurring within the 50 and 100 m depth bins, respectively (Fig. 3B). Dives more than 100 m were rare (7.7% of dives in depth bins >100 m), and the maximum depth bin utilized was >800 m (17 occasions, 0.2%) (Fig. 3B). About half of dives (48.4%) were 10 min or less in length, with 3.6% of dives exceeding 1 h (Fig. 3C). TAD was fairly evenly distributed among depth bins to 35 m, with increased frequency within the 35.1 to 100 m bins, after which it begins to decline (Fig. 3A).

There were significant differences among categories for TAD (KW; $\chi^2_3 = 1571.2$, $p < 0.001$; Table 3), with all comparisons of pairs differing significantly from one another ($p < 0.001$; Table 3) apart from day–shallow versus night–shallow ($p = 0.34$; Table 3). Most notably, turtles spent significantly more time conducting shallow dives than deeper dives during both the day (day–deep vs. day–shallow, $p < 0.001$;

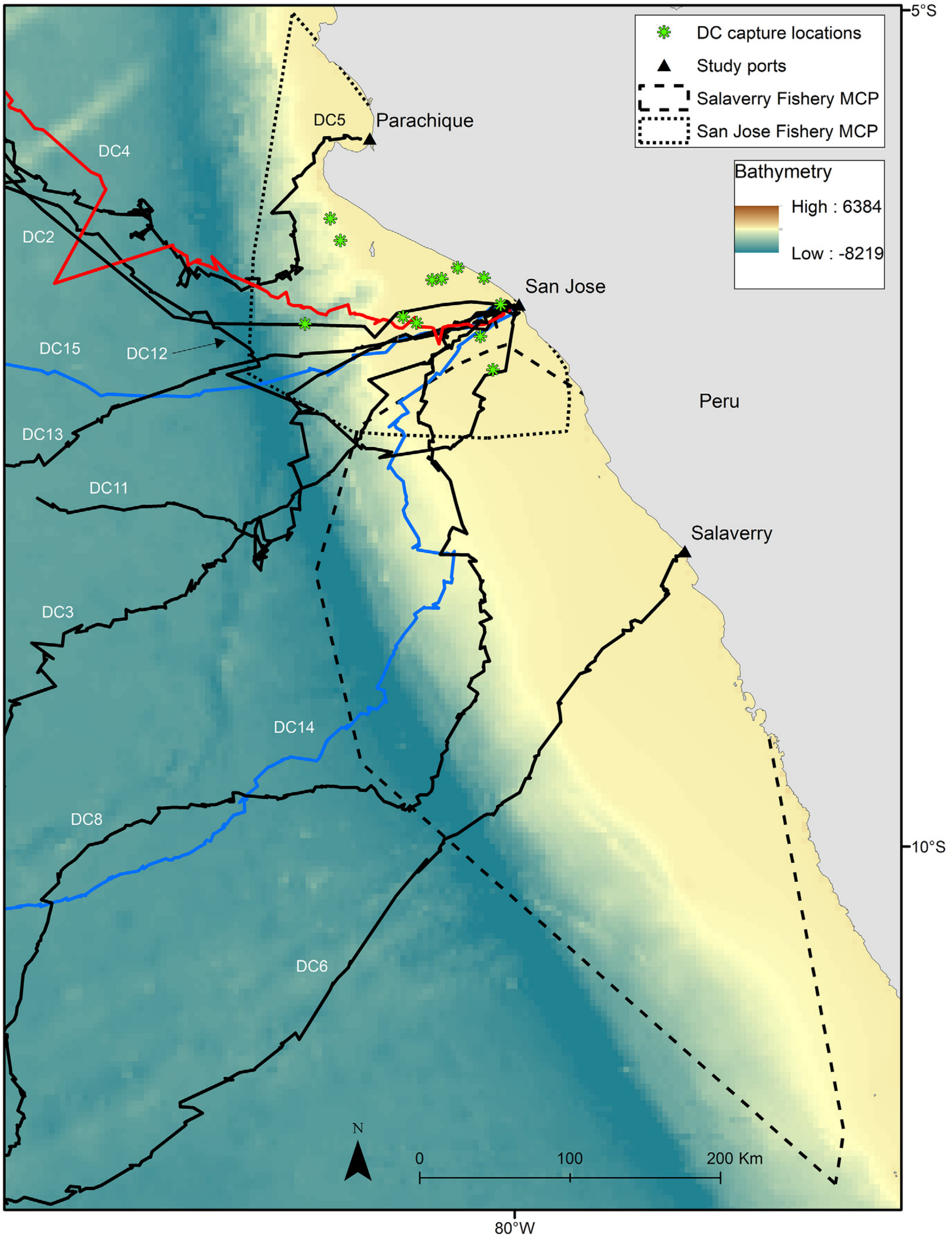

Fig. 1. Region-scale movements of 11 satellite-tagged leatherback turtles *Dermochelys coriacea* caught incidentally in small-scale driftnet fisheries in Peru, 2014–2018 in relation to driftnet fishing grounds. Animal ID designations are listed (e.g. DC1, DC2, etc.). Leatherback size classes are colored as black: juvenile; blue: subadult; red: adult. Also shown are turtle capture locations, locations of study ports, and San Jose and Salaverry port small-scale gillnet fishing grounds (MCP: minimum convex polygons). Bathymetry data were obtained from the General Bathymetric Chart of the Oceans (GEBCO Compilation Group 2023)

Table 3, Fig. 3A) and night (night–deep vs. night–shallow, $p < 0.001$; Table 3, Fig. 3A). Leatherback turtles did not spend significantly different amounts of time in shallower depths when comparing day and night (day–shallow vs. night–shallow, $p = 0.34$; Table 3, Fig. 3A). There were significant differences among categories for maximum dive depth (KW; $\chi^2_3 = 161.06$, $p < 0.001$; Table 3), with all comparisons of pairs differing significantly from one another ($p < 0.001$; Table 3) apart from between day–deep

