PROCEEDINGS OF THE ROYAL SOCIETY B

FirstCite e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2010.2467
Published online

Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic

Matthew J. Witt[1], Eric Augowet Bonguno[2], Annette C. Broderick[1], Michael S. Coyne[1,3], Angela Formia[4,5], Alain Gibudi[6], Gil Avery Mounguengui Mounguengui[7], Carine Moussounda[8], Monique NSafou[2], Solange Nougessono[2], Richard J. Parnell[4], Guy-Philippe Sounguet[9], Sebastian Verhage[10] and Brendan J. Godley[1,*]

[1]*Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Exeter, UK*
[2]*Agence Nationale des Parcs Nationaux, Batterie IV, BP 20379, Libreville, Gabon*
[3]*SEATURTLE.org, 1 Southampton Pl, Durham, NC 27705, USA*
[4]*Wildlife Conservation Society, Global Conservation Program, 2300 Southern Boulevard, Bronx, NY 10460, USA*
[5]*Dipartimento di Biologia Animale e Genetica, University of Florence, Via Romana 17, 50125 Firenze, Italy*
[6]*PROTOMAC, BP 2104, Libreville, Gabon*
[7]*IBONGA-ACPE, BP 178, Gamba, Gabon*
[8]*Centre National des Données et de l'Information Océanographiques, BP 10961, Libreville, Gabon*
[9]*Aventures Sans Frontières, BP 7248, Libreville, Gabon*
[10]*World Wide Fund for Nature, BP 9144, Libreville, Gabon*

Despite extensive work carried out on leatherback turtles (*Dermochelys coriacea*) in the North Atlantic and Indo-Pacific, very little is known of the at-sea distribution of this species in the South Atlantic, where the world's largest population nests in Gabon (central Africa). This paucity of data is of marked concern given the pace of industrialization in fisheries with demonstrable marine turtle bycatch in African/Latin American waters. We tracked the movements of 25 adult female leatherback turtles obtaining a range of fundamental and applied insights, including indications for methodological advancement. Individuals could be assigned to one of three dispersal strategies, moving to (i) habitats of the equatorial Atlantic, (ii) temperate habitats off South America or (iii) temperate habitats off southern Africa. While occupying regions with high surface chlorophyll concentrations, these strategies exposed turtles to some of the world's highest levels of longline fishing effort, in addition to areas with coastal gillnet fisheries. Satellite tracking highlighted that at least 11 nations should be involved in the conservation of this species in addition to those with distant fishing fleets. The majority of tracking days were, however, spent in the high seas, where effective implementation of conservation efforts is complex to achieve.

Keywords: satellite tracking; fisheries bycatch; marine vertebrate; South Atlantic; foraging; conservation

1. INTRODUCTION

Long-lived marine vertebrates face risks throughout their range, and their life-history characteristics place them at risk of repeated and sometimes deleterious interactions with anthropogenic threats [1]. Management of human activities that pose risk to these species is complex, as multiple nations are involved and species can spend extended periods of time in the high seas. In these regions, only a limited range of specialized legal conventions exist to manage the human activities of abiding parties [2]. To quantify the level of threat posed by human activities, it is necessary first to gain an understanding of species movements in tandem with a coherent description of the nature and spatial footprint of potential risks (e.g. [3]).

Satellite telemetry offers a useful approach for tracking the movement of migratory species and has been used on all major taxonomic groups of marine vertebrates (e.g. pinnipeds [4], seabirds [5], cetaceans [6] and large pelagic fishes [7]). For leatherback turtles (*Dermochelys coriacea*), satellite tracking has provided important insights into their horizontal and vertical movements in the North Atlantic [8–11] and Indo-Pacific [12–15] (electronic supplementary material, table S1). Leatherback turtles are generally epipelagic reptiles (i.e. occurring in waters less than 200 m depth) [10]. They are the most widely distributed of all marine turtle species and appear to be bounded by the 10–12°C isotherms at mid-latitudes [16,17], although they can tolerate

* Author for correspondence (b.j.godley@exeter.ac.uk).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2010.2467 or via http://rspb.royalsocietypublishing.org.

Received 11 November 2010
Accepted 7 December 2010

near-freezing waters for short periods of time during diving [18]. Adults return to breed and nest in the region of their natal tropical beaches on variable reproductive schedules [19], which are governed by food availability during years of non-breeding away from reproductive grounds [20].

Population trajectories observed at leatherback turtle rookeries are somewhat varied. In the Pacific, numbers have undergone precipitous decline [21] with no sign of rebound. The North Atlantic populations have seen varied trajectories, with some decreasing [22] while others are stable or are increasing [23–25]. Only recently, however, has the magnitude of the South Atlantic population—the world's largest—been fully described [26]; with as many as 40 000 females nesting in an area centred upon Gabon, the trajectory of this population nevertheless remains uncertain. Leatherback turtle movements in South Atlantic coastal habitats during the breeding season have been reported [27,28]. With the exception of a few flipper tag returns from South America [29] and the satellite tracking of four individuals from the Rio de la Plata Estuary (Uruguay, South America) [30] demonstrating seasonal movements along the South American coastline, there is no comprehensive knowledge of their at-sea distribution.

