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Post-capture movements of loggerhead turtles in the southeastern Pacific Ocean assessed by satellite tracking

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ABSTRACT: The post-capture movements made by loggerhead sea turtles *Caretta caretta* in the southeastern Pacific Ocean were monitored from 2003 to 2007. Fourteen loggerhead turtles were fitted with satellite transmitters and released off the coast of Peru. All turtles were juveniles (curved carapace length range: 40.5 to 68.5 cm) incidentally captured by small-scale longline fishing vessels from southern or central Peru. Track durations were highly variable (mean ± SD: 143 ± 90 d; range: 8 to 297 d) with no clear signs of immediate post-release mortality. Upon release, all turtles moved offshore beyond the continental shelf. Eight of 11 turtles tracked for >60 d had final displacements of <750 km, suggesting that loggerhead turtles often maintain extended residency in these waters and that this area is an important foraging zone for loggerhead turtles of southwest Pacific origin. Satellite tracks also showed a substantial overlap of areas used by turtles with known Peruvian longline fishing effort. Turtles spent 75% of their time within the area fished by this fleet (based upon observed sets). This suggests that turtles are vulnerable to fishery interactions and that bycatch mitigation measures should be employed to minimize fishery impacts on loggerhead turtles. The loggerhead turtles tracked during this study spent ca. 51% of their time in Peruvian waters, 39% in international waters and 9% in Chilean waters, which emphasizes the need for a multinational approach to sea turtle conservation and fisheries management in the region.

KEY WORDS: *Caretta caretta* · Peru · Chile · Small-scale fisheries · Bycatch · Habitat · Governance

INTRODUCTION

Many large marine vertebrates such as sharks, sea turtles, seabirds and marine mammals have complex life histories that encompass wide spatiotemporal scales. This situation places them at repeated risk of interaction with multiple anthropogenic threats that have been associated with the population declines seen in many species (e.g. Tasker et al. 2000, Baum et al. 2003, Read et al. 2006, Wallace et al. 2010). Key among these threats is incidental capture (bycatch) in marine fisheries gear (e.g. longlines and driftnets) operating in pelagic zones (Hall et al. 2000). The loggerhead sea turtle *Caretta caretta*, which is found worldwide in temperate and tropical waters (Bolten 2003), is one such species affected by bycatch and is in decline in many parts of its range (Lewison et al. 2004, Wallace et al. 2008).

The life history of loggerhead sea turtles operates at oceanic scales, with nesting sites, juvenile developmental habitats and adult foraging grounds for the same population often separated by thousands of kilometers (Bolten 2003). In the North Pacific Ocean, loggerhead turtle nesting, which is confined to Japan, has

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been linked through genetic analyses and satellite tracking to aggregations of juveniles and subadults found in the central and eastern Pacific (Bowen 1995, Nichols et al. 2000, Polovina et al. 2006, Howell et al. 2010). In the South Pacific Ocean, decades of intense monitoring in eastern Australia has helped in defining many aspects of the nesting and oceanic ecology of loggerhead turtles in the western South Pacific region and in describing declining trends in abundance of that population (Limpus & Limpus 2003a). However, it was not until 2004 that the species was confirmed in the southeastern Pacific Ocean (SEP) through a combination of onboard and shore-based fisheries monitoring (Alfaro-Shigueto et al. 2004). Genetic studies have shown that the juvenile loggerhead turtles found in the SEP originate from Australian and New Caledonian rookeries (Alfaro-Shigueto et al. 2004, Boyle et al. 2009). Additional reports now also confirm the occurrence of loggerhead turtles off Ecuador and Columbia (Alava 2008) and Chile to a latitude of 32° S (Donoso & Dutton 2010). Alfaro-Shigueto et al. (2008) report primarily small- to medium-sized juveniles and subadult-sized turtles found off the Peruvian coast (curved carapace length [CCL] range: 35.9 to 86.3 cm) while Donoso & Dutton (2010) and Alava (2008) reported similar-sized, and perhaps somewhat larger, loggerhead turtles captured by industrial swordfish longline vessels in Chile (CCL range: 47 to 84 cm) and small-scale longline vessels in Ecuador (CCL range: 50 to 80 cm). However, each of these studies was fishery dependent and thus may only represent those sizes of turtles vulnerable to capture by these particular fishing gears.

The wide dispersal of loggerhead turtles combined with their omnivorous feeding habits (which result in opportunistic foraging on fishing bait), leads to high levels of bycatch in coastal and pelagic fisheries, particularly near-surface longlines (Lewison et al. 2004, Peckham et al. 2008, Tomás et al. 2008, Wallace et al. 2008). These fishery interactions have led to sizeable takes of loggerhead turtles globally (Lewison et al. 2004, Gilman et al. 2006, Wallace et al. 2008). As a result of this situation, the need to improve our understanding of the pelagic life stages of sea turtles and their interactions with fisheries have been identified as research priorities (Hamann et al. 2010).

There has also been growing awareness of the need to assess and address the issue of post-release mortality, that is, the potential for animals to die from fishery-related injury after being released from fishing gear (Bjorndal et al. 2003, Hays et al. 2003). Such information is necessary in determining fishery-related morality rates but is particularly challenging to evaluate without a means to track animals after their release. Assessments of post-release mortality based upon satellite tracking of released animals has been attempted with sea turtles, including loggerhead turtles (Chaloupka et al. 2004, Swimmer et al. 2006, Sasso & Epperly 2007, Howell et al. 2010, Snoddy & Southwood Williard 2010) as well as with other marine megafauna including blue sharks *Prionace glauca* (Moyes et al. 2006) and blue marlin *Makaira nigricans* (Graves et al. 2002).