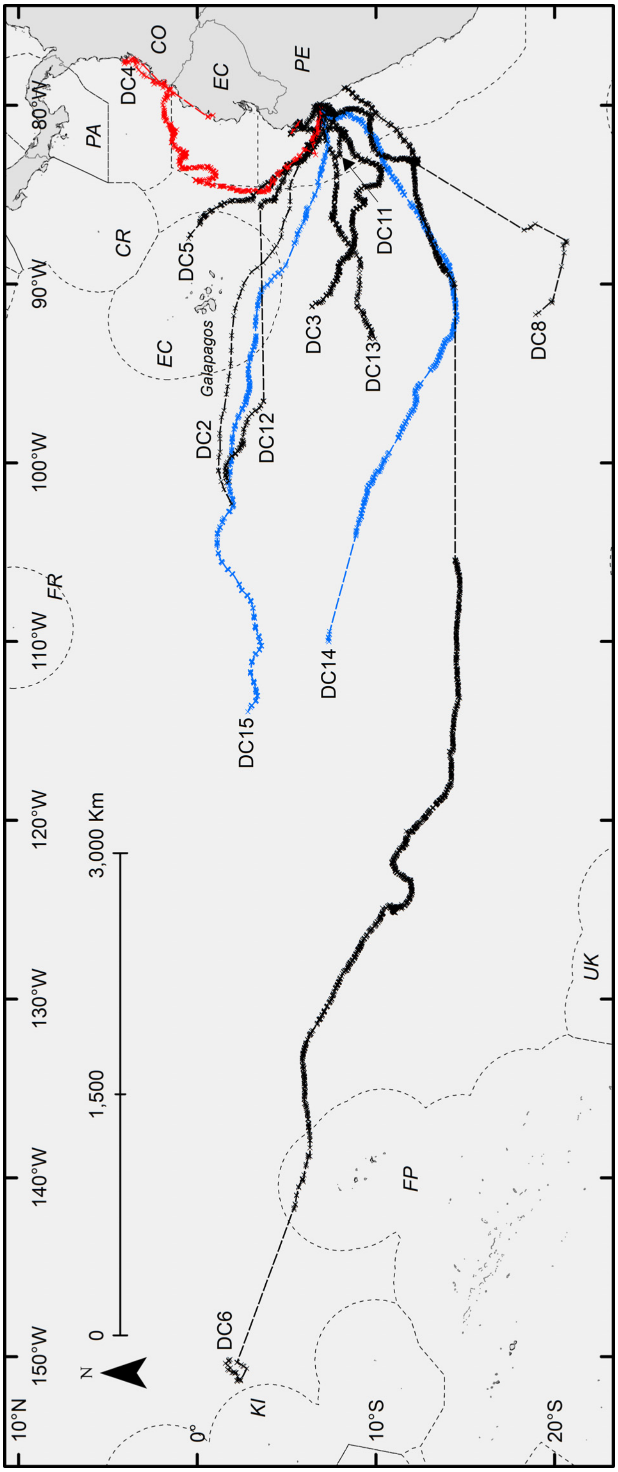

Fig. 2. Broad-scale movements through national and international waters of 11 satellite-tagged leatherback turtles *Dermochelys coriacea* caught incidentally in small-scale driftnet fisheries in Peru, 2014–2018. Animal ID designations are listed (e.g. DC2, DC3, etc.). Leatherback size classes are colored as black: juvenile; blue: subadult; red: adult. Exclusive economic zone boundaries are shown as dashed lines with nation designations italicized: CO: Colombia; CR: Costa Rica; EC: Ecuador; FR: France; FP: French Polynesia; KI: Kiribati; PA: Panama; PE: Peru; UK: United Kingdom

versus night—deep ($p = 0.052$; Table 3). Most notably, turtles carried out significantly more shallow dives compared to deep dives during both the day (day—deep vs. day—shallow; $p < 0.001$; Table 3, Fig. 3B) and night (night—deep vs. night—shallow; $p = 0.0033$; Table 3, Fig. 3B). Turtles also carried out significantly more shallow dives during the day compared to at night (day—shallow vs. night—shallow; $p < 0.001$; Table 3, Fig. 3B).

3.5. Tag cessation and post-release mortality

One objective of this project was to investigate whether we could assess post-release mortality from the telemetry data. This was in part due to the large number of relatively short-duration tracks we obtained. Three main possible causes for tag 'failure' were assessed: (1) low battery voltage, (2) biofouling of the tag, and (3) injury or death of the turtle (Table 2).

3.5.1. Low voltage

There was no evidence of low battery voltage being the cause for the cessation of transmissions from any of the tags (Table 2, Table S2, Fig. 4).

3.5.2. Biofouling

Biofouling was identified as a possible cause for cessation of PTTs DC2, DC4, and DC8 due to the reduction in the maximum wet—dry state of the tags, a sign of biofouling (Table 2, Fig. 4). PTTs DC2 and DC8 showed evidence of possible biofouling after 18 and 17 d, respectively (despite being treated with the clear [DC8] or black [DC2] anti-fouling coatings). DC4 also showed evidence of possible biofouling but this did not result in tag failure (see Section 3.4.3). A drop-off in signal quality (only location quality 'B' signals received after 25 July 2016) toward the end of the track for DC6 also suggests