The precipitous decline in the Indo-Pacific leatherback turtle is thought to have been driven, at least in part, by fisheries interactions [21]. Given the increasing industrialization of fisheries in Africa [31], and demonstrable bycatch in longline [3,32] and gillnet fisheries [33], we set out to describe the at-sea distribution of leatherback turtles from this major rookery. In particular, we describe: (i) post-nesting dispersal patterns, including migratory routes; (ii) general patterns of movement in the South Atlantic, in contrast to those in the North Atlantic, to explore whether there is opportunity for stock-mixing across the Equator; and (iii) habitat-use contextualized with oceanographic data and known data on intensity of putative threats.

2. MATERIAL AND METHODS

(a) *Field sites and attachment methods*

Platform transmitter terminals (PTTs; $n = 25$) were attached to female leatherback turtles nesting in Gabon over four nesting seasons (2006: $n = 8$; 2008: $n = 5$; 2009: $n = 10$; and 2010: $n = 2$). Turtles were encountered while undertaking night-time patrols at Pongara ($n = 11$) and Mayumba ($n = 14$) National Parks, two of Gabon's most dense nesting regions [26]. Morphometric data (e.g. curved carapace length (cm)) were collected from each female leatherback turtle fitted with a PTT. In 2006, Kiwisat 101 PTTs ($n = 3$; mass 440 g; 2 × lithium C cells; Sirtrack, New Zealand) and Satellite Relay Data Loggers ($n = 5$; mass 400 g; 1 × lithium D cell; Sea Mammal Research Unit, UK) were deployed using a harness system fitted during the nesting process, analogous to the approach of Eckert & Eckert [34]. In 2008, Kiwisat 202 PTTs ($n = 5$; mass 150 g; 3 × lithium AA cells; Sirtrack) were deployed using a 'through-the-keel' approach, where PTTs were directly attached to the carapace, analogous to the method of Fossette et al. [35]. In 2009 and 2010, MK10-A ($n = 8$; mass 200 g; 4 × lithium AA cells) and MK10-AF PTTs ($n = 4$; mass 250 g; 4 × lithium AA cells; Wildlife Computers, Washington, USA) were deployed using the same 'through-the-keel' direct attachment method. These attachment methods represented state-of-the-art technology for the seasons in which they were used and all efforts were made to ensure PTTs and the associated attachments minimized impacts upon study animals. All PTTs were fitted with salt-water switches to suppress transmissions while individuals were submerged. PTTs were not duty-cycled, with the exception of Kiwisat 202 PTTs, which switched off for 6 h daily between 00.00 and 06.00 Coordinated Universal Time (UTC).

(b) *Preparing Argos location and PTT data*

Argos data were automatically downloaded from CLS Argos [36] using the Satellite Tracking and Analysis Tool [37]. To reconstruct the movements of leatherback turtles, we used Argos locations assigned the standard location classes (LC) of 3, 2, 1 and 0, and auxiliary LC of A and B. These classes represent the estimated spatial accuracy of each location. Locations assigned LC 3 are of greatest accuracy ($\leq$ 350 m) and locations assigned LC A or B have no estimate of accuracy. Locations classified as invalid (LC Z) were discarded as they did not pass at least two of Argos's plausibility tests (i.e. minimum residual error, transmission frequency continuity, minimum displacement and plausibility of velocity between locations [36]). The time series of locations for each leatherback turtle were subject to speed and azimuth filtering (10 km h^{-1} and 40°, respectively) [38]. Location data were then resolved to single best daily locations, representing the location with the greatest spatial accuracy (highest LC) received in each 24 h period (00.00–23.59 UTC). When more than one location of equal accuracy was received in any 24 h period, we selected the first. For days when no locations were received, we interpolated locations using cubic (curvilinear) interpolation [39], but only for periods of up to 7 days following receipt of a valid Argos location. From these location data, a spatial density map was constructed to estimate potential areas of high occupancy. This process used a hexagonal polygon binning process (polygon areas approx. 50 000 km^2) summing spatially coincident leatherback turtle locations to each polygon.

For each leatherback turtle location, we determined: (i) spatially coincident geopolitical zone; (ii) spatially and temporally coincident chlorophyll a concentration (mg m^{-3}) and night-time sea surface temperature (°C) from the satellite-derived MODIS Aqua monthly chlorophyll a and sea surface temperature products (4 km resolution); (iii) longline fisheries effort as occurring in 2000 [3]; and (iv) human impact score [40] representing an integration of anthropogenic drivers of ecosystem change, which includes commercial fisheries catch data for the period 1993–2003. Cumulative impact scores (I_c) are divided into six categories of impact ranging from very low (<1.4) to very high impact (>15.52).

PTTs in 2009 and 2010 (models MK10-A and MK10-AF) also provided summary dive data at 4 h intervals (starting 00.00 UTC) on the proportion of time spent within pre-specified depth ranges.

(c) *Dispersal behaviour and transit speeds*

Reconstructed horizontal movements were visually assessed to determine commonalities in post-nesting dispersal behaviour. The movements of each individual were assigned to one of the three apparent groups: (i) dispersal into habitats of the equatorial Atlantic, south of the Equator and north of the Tropic of Capricorn (23.4°S); (ii) dispersal to temperate habitats off South America; and (iii) dispersal to temperate habitats off southern Africa to a region south of the Tropic of Capricorn and east of the Prime Meridian (0°E).