The SEP (Fig. 1) is 1 of 4 eastern boundary current systems on earth and is a highly dynamic and productive marine ecosystem (Carr 2001). It is dominated by the Humboldt Current System (HCS), which is a wind-induced coastal upwelling system. Winds in this system move along the Peruvian coast toward the equator before turning westward into the Pacific Ocean and result in year-round, nutrient-rich upwelling (Bakun & Weeks 2008). This cold, nutrient-rich coastal upwelling yields high levels of primary and secondary productivity and makes the HCS one of the world's most productive marine ecosystems (Carr 2001, Taylor et al. 2008).

Aside from supporting a considerable abundance of flora and fauna, the HCS also supports large fishing industries (Bertrand et al. 2004, Jahncke et al. 2004, Thiel et al. 2007). Indeed, ~16 to 20% of global annual fish production is derived from the region (Heileman et al. 2009). There are also very large and dispersed small-scale fleets, with ~40 000 small-scale vessels fishing the coastal and offshore waters of Ecuador, Peru and Chile (Arriaga & Martinez 2003, OECD 2009, Alfaro-Shigueto et al. 2010). Bycatch of seabirds, cetaceans and sea turtles, including loggerhead turtles, has been documented in these small-scale fisheries in Peru (Awkerman et al. 2006, Alfaro-Shigueto et al. 2010, Gilman et al. 2010, Mangel et al. 2010). This is of concern given the 86% decline in loggerhead turtle nesting reported for eastern Australia nesting beaches over a 23 yr period, despite local conservation efforts including nesting beach and in-water protected areas, and hatchling management and controls on some fisheries known to affect the species (Limpus & Limpus 2003b).

The purpose of the present study was to improve our understanding of the ecology of loggerhead turtles in the SEP region. More specifically, we were interested in (1) assessing loggerhead turtle at-sea movements and distribution, (2) determining their habitat selection and (3) gaining preliminary insights into the effects of injury and potential for post-hooking mortality.

MATERIALS AND METHODS

Turtle characteristics. Fourteen loggerhead turtles were fitted with satellite transmitters between March 2003 and February 2007 (Table 1). The turtles were incidentally entangled or hooked by longline gear set

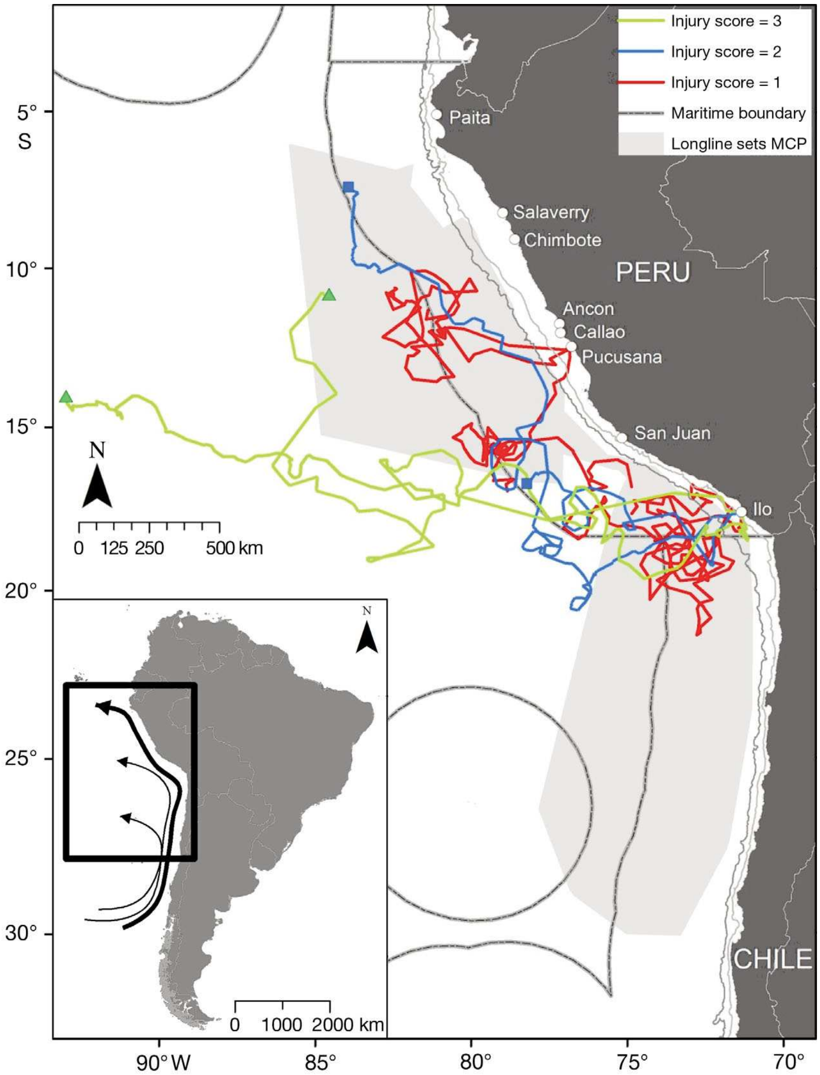

Fig. 1. *Caretta caretta.* All turtle track locations (turtles tracked for 60+ d) by level of injury and showing a polygon of longline fishing effort monitored from 8 ports (242 trips, 1771 sets) collected by fisheries observers from 2000 to 2007 (Alfaro-Shigueto et al. 2008). Color shading of tracks indicates injury scores. Red: injury score 1 (n = 7); blue: injury score 2 (n = 4); green = injury score 3 (n = 3). The termination points of tracks of injury scores 2 and 3 are also marked with colored squares and triangles, respectively. Tracked loggerhead positions were within fishing area boundaries from 75 ± 33 % of the time (range, 13 to 100 %) (500 and 2000 m bathymetric contours are also shown). Inset shows the predominant current patterns (arrows) of the southeastern Pacific Ocean. MCP: minimum convex polygon