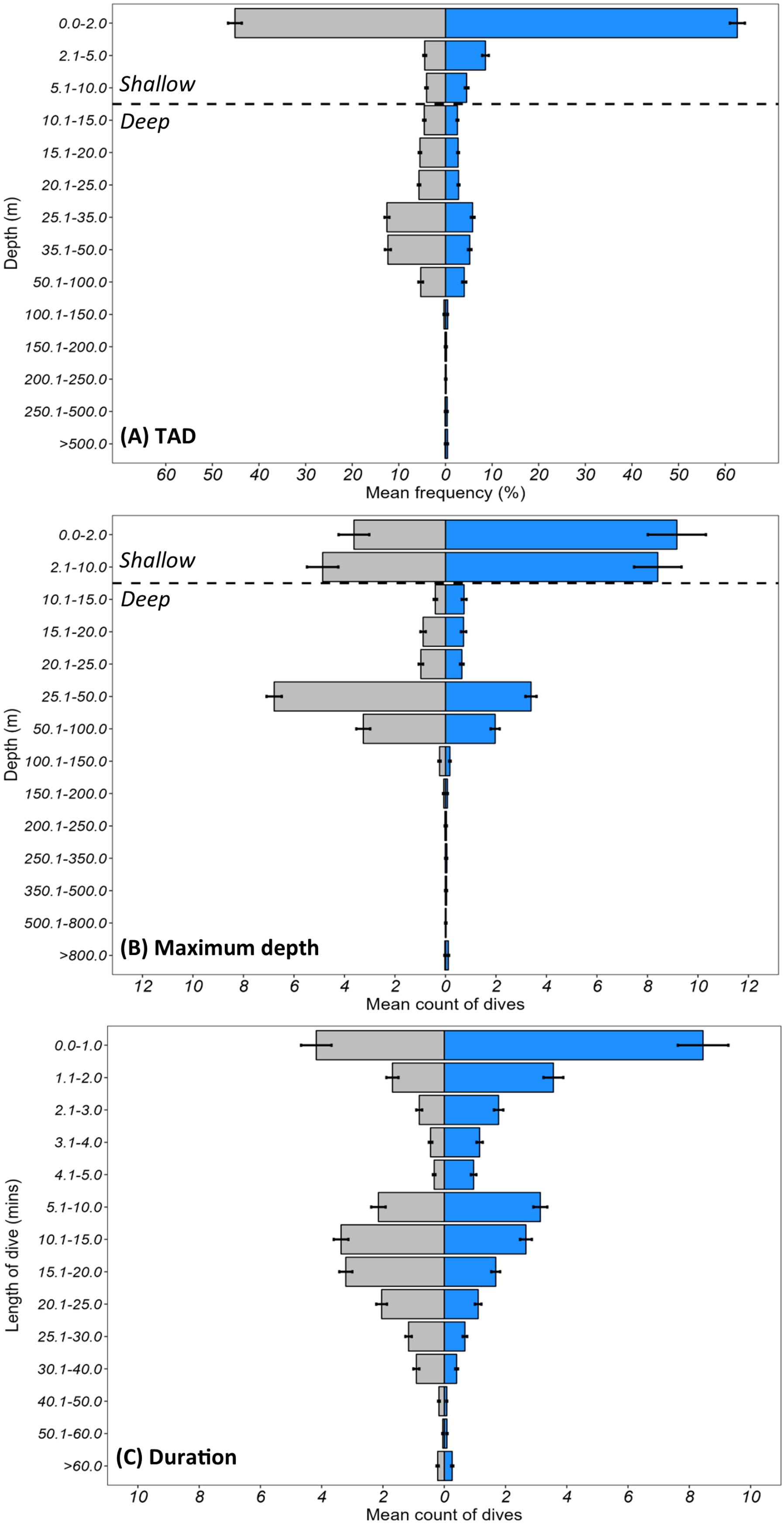

Fig. 3. Dive summary histograms for (A) Time-at-Depth (TAD), (B) maximum dive depth, and (C) dive duration of leatherback turtles (n = 6). Mean ± standard error split by night (grey bars) and day (blue bars). Horizontal dashed lines: separation between 'shallow' and 'deep' dive categories

Table 3. Results from Kruskal-Wallis and Dunn's pairwise comparisons for depth use and time of day

Pairwise comparison	Dunn's test	p
Time-at-depth		
Kruskal-Wallis rank sum test; $\chi^2_3 = 1571.2$, $p < 0.001$		
Day—deep vs. day—shallow	29.23	<0.001
Day—deep vs. night—deep	9.09	<0.001
Day—deep vs. night—shallow	31.58	<0.001
Day—shallow vs. night—deep	22.92	<0.001
Day—shallow vs. night—shallow	1.91	0.34
Night—deep vs. night—shallow	25.27	<0.001
Maximum dive depth		
Kruskal-Wallis rank sum test; $\chi^2_3 = 161.06$, $p < 0.001$		
Day—deep vs. day—shallow	12.24	<0.001
Day—deep vs. night—deep	2.63	0.052
Day—deep vs. night—shallow	4.92	<0.001
Day—shallow vs. night—deep	10.62	<0.001
Day—shallow vs. night—shallow	5.61	<0.001
Night—deep vs. night—shallow	3.34	0.0033

either biofouling or damage to the antenna as a possible cause of tag failure. We also note that PTTs DC6, DC8, DC12, and DC14 all experienced extended periods of no transmissions (ranging from 20 to 75 d), only to later continue transmitting (after departing continental shelf waters) (Fig. 2).

3.5.3. Turtle injury or death

The track of turtle DC4, an adult female, showed that it moved to land at the end of its track (Fig. 2). Colleagues in Ecuador were able to travel to the location of the tag's continued transmission and recover the tag. The tag was in the possession of fishers who indicated that they came upon the turtle dead and floating in the water and removed the tag. While this may be true, it also seems possible that the turtle was injured or died after being entangled as bycatch by that fishing vessel. The change in behavior of this animal is also illustrated by its percent time spent above 10 m (Fig. S2) which indicates its possible time of capture at the end of the track.