Time series of movement speed (derived ground-speed, km h^{-1}) and minimum straight-line displacement from the first post-nesting location to all subsequent locations were calculated for each leatherback turtle. Patterns in movement speed were subsequently examined with respect to dispersal groups and PTT attachment methods (i.e. harness or direct attachment) using linear mixed-effects models with maximum-likelihood error estimation in GenStat (v. 12, VSN International, UK). Mean movement speed (km h^{-1}) was calculated over 10-day periods to minimize both potential diurnal effects on speed of movement and variable accuracy estimates from Argos. Mean movement speed was subsequently used as the response variate in the statistical model. Three fixed-effects were used in the model: (i) time since deployment, as turtles generally reduced transit speed as tracking duration increased; (ii) dispersal group; and (iii) PTT attachment method. An identification number for each tracked turtle was included as a random factor, which allowed for repeated observations and variable data volumes for each individual [41]. Only data gathered within the first 150 days of satellite tracking (approx. mean tracking duration) were used from each individual.

3. RESULTS

(a) *Tracking summary*

Female leatherback turtles ($n = 25$; curved carapace length 151 ± 6 cm, mean ± 1 s.d., range 141–163 cm) were satellite-tracked for 154 ± 104 days (mean ± 1 s.d., range 39–504 days) while undertaking post-nesting dispersal from the coast of Gabon (figure 1 and electronic supplementary material, table S2). Of these individuals, 17 were satellite-tracked for more than 100 days and one for more than 365 days. PTTs (mass 267 ± 109 g, mean ± 1 s.d., range 150–440 g) represented $0.1 \pm 0.4\%$ (mean $\pm$ 1 s.d., range 0.4–1.7%) of leatherback turtle body mass. Body mass was estimated using y (mass kg) $= -468.84 + (5.2076 \times \text{CCL (cm)})$ from [42].

The horizontal movements of leatherback turtles (figure 2) allowed individuals to be assigned to one of the three dispersal groups: (i) dispersal to habitats of the equatorial Atlantic ($n = 15$; mean minimum displacement distance 2190 ± 685 km, mean ± 1 s.d., range 1079–3277 km); (ii) dispersal to temperate habitats off South America, including Brazil, Uruguay and Argentina ($n = 5$; mean minimum displacement distance 5378 ± 1970 km, mean ± 1 s.d., range 2527–7563 km); and (iii) dispersal to temperate habitats off southern Africa ($n = 2$; mean minimum displacement 4248 ± 679 km, mean ± 1 s.d., range 3768–4728 km). Two individuals could not be assigned to a dispersal group. No satellite-tracked individual moved further north of the Equator than 0.7°N. The median curved carapace lengths of the three dispersal groups did not differ significantly (Kruskal–Wallis, $\chi^2_{0.05,2}$ 0.27, $p = 0.87$).

(b) *Geopolitical zones and at-sea density*

Female leatherback turtles ranged widely while undertaking their post-nesting movements over the four seasons of satellite tracking (figure 1). Turtles occupied waters of 11 countries bordering the South Atlantic, as follows. African waters: Angola 0.9 per cent of all locations, Equatorial Guinea 3.0 per cent, Gabon 4.7 per cent, Namibia 2.4 per cent, Republic of the Congo 0.7 per cent, Sao Tome and Principe 1.0 per cent, and South Africa 2 per cent. South American waters: Brazil 3.8 per cent, Argentina 0.4 per cent and Uruguay 0.8 per cent. Two per cent of locations occurred in the waters of the UK Overseas Territories of Ascension Island and St Helena. Notably, 78 per cent of all leatherback turtle locations were received from the high seas. Leatherback turtles dispersing into the equatorial Atlantic spent the greatest proportion of time in the high seas (group I; 83.6%) when compared with those destined for temperate habitats off South America (group II; 67.4%) and temperate habitats off South Africa (group III; 77.1%).

Density mapping of leatherback turtle movements (figure 3*a*) highlights the potential importance of the equatorial Atlantic for this species, particularly for individuals assigned to group I, the dominant dispersal group in this study. Density mapping (figure 3*a*) further highlights a putative migratory corridor reaching from Gabon following a south-westerly direction into the high seas from both Pongara and Mayumba National Parks. The circular mean (± 1 s.d.) heading between the first post-nesting location (first Argos location occuring at sea after the final nesting event) and the location at 10 days following departure for each individual (mean time to cross 200 nm EEZ limit of Gabon) was $235 \pm 15°$ ($n = 25$; range 210–271°).

(c) *Ocean sea surface temperature and surface chlorophyll*

In continental shelf habitats, female leatherback turtles moved close to the regions where they are thought to be thermally limited (figure 3*b*) [16,17], extending as far as 39.5° S in temperate habitats off South America (group II) and 40.6° S in temperate habitats off southern Africa (group III).

Movements of female leatherback turtles dispersing into the equatorial Atlantic (group I) were generally restricted to regions of elevated surface chlorophyll (figure 3*b*). Median concentration of satellite-derived surface chlorophyll *a* for the locations of leatherback turtles was 0.15 mg m^{-3} (grand median, $n = 15$; range of medians 0.1–0.6 mg m^{-3}). Median sea surface temperature for this group was 26.3°C (grand median, $n = 15$; range of medians 21.2–28.6°C).