from small-scale fishing vessels targeting sharks (mainly blue sharks and short-fin mako sharks *Isurus oxyrinchus*) and dolphin fish *Coryphaena hippurus* in oceanic waters. The vessels operated out of the ports of Ilo (71.33° W, 17.63° S) and Pucusana (76.78° W, 12.48° S) in southern and central Peru, respectively (Fig. 1). These vessels used Mustad classic J type fishing hooks with a 10° offset and ranged in size from 1 to 3 (for a detailed description of the fishery see Alfaro-Shigueto et al. 2010). The precise location of capture is known for 11 of the 14 turtles. The study animals ranged in size from 40.5 to 68.5 cm CCL, measured from nuchal notch to posterior most tip, and were thus classified as juveniles, as reported by Alfaro-Shigueto et al. (2008).

The turtles used in our study were captured by collaborating fishers during the final set of each fishing trip to allow prompt return to port for transmitter attachment. To further minimize time in captivity, turtles were released within ~30 min of the completion of transmitter attachment several kilometers offshore, typically within 24 h of their original capture. All loggerhead turtles used in the study were active at time of capture (not moribund or comatose) and fishers were given detailed instructions on how to safely handle and maintain the turtles aboard. All visible fishing hooks and entangling line were removed from the turtles before release.

We assigned an injury score to each turtle based upon the location and severity of any visible injuries sustained during the capture process following criteria described by Chaloupka et al. (2004). We used a 3 point injury scale in which level 1 referred to turtles with external injuries only (including those that were only entangled in longline branchlines), level 2 indicated minor injuries to the mouth cavity or lower mandible and level 3 indicated more severe injuries including turtles deeply hooked in the esophagus or soft palate. This examination was primarily external in nature (except in those cases of level 3 injuries) and was not meant as an overall turtle health assessment (as in Heithaus et al. 2007), but rather as a scoring of the injuries associated with the turtle's capture.

Transmitter application and data analysis. We used satellite transmitters (platform transmitter terminals [PTTs] from Telonics and from Wildlife Computers) in the study (Table 1). We attached PTTs to the anterior central scutes of the carapace using the fiberglass cloth and polyester resin method described by Balazs et al. (1996) or with PowerFast™ 2-part marine epoxy (Coyne et al. 2009; Table 1). PTTs had one of 2 laddered duty cycles (Table 1) where Duty Cycle 1 was set to transmit 24 h on (Month 1), 6 h on and 13 h off (Months 2 to 3) and 6 h on and 25 h off (>Month 3). Duty Cycle 2 was set to transmit 24 h on (Month 1), 24 h on and 48 h off (Months 2

Table 1. *Caretta caretta*. Summary of environmental and tracking variables for 14 loggerhead turtles captured as bycatch off the coast of Peru. Ports are Ilo (I) and Pucusana (P). Platform transmitter terminal (PTT) models SPOT5 and SDR-T16 were obtained from Wildlife Computers, while the remainder (ST-18, ST-20, ST-20D, A1010) were from Telonics. Attachment methods referred to used fiberglass resin (F) or Powerfast epoxy (P). Duty cycle 1 was a laddered program set to transmit 24 h on (Month 1), 6 h on and 13 h off (Months 2 to 3) and 6 h on and 25 h off (>Month 3). Duty cycle 2 was a laddered program set to transmit 24 h on (Month 1), 24 h on and 48 h off (Months 2 to 3), 24 h on and 72 h off (Months 4 to 5) and 24 h on and 96 h off (>Month 6). Injury score 1: external injuries (including entanglement); injury score 2: minor internal injuries to mouth or lower mandible; injury score 3: severe injuries due to deep hooking. D refers to displacement (Columns 10 and 11). CCL = curved carapace length