DC3 showed a similar behavior during the first tracking month when this animal then appeared to make fewer and fewer dives exceeding 10 m until 10 October 2014, after which time the turtle was at the ocean surface 100% of the time, perhaps injured or floating dead until the tag ceased transmitting on 8 December 2014 (Fig. S2).

In addition, we deployed DC10 for the first time in March 2016, but after 4 d it was transmitting high-quality signals from an inland location. We were able to travel to the location of signal transmission and recover the PTT from a fisher who indicated that he found the turtle stranded along the coast and removed the tag.

4. DISCUSSION

Previous telemetry studies of leatherbacks in the eastern Pacific were conducted with adult females, with deployments occurring from nesting beaches in Costa Rica (Shillinger et al. 2008, 2011) and Mexico (Eckert & Sarti 1997, Bailey et al. 2012a). These animals followed largely similar offshore routes to feeding grounds in the SEP. In this study, we see a different pattern: that of coastal habitat use by juveniles, subadults, and adults. Our results corroborate that coastal Peruvian waters are a leatherback foraging habitat (Saba et al. 2008, Degenford et al. 2021, Quiñones et al. 2021, Liang et al. 2023) and add insights into the distinct movements and behaviors of leatherback turtles between Peruvian and other territorial and international waters. This small sample of tracked animals encompassed a vast area of ocean extending from the release location 8000 km westward approaching Kiribati in Micronesia, 1200 km northward to Colombia (crossing the equator), and 1500 km to the south into high seas waters.

4.1. Movement patterns, fisheries, and governance

All turtles in this study were caught by the small-scale driftnet fleet in continental shelf or slope waters ranging from <1 to 80 km from shore. However, upon release, these animals departed this foraging area and fishing ground. Of those animals tracked for >30 d, only one animal, an adult female, remained relatively nearshore and returned to continental shelf waters near the end of the tracking period. All the other turtles (including both juveniles and subadults) departed continental shelf waters and had relatively constant rates of displacement and directions of travel for the duration of their tracking periods. This suggests that leatherbacks may be highly sensitive to fisheries bycatch and/or handling. Benson et al. (2011) reported a similar response, with 89% of turtles tagged in California (USA) foraging grounds (~37° N) departing the area after capture, but most (72%) later returning after 2 to 3 mo. Sherrill-Mix & James (2008) also noted that of the leatherbacks fitted with harness-type PTT attachments, 17 of 42 immediately