Female leatherback turtles dispersing to temperate continental shelf habitats off South America (group II) undertook migratory movements traversing the South Atlantic. Median concentration of satellite-derived surface chlorophyll *a* was 0.08 mg m^{-3} (grand median, $n = 6$; range of medians 0.05–0.12 mg m^{-3}). Median sea surface temperature for this group was 26.5°C (grand median, $n = 6$; range of medians 22.3–27.6°C). For two individuals assigned to this group (II) that arrived in continental shelf habitats off South America, and whose movements in these habitats were suggestive of foraging (i.e. increased path tortuosity relative to the comparatively straight trans-oceanic migration), the individual median satellite-derived surface chlorophyll *a* concentrations were 0.4 and 0.3 mg m^{-3}, respectively, and median sea surface temperatures were 18.3°C and 17.3°C, respectively.

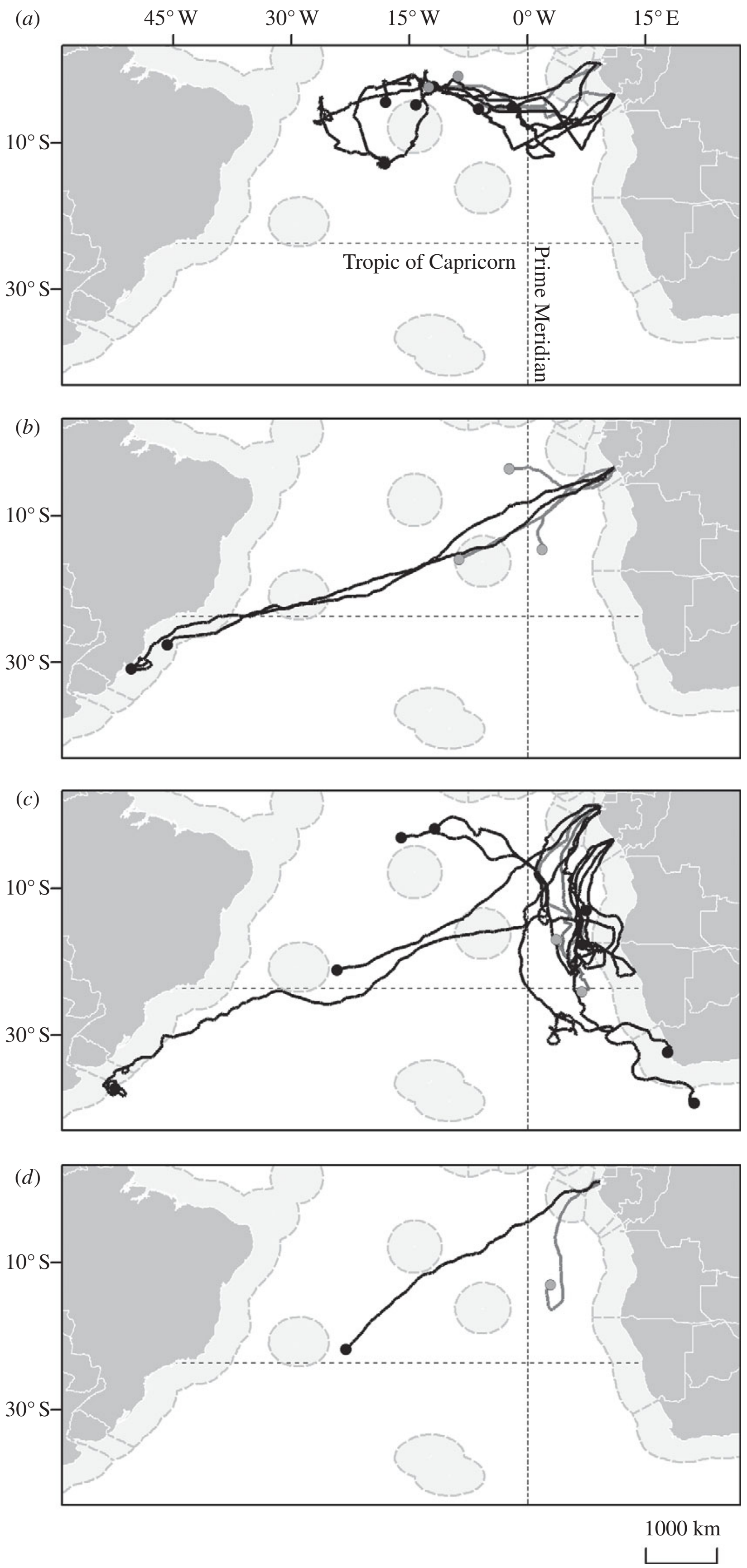

Figure 1. Movements of female leatherback turtles in the South Atlantic highlight different dispersal strategies. (*a*) 2006, $n = 8$; (*b*) 2008, $n = 5$; (*c*) 2009, $n = 10$; and (*d*) 2010, $n = 2$. Leatherback turtle movements recorded for greater than or equal to 100 days (black lines); movements recorded for less than 100 days (grey lines). Final locations of satellite-tracked leatherback turtles (filled circles).