Turtle no.	CCL (cm)	Deployment date	Port	PTT model	Attachment method	Duty cycle	Injury score	Track duration (d)	Maximum D (km)	D rate (km d^{-1})	Maritime zone (%) Peru	Chile	High seas	Time in fishing zone (%)	Capture to release distance (km)	Closest approach to capture (km) | (d)
CC1	63.2	25 Mar 03	I	ST-18	F	1	1	223	446	2.00	16	82	2	100		
CC2	64.0	24 Oct 03	I	ST-18	F	1	1	136	479	3.52	73	0	27	39	394	248 | 71
CC3	68.0	24 Oct 03	I	ST-18	F	1	1	142	593	4.18	78	7	15	55	399	89 | 85
CC4	61.5	7 Apr 05	I	ST-20	F	1	3	297	2 337	7.87	29	4	67	20	295	118 | 55
CC5	65.9	14 Jul 05	I	SDR-T16	F	1	3	289	1 658	5.74	7	0	93	13		
CC6	56.5	3 Feb 06	P	ST-18	F	1	1	147	672	4.57	33	0	67	100	249	228 | 5
CC7	54.2	5 Feb 06	P	ST-18	F	1	1	114	581	5.10	59	0	41	100	229	142 | 8
CC8	68.5	14 Nov 06	P	ST-20D	F	1	1	94	522	5.55	68	0	32	98	593	187 | 81
CC9	65.5	13 Jan 07	I	SPOT5	F	2	1	79	372	4.71	66	11	23	100	124	62 | 18
CC10	64.1	13 Jan 07	I	SPOT5	P	2	2	51	395	7.74	0	63	37	100	117	48 | 4
CC11	40.5	13 Jan 07	I	SPOT5	P	2	2	48	361	7.53	16	75	9	100	126	58 | 34
CC12	60.8	16 Jan 07	I	SPOT5	P	2	3	8	60	7.50	100	0	0	100		
CC13	51.3	5 Feb 07	I	A-1010	P	1	2	121	721	5.96	97	3	0	70	98	25 | 3
CC14	65.0	8 Feb 07	I	A-1010	P	1	2	249	1 752	7.04	35	1	64	61	245	101 | 7

to 3), 24 h on and 72 h off (Months 4 to 5) and 24 h on and 96 h off (>Month 6).

Positional data were received from Service ARGOS and managed with the Satellite Tracking and Analysis Tool (STAT, Coyne & Godley 2005). Argos positional data are accompanied by indicators of their spatial accuracy where positions assigned location Class 3 are of greatest accuracy (<350 m), and those with location Class 0 are the least accurate (>1 km). Positions assigned Classes A and B have no estimate of their accuracy. These data were subjected to a combination of filtering procedures to eliminate potential outliers. Argos-derived location Classes 3, 2, 1, 0, A and B for turtle positions were retained for this analysis (Witt et al. 2010) and filtered based upon speed (>5 km h^{-1} excluded, Luschi et al. 1998) and turning angle (<25° excluded). Tracks were also reduced to one location per day to produce an unbiased data set of all environmental and behavioral variables (see De Solla et al. 1999 for further discussion of handling autocorrelation in animal movement data sets). For days when more than one location was obtained, the position of highest quality Argos location class was retained. If multiple positions for a given day were of the same highest quality, the location nearest to 12:00 h local time was selected. Following track filtering, the first 7 d of each track after release were eliminated to minimize any artifact introduced by transporting and releasing turtles relatively close to the coast. We used ArcMap 9.2 (ESRI) to display turtle positions and the Hawth's Tools Extension (www.spatialecology.com/htools) to create minimum convex polygons of longline fishing effort.

Longline fishing effort data detailed in Alfaro Shigueto et al. (2008) was used to examine the overlap with the turtles tracked in this study. Trained onboard observers collected data on fishing effort and catch, including set positions (using handheld GPS), aboard fishing vessels from 8 ports (242 trips, 1773 sets) for the years 2004 to 2007. This is the same fleet from which the loggerhead turtles in this study were captured. A polygon of Peruvian fishing effort was created by combining minimum convex polygons of fishing effort from the 8 ports.

Satellite tracking data were compared with bathymetry and sea surface temperature (SST) data. Bathymetric values were obtained from the Global Bathymetric Chart of the Oceans (GEBCO, www.gebco.net; IOCIHO 2003). An 8 d composite 4 km spatial resolution Nighttime

(4 micron) Sea Surface Temperature Dataset from the MODIS-Aqua satellite was used to determine SST at the location of each turtle's daily position (Feldman & McClain 2009). Maritime political boundaries were obtained from the Flanders Marine Institute maritime boundaries geodatabase v. 5.0 (www.vliz.be). Time within a given boundary was calculated by tabulating entry and exit dates and times from the tracking data and assigning those time periods to their appropriate polygons. Any period >7 d that could not be accounted for owing to lack of positions was discarded (2% of cases), but times <7 d were attributed to the dominant polygon (7% of cases). Data regarding environmental variables, as well as speed of movement, displacement from release location (including 7 d release period) and political boundaries were limited to turtles tracked for 60 d or more (n = 11). Swim speeds are reported as 'minimum overall average' since our speed calculations assume straight line travel between consecutive positions. Descriptive statistics are presented as mean ± SD.

RESULTS

Environmental variables

After their release, all turtles returned to oceanic waters (Fig. 1) and did not appear to return to coastal waters (<200 m). The overall mean depth of the waters occupied was 4286 ± 376 m (range of means: 3392 to 4704 m, median = 4352 m, n = 11). The average SST was 21.1 ± 2.2°C (range of means: 16.2 to 23.8°C, median = 21.6°C, n = 11; Fig. 2), with only 4% of SST values being <15°C.