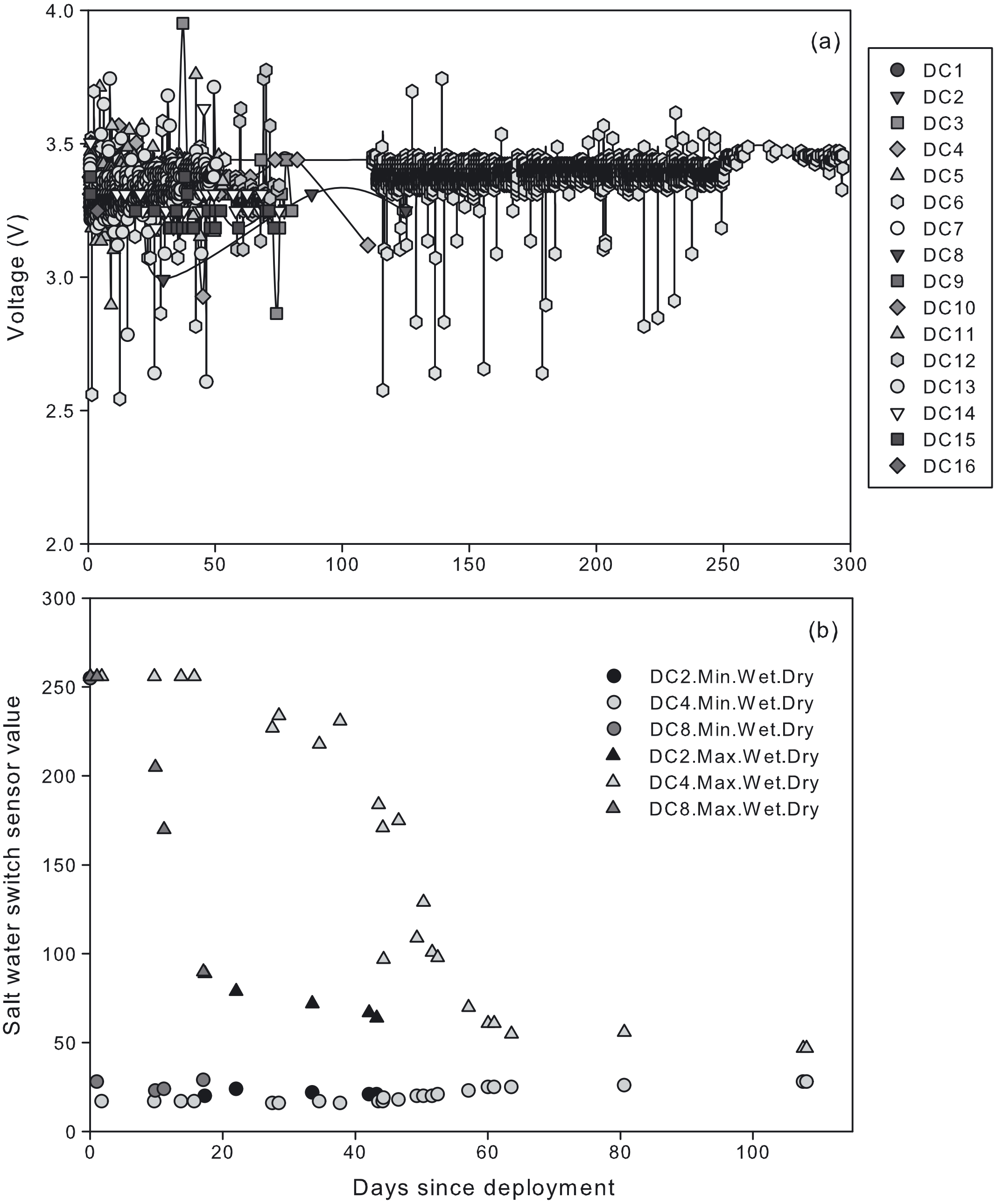

Fig. 4. Two potential causes of cessation of platform transmitter terminal transmission were assessed. (A) Battery voltage values taken from the status.csv files for 16 leatherback turtles, showing no evidence of sustained declines below 3.1 V, which would be indicative of battery exhaustion as a potential cause of PTT failure. (B) Saltwater switch sensor values taken from the status.csv files for leatherback turtles DC2, DC4, and DC8, showing evidence of biofouling due to declines in 'Max.Wet.Dry' values

departed the area of capture and increased speeds in the first week compared to those that remained in the foraging area. Indeed, turtles in that study (subadults and adults) were 500 times more likely to begin migrating if bycaught (Sherrill-Mix & James 2008). Wallace et al. (2005) noted a similar pattern in nesting female leatherbacks in Costa Rica — longer internesting periods and altered diving by more intensively handled animals. Our results counter those of Hamelin & James (2018), which indicated minimal impact on movement patterns with direct carapace attachment compared with harnesses. This difference could be related to the stress from the combination of bycatch, transport, and handling, highlighting the importance of releasing turtles as quickly as possible after capture and with as little handling as necessary. Several institutions have developed protocols for the safe handling and release of sea turtles from fishing gear, which, when shared with fishers in Peru and elsewhere, can help reduce injuries and promote post-release survival (e.g. Mires-Rojas et al. 2021).