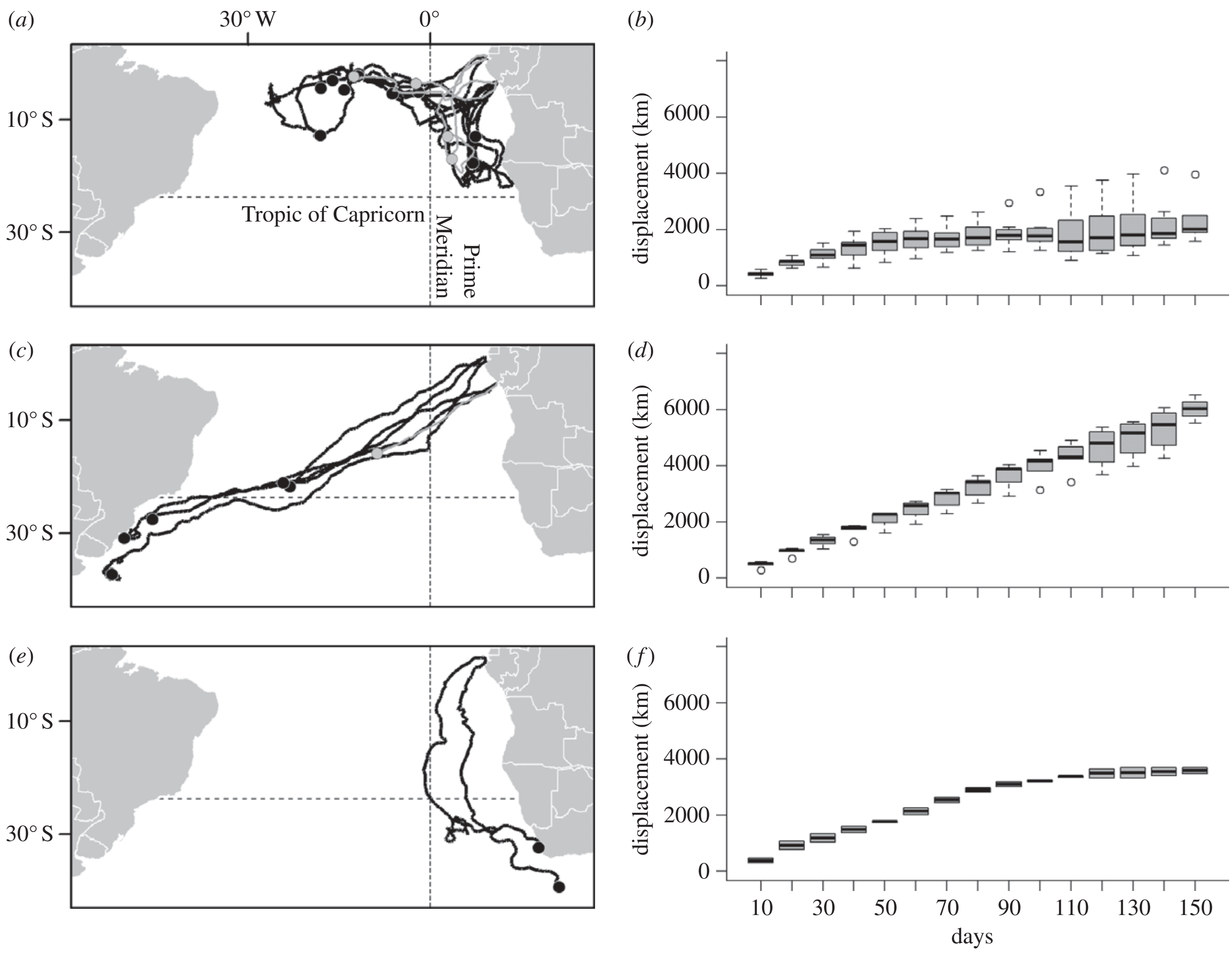

Figure 2. Movements and displacement time series of female leatherback turtles highlighting differing dispersal strategies. (*a*,*c*,*e*) Satellite-tracked movements and (*b*,*d*,*f*) box and whisker plots; boxes show 25th, 50th (median) and 75th percentiles (whiskers extend to the 2.5th and 97.5th percentiles, extremes are identified by empty circles), summarizing leatherback turtle displacement at 10-day intervals for up to 150 days from Gabon to South Atlantic habitats for the three dispersal groups: (*a*,*b*) habitats of the equatorial Atlantic; (*c*,*d*) habitats off South America, and (*e*,*f*) habitats off South Africa. (*a*) $n = 15$; (*c*) $n = 6$; (*e*) $n = 2$.

Leatherback turtles dispersing into temperate habitats off southern Africa (group III; $n = 2$), whose movements were also suggestive of foraging behaviour, moved into waters of the Benguela and Agulhas Currents, where median satellite-derived surface chlorophyll *a* concentrations for these individuals were 0.17 and 0.16 mg m^{-3}, respectively; median sea surface temperatures were 21.2°C and 18.5°C, respectively.