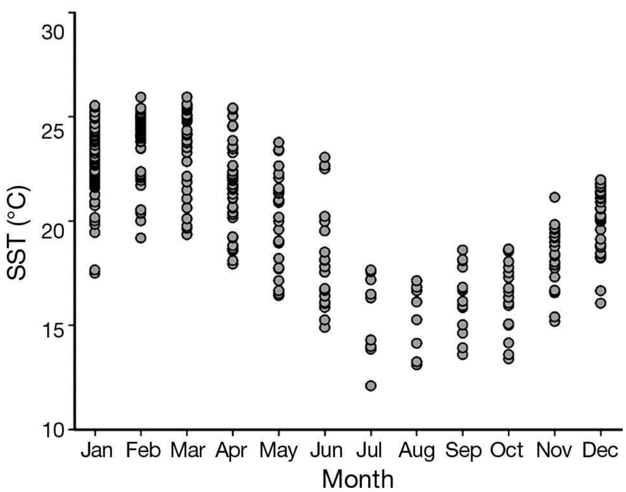

Fig. 2. *Caretta caretta*. Pooled monthly sea surface temperature (SST) for all turtles tracked for >60 d (n = 11)

Track durations

Track durations ranged from 8 to 297 d (mean duration: 143 ± 90 d, median = 129 d, n = 14; Table 1). The minimum overall average swim speed was 0.70 ± 0.11 km h^{-1} (range: 0.57 to 0.90 km h^{-1}, median = 0.66 km h^{-1}, n = 11). There was no effect of turtle size on track duration (randomization test with 10 000 iterations and within and between group randomization: 2-tailed p = 0.96; Fig. 3a). Likewise, there was no effect of level of injury upon track duration (Randomization test: 2-tailed p = 0.99; Fig 3b). There was also no effect of either turtle size (Randomization test: 2-tailed p = 0.96; Fig 3c) or injury score on minimum overall average swim speed (Randomization test: 2-tailed p = 0.12; Fig 3d).

The number of uplinks received per day for each turtle was also examined because an increase in daily signals received could indicate that an animal is floating injured or dead at the surface (Hays et al. 2007). There was no evidence of an increase in daily signals received for any of the tracked turtles (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m433p261_supp.pdf). We also reviewed the battery voltage information for the 4 SPOT5 tags (the only tags for which this information was available) to assess transmitter battery life as a possible reason for termination of the tracks for those turtles. There was no sign of voltage declines sufficient to halt transmission toward the end of the track periods for any of the 4 tags.

Displacement

Maximum displacement ranged from 372 to 2337 km (mean: 921 ± 667 km, median = 593 km; Table 1, Fig. 1 & Fig. S3 in the supplement). Eight of the 11 turtles with tracks lasting >60 d (track duration range: 79 to 223 d) had a final displacement of <750 km. The remaining 3 turtles had track durations ranging from 249 to 297 d and maximum displacements from 1607 to 2337 km.

There was no effect of turtle size on displacement rate (Randomization test: 2-tailed p = 0.64; Fig. 3e), nor was there an effect of capture to release distance on maximum displacement (r = 0.07; Fig. S2a in the supplement). However, there was an effect of level of injury upon displacement rate (Randomization test: 2-tailed p = 0.002; Figs. 3f & S3) in which turtles with injury scores of 2 and 3 had greater displacement rates than those with an injury score of 1.

Logistical constraints meant that turtles could neither be fitted with transmitters *in situ* nor returned to capture location for release. The average distance

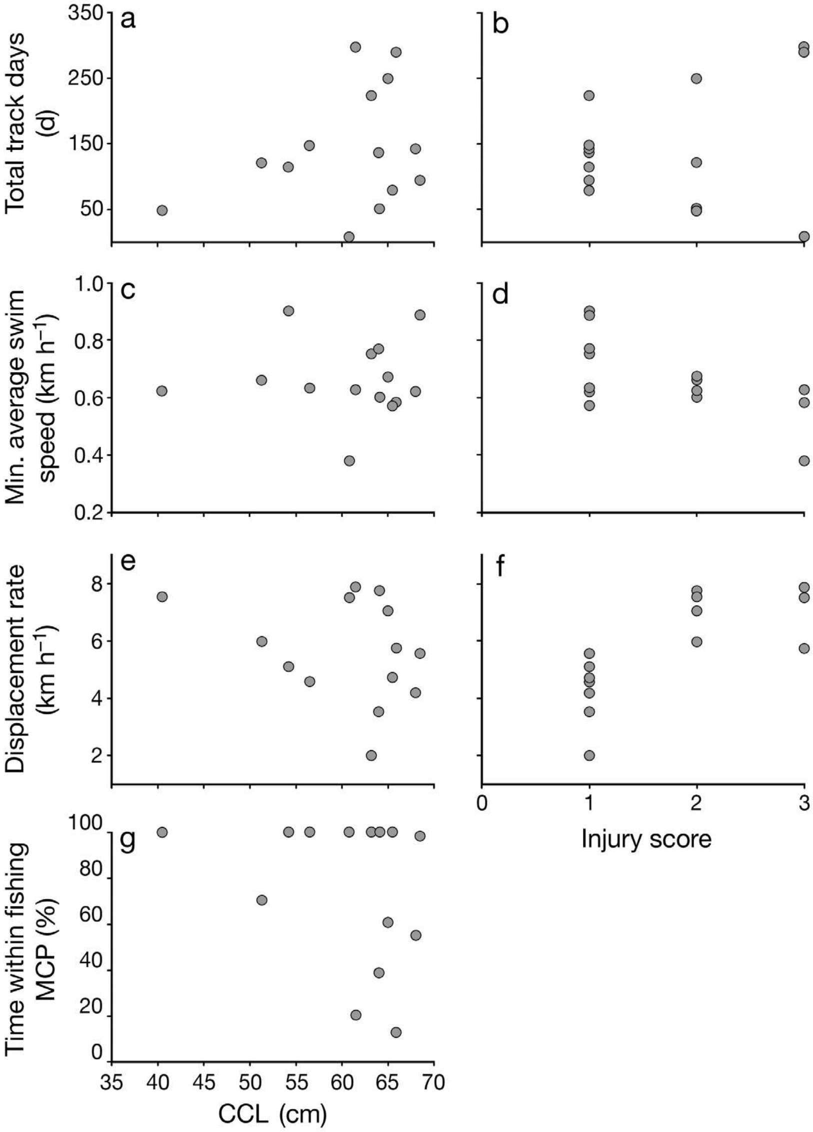

Fig. 3. *Caretta caretta*. Track durations, minimum overall average swim speeds, displacement rates and time within fishing grounds minimum convex polygon (MCP) grouped by turtle size (curved carapace length, CCL) and injury score