Previous telemetry work in the eastern Pacific on nesting adult females in Costa Rica and Mexico showed that most animals passed 100s to 1000s of km westward of Peru's EEZ boundary as they migrated into the southern Pacific Ocean (Eckert & Sarti 1997, Shillinger et al. 2008, Bailey et al. 2012a). Evidence of leatherbacks in coastal waters in the eastern Pacific derived from fisheries bycatch monitoring, direct observations, and fisher interviews has since accumulated (sometimes very close to shore), including reports from Panama (Flores 2022) and Peru (Alfaro-Shigueto et al. 2007, 2012, Costanza et al. 2021, Quiñones et al. 2021) and is further reinforced by the results reported here.

Leatherbacks in coastal waters such as those off Peru are at high risk of fishery interactions (Saba et al. 2008). There are tens of thousands of small-scale and industrial fishing vessels operating in the continental waters of Ecuador and Peru alone (Alfaro-Shigueto et al. 2018). It is noteworthy and concerning that the one animal in this study (DC4, an adult female) that remained in coastal waters for an extended time was later reportedly recovered dead by fishers in Ecuador, possibly as fishery bycatch, further demonstrating the risks such animals face in continental shelf waters. Turtles in this study also passed through multiple national jurisdictions (Peru, Ecuador, Colombia, French Polynesia) and high seas waters, reinforcing their highly migratory nature. This calls for international collaborations to effectively recover the population (The Laúd OPO Network 2020), with coastal areas having a high-priority need for protection from fishery interactions, including along the Pacific coasts of Mexico and Central America (Ortiz-Alvarez et al. 2020, Liang et al. 2023).