(d) *Threats*

When considering patterns of horizontal movement with respect to putative threats, female leatherback turtles dispersing into the equatorial Atlantic (group I) occupied waters that in 2000 [3] received some of the world's highest longline fisheries effort (figure 3*c*). Surveys to quantify leatherback turtle longline interactions in this area have demonstrated that they occur and that some of these are fatal (figure 3*c* [32]; catch per unit effort (CPUE): 0.3–0.7 leatherbacks per 1000 hooks set with gear set at 40–60 m depth). Median human impact score [40] sampled at leatherback turtle locations (group I) was 7.5 (grand median, $n = 15$; range of medians 4.6–8.7). For the ocean basin (5° N–43° S, 55° W–25° E), the median human impact score was 7.8 (IQR 4.8–9.1), corresponding to impacts ranging from low to medium-high as described by Halpern *et al.* [40].

Leatherback turtles dispersing to temperate habitats off South America (group II) moved through equatorial regions of longline fisheries, where effort was greatest (in 2000) in the South Atlantic (figure 3*c*). Human impact scores (medians) sampled at the locations of two turtles while within temperate continental shelf habitats adjacent to Brazil, Uruguay and Argentina were 10.4 and 9.1, respectively (figure 3*d*). Leatherback turtle interactions with fisheries have been reported within these habitats (longline CPUE: 0.59 leatherbacks per 1000 hooks set [43], 0.22 marine turtles per 1000 hooks set [33]; gillnet CPUE: 0.13 marine turtles per gillnet set [33]).

Individuals arriving in temperate habitats off southern Africa (group III) moved into regions where longline fisheries effort is somewhat lower than in equatorial regions (figure 3*c*). Median human impacts scores determined at locations of the two turtles in this region were 7.5 and 8.6 (figure 3*d*).

(e) *Depth utilization*

Summary and individual dive metrics collected by PTTs deployed during 2009 and 2010 indicated that