between capture and release locations was 261 ± 153 km, (range: 98 to 593 km, median = 245 km, n = 11), but there was no correlation between capture to release distance and distance traveled after 1 mo from the release date ($r = 0.02$, $p = 0.96$; Fig. S2b). There was no clear evidence of high precision homing per se although turtles approached to within 119 ± 75 km (range of minimum distances: 25 to 248 km, median = 101 km, n = 11) of their capture location and did so 34 ± 33 d post-release (range: 3 to 85 d, median = 18 d) (Table 1). As would be expected, there was a correlation between capture to release distance and nearest approach to capture location ($r = 0.66$, $p < 0.05$; Fig. S2c).

Fisheries and governance

Although captured and released in Peruvian waters, our study turtles also moved within Chilean and international waters during tracking periods (Peru: mean = 51 ± 29%, median = 59%, range for individuals = 7 to 97%; Chile: mean = 10 ± 24%, median = 1%, range = 0 to 82%; international waters: mean = 39 ± 30%, median = 32%, range = 0 to 93%; Table 1, Fig. 1). The combined tracks of all turtles covered an area of ~2500 km from east to west and 1600 km from north to south. There was also a large overlap of turtle movements with longline fishing areas. Turtles spent 75 ± 33% (range: 13 to 100%, median = 99%) of their time within previously defined Peruvian small-scale longline fishing grounds (Alfaro-Shigueto et al. 2008). There was no effect of turtle size on time spent within the fishing grounds (Randomization test: 2-tailed $p = 0.86$; Fig. 3g).

DISCUSSION

This work offers insights into post-capture movements of loggerhead turtles in the SEP and represents the first work of its kind with sea turtles in the region. As such, while based upon a relatively small sample, it provides a valuable point of comparison with similar studies of conspecifics elsewhere and can help inform regional and global efforts to better understand fishery impacts on sea turtles (Lewison et al. 2004, Blumenthal et al. 2006, Wallace et al. 2008, McClellan et al. 2009, Alessandro & Antonello 2010) and their post-release mortality (Bjorndal et al. 2003, Hays et al. 2003, Chaloupka et al. 2004, Swimmer et al. 2006, Sasso & Epperly 2007).

Environmental factors

Our work indicates that many of these turtles were ‘resident’ in the waters off Peru and Chile, where they maintained a pelagic lifestyle for the duration of tracking. Turtles spent >97% of their time in waters in excess of 1000 m depth. Moreover, 8 of 11 turtles had final displacements of <750 km from their release point even though track durations extended up to 223 d. These results, while based upon instrumented animals released at locations distinct from their site of capture, support findings from other regions indicating that juvenile loggerhead turtles may be actively selecting key pelagic habitats and are not simply passively distributed by ocean currents (Polovina et al. 2006, Monzón-Argüello et al. 2009, Hays et al. 2010, McCarthy et al. 2010). Furthermore, given the sizes of turtles in this study, this would also be consistent with a transition by juvenile loggerhead turtles from passive to active swimmers at ~40 to 60 cm straight carapace length, as has been reported in the Atlantic Ocean and Mediterranean Sea (Bolten 2003, Cardona et al. 2005, Revelles et al. 2007). However, 3 loggerhead turtles, nos. CC4, CC5 and CC14, did make relatively long movements both north and west, which match the general surface current patterns in the region (Fig. 1). Therefore, loggerhead turtle movements may comprise a combination of active station holding and passive current-driven drifting (Cardona et al. 2005, Hays et al. 2010).

Studies off the Baja California Peninsula indicate that juvenile loggerhead turtles may take up residency for extended periods before returning to the western Pacific Ocean (Nichols et al. 2000, Peckham & Nichols 2003, Seminoff et al. 2004, Etnoyer et al. 2006). Our findings suggest that a similar scenario occurs in the waters off Peru and northern Chile. Moreover, as has been observed in several studies of juvenile loggerhead turtles in the Mediterranean Sea, the animals in our study appeared to avoid the waters of the continental shelf (Cardona et al. 2005, Revelles et al. 2007, Monzón-Argüello et al. 2009). This observation is reinforced by similar findings by Donoso & Dutton (2010) who report loggerhead turtles in pelagic waters offshore from northern Chile. Given the size class of turtles in the present study and for the region (Alfaro-Shigueto et al. 2008), which is primarily the oceanic juvenile stage (Bolten 2003, Limpus & Limpus 2003a), this may be as expected. The findings of Howell et al. (2010) that juvenile loggerhead turtles in the central North Pacific Ocean spent >90% of their time in the upper 15 m of the water column supports the notion of a pelagic foraging lifestyle for this life history stage in this species. Furthermore, if these juvenile turtles have poorly developed diving abilities (Bolten 2003, Cardona et al. 2005, Revelles et al. 2007) then they would not be able to exploit benthic prey found over the shelf and may therefore specialize in pelagic prey, similar to Baja California where the loggerhead turtle population feeds primarily or exclusively upon pelagic red crab *Pleuroncodes planipes* (Nichols et al. 2000, Peckham & Nichols 2003).