As leatherbacks must come to the surface to breathe, this puts them at heightened risk of interactions with surface fisheries, but the dive data also indicates extensive time spent within 10 m of the surface. The leatherback dive-depth distributions in this study indicate that most of these animals' time was spent at or near the ocean surface (an average of 40% of time above 10 m). A similar result was reported for subadult and adult leatherbacks in North Atlantic foraging grounds, where turtles spent 43 and 50% of their time at the surface during the night and day, respectively (James et al. 2006). This suggests that they are almost at constant risk of entanglement in driftnets while they remain in this foraging area over the Peru continental shelf (driftnets in the Peru small-scale fishery exceed 10 m in height and set their nets around dusk and retrieve them at dawn; Alfaro-Shigueto et al. 2010). Clearly, these animals also remain at risk of interactions with the other fishing fleets operating in this area, including pelagic longlines and purse-seines (Donoso & Dutton 2010, Escalle et al. 2022). This should also be taken into consideration by regional fishery management organizations like the Inter-American Tropical Tuna Commission in their programs to monitor and mitigate bycatch. Leatherbacks will also be vulnerable to other pronounced and persistent risks, including plastics, noise, and oil pollution (Schuyler et al. 2016, NMFS—USFWS 2020)

4.2. Use of the water column

The subset of tags with dive data showed that shallow dives predominated in both day and night. A similar result was reported by James et al. (2006), who indicated that leatherbacks in their northern Atlantic foraging area spent most of their time in the upper 6 m, with little difference observed between day and night. Similarly, Fossette et al. (2010) reported that shallow diving behavior was observed homogenously in neritic and oceanic residence areas. After the preference for shallower dives, dives to the 50 and 100 m depth bins were the next most abundant. Fossette et al. (2010) also reported dives to be concentrated in the epipelagic layer from 50 to 80 m, and Okuyama et al. (2021) noted that the modal bin of maximum depth was within 50 to 100 m. An individual response by leatherbacks to concentrations of zooplankton at either the ocean surface or at depth has also been reported (Schick et al. 2013). This observed pattern in our study may be related to the vertical distribution of leatherback prey in the SEP, as one of its main prey species, the scyphozoan jellyfish *Chrysaora plocamia*, which is distributed in the upper 100 m of the water column (Quiñones et al. 2015), is abundant close to the Peru coast (Quiñones et al. 2018) and is strongly correlated with the presence of leatherbacks (Quiñones et al. 2021). The vertical and horizontal distributions of *C. plocamia* are themselves impacted by environmental changes such as El Niño—Southern Oscillation-related fluctuations (Quiñones 2018), with leatherback forage quality and foraging success likely impacted by these fluctuations (Schick et al. 2013).

4.3. Tag loss and post-release mortality

Previous studies have assessed tag failure to include biofouling, animal injury or death, battery exhaustion, and tag and/or antenna damage (Hays et al. 2007, Hamelin & James 2018, Hart et al. 2021). We were also able to assess possible causes of tag failure, including post-release mortality. There was no identifiable cause of failure for most PTTs (62.5%) and no evidence to suggest battery exhaustion leading to tag failure. Biofouling was the most likely factor in the cessation of 3 of 16 tags (18.8%). Four tags (25%) had evidence to suggest biofouling at some point during the track period, despite all tags having been treated with anti-fouling coatings. In 2 cases, biofouling was evident after only 17 and 18 d, with the potential for rapid biofouling in subtropical and tropical areas having been noted previously (Maréchal & Hellio 2009). These observations suggest that the neritic waters of the eastern tropical Pacific may be prone to biofouling and that as animals leave the continental shelf area, they are sometimes able to eliminate this load of fouling organisms or contaminants. A similar loss and return of signal attributed to PTT biofouling was also observed in the Atlantic Ocean, with leatherbacks moving between high-latitude foraging grounds and low-latitude nesting areas (James et al. 2005b, Hays et al. 2007). Behavioral differences, such as differences in travel speed, may also impact the potential for or rate of biofouling.