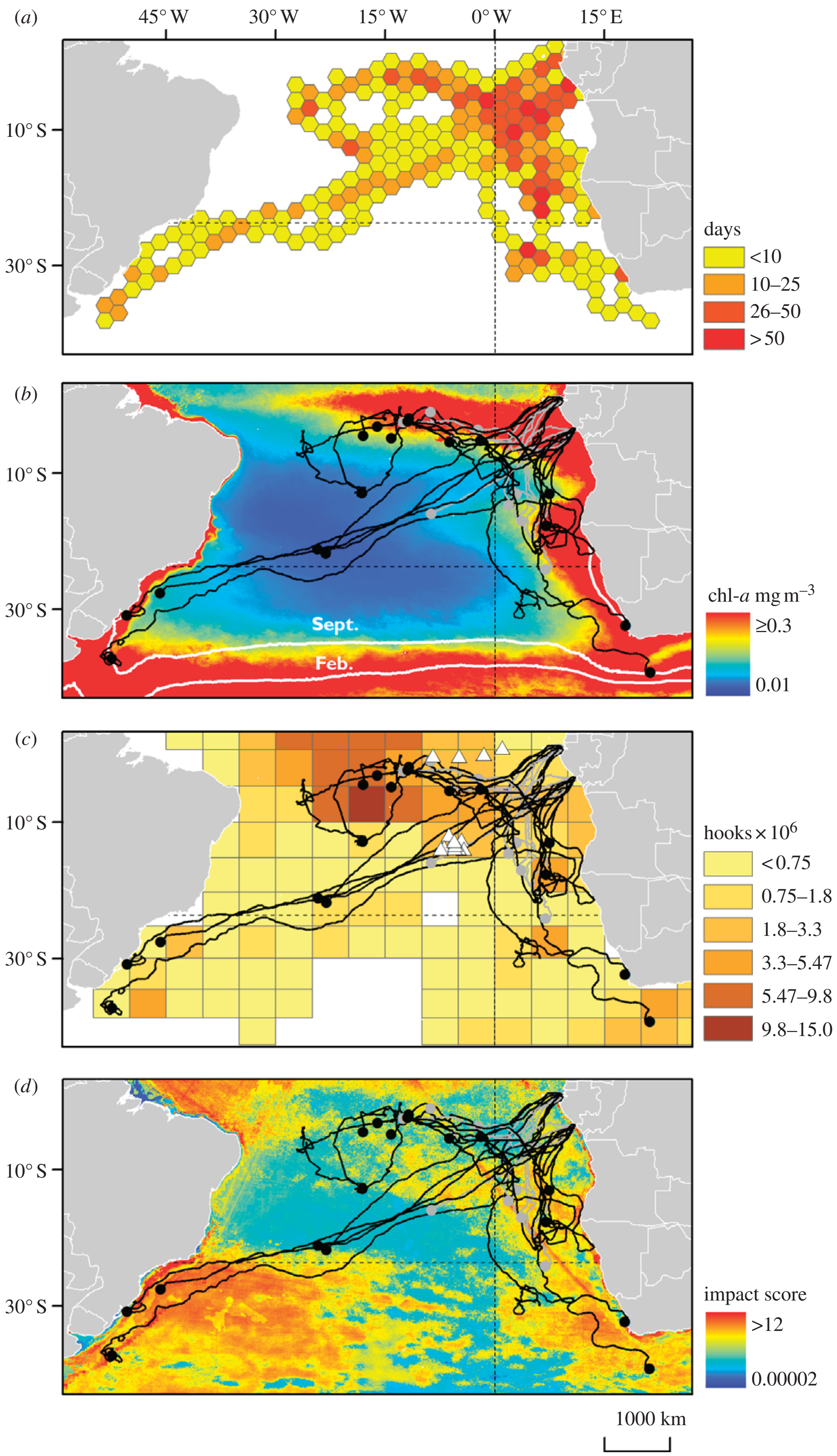

Figure 3. Movements of female leatherback turtles contextualized with satellite-derived surface chlorophyll *a* and potential threats, highlighting intra-population variability in encountered environment. (*a*) Density of female leatherback turtle daily locations occurring within tessellating hexagons of area approximately 50 000 km^2. (*b*) Movements of leatherback turtles (solid lines) with respect to mean of annual chlorophyll *a* (4 km product; 2006–2009 [60]). Mean northerly and southerly position of 15°C sea surface isotherm (white contours) derived from annual MODIS Aqua night-time sea surface temperature (4 km product; 2006–2009 [60]). (*c*) Longline fisheries effort in 2000 in the South Atlantic. Number of longline hooks deployed per 5° square in the South Atlantic [3]. Reported interactions of leatherback turtles with longline fisheries [32] (white filled triangles). (*d*) Cumulative human impact scores of anthropogenic drivers of ecological change for the South Atlantic [40].

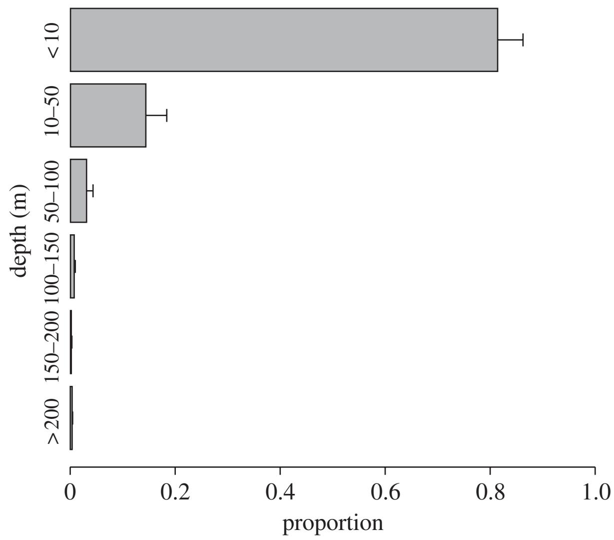

Figure 4. Depth utilization behaviour of female leatherback turtles undertaking post-nesting dispersal. Bar plot with errors bars (1 s.d.) showing mean percentage of time spent at specific depth intervals for female leatherback turtles in 2009 and 2010 undertaking post-nesting movements.

leatherback turtles predominantly occupied the epipelagic zone between the surface and 200 m depth (figure 4). Exceptionally deep dives were, however, recorded with an absolute maximum dive depth of 1080 m and mean maximum dive depth of 590 ± 314 m (mean ± 1 s.d., $n = 8$; range 272–1080 m).

(f) *Transit speeds and attachment methods*

There were significant effects of increasing migration duration (linear mixed model, Wald = 35.7, d.f. = 1, χ^2 $p = <0.001$) and attachment method (linear mixed model, Wald = 9.0, d.f. = 1, χ^2 $p = 0.003$) on movement speed. Yet there was no apparent effect of post-nesting dispersal strategy on movement speed (linear mixed model, Wald = 2.3, d.f. = 2.3, χ^2 $p = 0.3$). Predicted mean movement speed taken from the statistical model was 1.6 ± 0.3 km h^{-1} (mean ± 1 s.d.) for individuals fitted with PTTs using direct attachment, whereas for leatherback turtles with PTTs fitted using a harness it was 1.3 ± 0.5 km h^{-1} (mean ± 1 s.d.)—18.8 per cent slower than those turtles fitted with PTTs using a direct attachment method.

4. DISCUSSION

As shown in conspecifics satellite-tracked in other parts of the world [8–10,12,15,44], leatherback turtles in the South Atlantic are wide-ranging, with movement encompassing much of the South Atlantic basin within thermal tolerance limits [16,17]. Density mapping of leatherback turtle movements, considered in unison with surface chlorophyll *a*, highlights the potential importance of habitats within the South Equatorial system for this species. Individuals assigned to group I remained north of the South Atlantic gyre, the core of which is characterized by exceptionally low surface chlorophyll *a* concentrations, when compared with the ocean basin. Surface chlorophyll *a* within the dynamic equatorial habitats is predominantly governed by upwelling of nutrients (see [45]). Individuals dispersing to temperate habitats off South America (group II) appear to transit through the equatorial area of increased surface chlorophyll *a* and also the South Atlantic gyre, to more productive habitats where productivity is governed by wind-driven mixing and the characteristic eutrophic nature of continental shelves [45]. For individuals dispersing to temperature habitats off southern Africa (group III), regional ocean current systems including the Benguela system appear important. This region is highly productive, particularly for gelatinous organisms [46], which are thought to comprise the majority of the leatherback turtle diet. One individual within this group also interacted with the Agulhas retroflection, a physical feature of the western boundary current of the South Indian Ocean, which is similarly used by foraging leatherback turtles from the Indo-Pacific population (see [13] for review).