The mean SST of 21.1 ± 2.2°C experienced by these turtles was well within their thermal tolerance (Witherington & Ehrhart 1989, Coles & Musick 2000, Milton & Lutz 2003), but the minimum SST experienced by some individuals reached <15°C on several occasions and could therefore be approaching the species' lower thermal tolerance (Coles & Musick 2000, Milton & Lutz 2003). As Howell et al. (2010) note, however, this lower limit may be better considered as a species preference and less as an absolute value. But these cool temperatures do suggest the potential for seasonal north–south movements, as seen in the western Atlantic Ocean (Coles & Musick 2000, Hawkes et al. 2007, Mansfield et al. 2009) and Mediterranean Sea (Bentivegna et al. 2007), that in cooler months probably bring loggerhead turtles that have been recorded in waters off northern Chile (Donoso & Dutton 2010) north into the relatively warmer waters of Peru. It is also interesting to note that Donoso & Dutton (2010) report an increase in loggerhead turtle bycatch associated with an incursion of a 21°C warm zone for the year 2001, and also found a bimodal association of SST (18 and 21°C) with the occurrence of loggerhead turtles off Chile. This coincides closely with the mean SST for the loggerhead turtles tracked in our study and with findings in the central North Pacific Ocean that loggerhead turtle bycatch by the Hawaii-based longline fleet was highest when setting at oceanic fronts of 17 and 20°C (Polovina et al. 2000). That loggerhead turtles may aggregate in waters of certain temperatures may also help explain their absence from continental shelf waters in Peru. These areas are dominated by cold, coastal upwelling waters ranging from 15 to 17°C in the winter and 15 to 19°C in the summer months (Bertrand et al. 2004). The apparent avoidance of the continental shelf by loggerhead turtles in our study may therefore be driven by one or more of the (possibly related) drivers of avoidance of cold coastal waters, active selection of preferred foraging habitat or lower risk of predation (Bolten 2003, Hawkes et al. 2007, Eckert et al. 2008). Additional studies to further detail loggerhead turtle prey species and foraging behavior in the SEP would help resolve this question.

Fisheries and governance

The turtle movements we describe overlapped with the area operated by the Peruvian small-scale longline fishery (Alfaro-Shigueto et al. 2008; our Fig. 1). Indeed, they fell within the fishing grounds of vessels monitored from 8 ports for 75% of their track durations and one-half of the study turtles spent the entire track period within the fishing zone. This profoundly underestimates the extent of overlap with this one fishery since it operates from at least 19 ports and sets an estimated 80 million hooks per annum (Alfaro-Shigueto et al. 2010). Alfaro-Shigueto et al. (2010) also note that the Peruvian small-scale longline fleet sets their mainline at the ocean surface. Therefore, if juvenile loggerhead turtles spend >90% of their time within the upper 15 m, as has been reported in the central North Pacific Ocean (Howell et al. 2010), then they have a heightened risk of interacting with this fishing gear. There are, in addition, other fisheries such as driftnets, industrial purse-seines, and longline fleets in international waters that have not been assessed but are of concern because of their potential for interactions with loggerhead turtles in the region.

Chaloupka & Limpus (1997, 2001) have reported on fisheries in the western Pacific Ocean that have bycatch of loggerhead turtles. But it is now clear that at least some of the loggerhead turtles from the Australian and New Caledonian stocks spend extended periods of time outside the western Pacific region. Research has shown that loggerhead turtle maturation, and the oceanic movements that accompany it, may take decades, with age at maturity estimates ranging from 10 to >30 yr (Zug et al. 1995, Parham & Zug 1997, Chaloupka 1998, Bjorndal et al. 2000, Bjorndal & Bolten 2001, Casale et al. 2009). This implies extended periods, possibly decades, in a given life stage and its accompanying habitat during which pelagic juveniles in particular are exposed to contact with the other fisheries operating in international waters. While there is some information for the central North Pacific Ocean for loggerhead turtle interactions with the Hawaii-based longline fleet, similar information is absent for the central South Pacific. However, Domingo et al. (2010) observed a bycatch of loggerhead turtles by Uruguayan-flagged vessels operating in this region. Donoso & Dutton (2010) document loggerhead turtle interactions with the Chilean industrial swordfish longline fishery, but also note the lack of information on other fleets in the area, including the Spanish longline fleet operating out of southern Peru. Peckham et al. (2007, 2008) have shown for the North Pacific region that fisheries impacts on loggerhead turtles, including small-scale (or artisanal) fisheries, can be severe. Likewise, in other regions and with other sea turtles species, similar, but not fully understood, trends of prolonged exposure to fishery interactions, including small-scale fisheries, have been reported (Lewison et al. 2004, Alfaro-Shigueto et al. 2007, Casale 2010, Wallace et al. 2010). There is clearly a need for a full, detailed assessment of bycatch and potential mitigation measures in the Peruvian small-scale fleet as well as the full suite of substantial industrial and small-scale fisheries operating in the region, especially given the rapid and sustained decline of this species in Australia (Limpus & Limpus 2003b).