The telemetry data also suggests that 3 turtles (18.75%; DC3, DC4, DC10) became injured or died after release. Turtle DC4 also appears to have been captured again by another fishing vessel, making it an example of post-release mortality from subsequent fisheries bycatch (6.25% of tracked animals). Although it is a small sample size, this information can help inform bycatch mortality estimates, bycatch mortality reduction targets, and population trend estimates (e.g. The Laúd OPO Network 2020, Griffiths et al. 2020). Dodge et al. (2022), reporting on a leatherback disentanglement network in the North Atlantic, in some cases were able to assess post-release survival. They reported 25% of monitored turtles stranding or dying within 39 d (2 from subsequent fishery interactions). In general, interpreting turtle fate from limited diagnostic telemetry data remains challenging, and additional work is recommended (Swimmer & Gilman 2012, Hamelin & James 2018). Unfortunately, given resource constraints and limited reporting of entangled animals, it would be challenging to set up a SEP sea turtle disentanglement or monitoring network such as that described by Dodge et al. (2022).

4.4. Next steps

While providing valuable insights about eastern Pacific leatherbacks, we also acknowledge this study's limitations. All animals in the study were captured by fishing vessels and thus represent only a snapshot of habitat use, albeit an under-sampled component of habitat use. Moreover, it is possible that capture stress (i.e. bycatch and extended period entangled in a net and subsequent manipulation) impacted post-release behavior such that the observed habitat use may not be representative of free-swimming animals or those that may occur outside the fishing grounds of Peru's small-scale driftnet fishery (Innis et al. 2014). There are also other, more robust data modeling procedures (e.g. state-space models) that could be applied (e.g. Liang et al. 2023) to this data set toward revealing more fine-scale detail (e.g. foraging vs. travel), with some of these currently underway. The sample size of the study was also notably small but — given the precariously small eastern Pacific population and the relative rarity of bycatch events and tag attachment opportunities from an active fishery — we believe this remains a unique and valuable contribution. Given this situation, alternative monitoring methods might be considered, such as aerial surveys or use of unmanned aerial systems (e.g. Marsh & Saalfeld 1989, Sykora-Bodie et al. 2017), to help inform estimates based upon the time at the surface we observed (James et al. 2006).

In conclusion, in this study we sought to assess the movements of a range of life stages of leatherback turtles in Peruvian waters in relation to fishing pressure and post-release mortality. We found that while animals were caught fairly close to shore and over the continental shelf and slope, the majority departed this area (and the threat of interacting with the Peruvian driftnet fleet) for the high seas, where potential interactions with other industrial fisheries await. Of the 16 total tracks, biofouling and turtle injury or death were identified as the cause of tag cessation in 6 cases. Future research efforts could further explore, through extended tracking, whether coastal foragers would eventually return to their capture area or whether this represents a more permanent movement beyond the continental shelf. Moreover, questions remain regarding whether movement away from these coastal foraging grounds results in a decline in foraging success or fitness, and to what extent these animals interact with the myriad other fisheries in the SEP region and beyond, including high seas jig fisheries (Seto et al. 2023), high seas longlines (Roe et al. 2014), and purse seines (IATTC-SAC 2023). Future work should also develop and refine estimates of post-release mortality of bycatch, including evaluating the effectiveness of handling and release protocols at increasing survival. This will inform ongoing population modeling and bycatch mitigation initiatives which have defined the degree to which bycatch mortality must decline for the population to recover (Griffiths et al. 2020, The Laúd OPO Network 2020). Advanced spatial modeling efforts that combine telemetry, fishery, and environmental data (e.g. Griffiths et al. 2019, 2020, Degenford et al. 2021, Lopez et al. 2022, Liang et al. 2023) can help predict bycatch interactions and mortalities. Such information should also be consolidated into national action plans for sea turtles (e.g. SERFOR 2019), while regional collaborations like Red Laúd del Oceano Pacifico Oriental (Laúd OPO, https://laudopo.org/) and multi-national institutions like the Inter-American Sea Turtle Convention for the Protection and Conservation of Sea Turtles and the Comisión Permanente del Pacífico Sur, with publicly available data like that of the South Pacific TurtleWatch website (https://www.upwell.org/sptw) can help catalyze regional action and work to prevent fishery interactions with this Critically Endangered population.

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