Injury effects

One of the objectives of this study was to use satellite tracking movement data to gain insights into the effects of injury to bycaught sea turtles. We found no effect of injury on track duration. However, there appears to have been an effect of injury on the rate of displacement. Turtles we scored as having minor or severe injuries (scores 2 and 3) displaced at a much faster rate than turtles with only external injuries (score 1). The reason for this difference is not clear. Turtles with the fastest displacements tended to move in the same general direction as main surface currents in the region (Fig. 1 inset) so they could be exhibiting some passive drifting. But the long duration and characteristics of the tracks (i.e. battery voltage, uplinks per day) suggest that injuries were not fatal. We also acknowledge that the turtles in this study may have had pre-existing injuries that were not visible or accounted for in our ranking. Thus our results, while indicative of a turtle's injury status, do not represent a complete understanding. Similar to the findings of Howell et al. (2010) 2 of our longest track durations came from animals we categorized as having severe injuries. Sasso & Epperly (2007), reporting on juvenile loggerhead turtles in the North Atlantic Ocean, also observed that lightly hooked loggerhead turtles in their study had a similar survival rate to uninjured, control turtles. While acknowledging the small sample size of the present study, these results suggest that loggerhead turtles are able to survive for extended periods with injuries, including severe injuries. Or they might indicate that our understanding of what entails a minor or severe injury to a sea turtle is incomplete. One transmitter failed after only 8 d but could not be attributed to death of the turtle, nor could death be attributed to any of the remaining turtles, which transmitted from 48 to 297 d. Use of PTTs or pop-up satellite archival tags (PSAT) with dive data or depth sensors could help investigators make more informed determinations, but still do not provide clarity in revealing a turtle's fate (Chaloupka et al. 2004, Swimmer et al. 2006). Future studies in this fishery should determine the prevalence of entanglements as well as minor and severe hookings of turtles in order to help evaluate their likelihood of survival and the relative risk posed by the fishery. The effects of sublethal injuries also need to be explored further as these could lead to reduced fitness as a result of tissue damage, infection, impaired feeding or swimming, or lead to a greater risk of predation (Watson et al. 2005, Sasso & Epperly 2007). Such effects may be particularly important in areas where turtle habitat strongly overlaps fishing grounds and turtles thus may face repeated capture and injury. Studies of longline fisheries bycatch of loggerhead turtles in the region do indicate that the majority of bycaught turtles are released alive (Alfaro-Shigueto et al. 2008, Donoso & Dutton 2010), as do reports of longline fisheries in other regions (Kotas et al. 2004, Gilman et al. 2007, Casale 2010). This situation could be further improved through fisher training in sea turtle safe handling and release methods and the adoption of bycatch mitigation measures such as the use of circle hooks or mackerel type bait, which have been shown to reduce sea turtle bycatch and injury type and severity in other fisheries (Watson et al. 2005, Gilman et al. 2007, Yokota et al. 2009).

The pelagic distribution of loggerhead turtles observed in the present study highlights the challenges of research on this species in the SEP region, and generally of other highly mobile, pelagic species. Monitoring through the use of onboard observers on fishing vessels has provided valuable information on size classes and distribution (Alfaro-Shigueto et al. 2004, 2008). But this type of fishery-dependent data does not necessarily describe the full ecology of the species in the region. Here we have reported on the movements of loggerhead turtles bycaught by small-scale longline fishing vessels. While we have limited our analyses to only those turtles that have tracks of 60 d or more (as a means to control for potentially aberrant behavior by injured animals), it is possible that these tracks do not fully represent the normal habitat or behavior of the species in the region. We also recognize that other variables could have an effect on track duration (e.g. attachment method, location of capture, transmitter type), but small sample size limits the degree to which these variables can be fully explored. However, given the extremely high level of fishing effort in the region (Alfaro-Shigueto et al. 2010) and the resulting high likelihood of interactions between fisheries and loggerhead turtles, this information is extremely valuable in improving our understanding of the species in the SEP and its interactions with fisheries.

Future directions

Much remains to be learned about loggerhead turtles. While we believe results from the present study provide extremely useful information on many aspects of loggerhead turtles in the SEP, satellite tracking of uninjured animals is recommended to obtain additional fishery-independent data. Moreover, similar to research in other ocean basins and with other species (e.g. Moyes et al. 2006, Swimmer et al. 2006, Howell et al. 2010), information on loggerhead turtle dive profiles and possible relationships to oceanographic variables like currents, fronts and eddies would be extremely valuable for defining 3-dimensional habitat use and further assessing their vulnerability to fisheries bycatch. Such research can also provide information to help manage these fisheries to minimize opportunities for sea turtle bycatch (Blumenthal et al. 2006, McClellan et al. 2009, Godley et al. 2010).

As we have noted, recent work has helped to better characterize some Peruvian and Chilean fisheries and their sea turtle interactions (Alfaro-Shigueto et al. 2008, 2010, Donoso & Dutton 2010), but almost nothing is known about those interactions in the other small-scale and industrial fleets from many nations operating in the southern Pacific Ocean. Evidence of interactions with Uruguayan-flagged commercial longliners operating in the Pacific Ocean have been reported (Domingo et al. 2010), but there remains a vast swath of the central South Pacific Ocean that loggerhead turtles most probably inhabit for many years before they return to neritic habitats in the western Pacific Ocean. There is clearly a need for a more complete assessment of the fisheries that loggerhead turtles are likely to encounter during that time to better identify, categorize and rank the threats they face and to identify and implement effective mitigation strategies.

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