Although leatherback turtle movements in the South Atlantic are on vast spatial scales, data on spatially explicit threats [3] and indices of general marine degradation [40] are becoming progressively more available, allowing an integrative approach to contextualize threats even for such a widely distributed species. The movement patterns described here highlight that a substantial proportion of the satellite-tracked turtles occupy regions which, in the year 2000, received some of the highest levels of longline fishing effort in the world. Unfortunately, we lack detailed knowledge on inter- and intra-annual variation in fisheries effort from both neritic and oceanic habitats, which would greatly facilitate a more holistic assessment of putative risk. Given the highly dynamic (oceanographic) and productive (biological) nature of habitats visited by the satellite-tracked leatherback turtles, it seems plausible that these areas represent important fisheries habitats, and therefore putative risks to long-lived vertebrates, over extended periods (years).

When movements of leatherback turtles are contextualized using spatial data on human impacts [40], we see a mixed picture with leatherback turtles moving through a wide spectrum of at-sea degradation, with a high degree of disturbance in much of the South Atlantic, albeit with lower levels of disturbance in mid-latitude waters. Fisheries data integrated by Halpern *et al.* [40] are derived from catch statistics and as such do not reflect fisheries effort [47], and may therefore not fully depict the spatial impact of fisheries. Pelagic longline fisheries may not, however, pose the greatest risk to leatherback turtles [48], particularly when considered in light of other fisheries techniques, including coastal gillnets [33,49], which may impact adults during breeding, migratory and foraging phases of movements. Fisheries pressure in coastal waters off South America (Atlantic), for example, could profoundly select for an offshore dispersal phenotype, as has been suggested for the Pacific population (see [50]). As described in this study, depth utilization data collected by PTTs indicate that female leatherback turtles are epipelagic in nature, as observed for conspecifics in the North Atlantic [10,51]. This behaviour places individuals at the operating depths of pelagic longline fisheries [32] and coastal gillnets [49].

Although the population from which individuals were satellite-tracked nests largely in one country, our tracking has shown that at least 10 other nations are involved in the future of leatherback turtles dispersing from Gabon. In recent decades, rising levels of fishing effort by European Union, eastern European and Asian fleets have become prevalent [31], further widening the range of countries needed to be involved in the conservation of this migratory species. Much of the fisheries activity described takes place on the High Seas, which makes deleterious interactions immensely difficult to manage.

To date, no leatherback turtle followed by satellite tracking has made any significant excursion across the Equator (Atlantic Ocean) in either direction, including 25 individuals tagged in this study, four individuals tagged by Lopez-Mendilaharsu *et al.* [30] in the southwest Atlantic and more than 100 animals from the North Atlantic (electronic supplementary material, table S1), suggesting that there may be a profound sub-structuring within the Atlantic. Leatherback turtles occupying the North and South Atlantic basins may be effectively reproductively isolated from one another. Such a division could be elucidated using forensic techniques [52]. This apparent pattern could, however, be an artefact of the short duration of post-nesting tracking (typically five to six months in this study) in comparison to the length of the multi-annual interbreeding interval. There are, however, areas in the South Atlantic where, as in the North Atlantic, different reproductive populations are likely to be mixing in shared foraging grounds. In continental shelf waters off South America, turtles from Gabon are likely to be sharing foraging areas with leatherback turtles originating from Brazilian rookeries [53], although these rookeries are significantly smaller. Perhaps more remarkable is the latitudinal extent of the range, with individuals nesting on the Equator in Gabon and subsequently dispersing into the productive waters of the Benguela upwelling along the Atlantic coast of South Africa and Namibia. There, two of our study animals used foraging grounds previously described for leatherback turtles dispersing from the Indian Ocean nesting areas of South Africa [13]. Data needed to complete a pan-Atlantic overview of patterns of movements should be sought from the nesting populations in Brazil [53] and Bioko (Equatorial Guinea) [54].

From the perspective of informing further satellite tracking work and to further refine our knowledge of leatherback turtle movements and the threats they face, there are two key lessons that should be highlighted. Firstly, wide-ranging dispersal results in marked intra-population variability in environmental conditions experienced in foraging areas, and hence variability in nutritional intake, which probably leads to variability in the magnitude of breeding in any given year [45,55]. The inter-annual variability in post-nesting migration we described underscores this phenomenon and shows that, in addition to increasing sample size of animals satellite-tracked to try and capture the major dispersal patterns, consideration should be given to tracking individuals from multiple breeding cohorts. Secondly, the animal satellite tracking community must continually appraise its methodologies to ensure that impacts on study animals are minimized for both ethical reasons and to ensure maximum robustness of the data gathered. A large number of leatherback turtles (Atlantic Ocean, $n > 100$; Indo-Pacific Ocean, $n > 100$; electronic supplementary material, table S1) have been satellite-tracked using harnesses and some authors have already suggested that, in addition to potential physical problems of abrasion [56], this method of attachment may impair speed of movement and diving behaviour [35]. To minimize the possible risk, we moved to direct attachment of smaller and lighter satellite transmitters in later study years. This has allowed us to compare the speed of movement (derived ground-speed) of two methods while controlling for dispersal strategy. It is clear from our data that the impact of harnesses is discernible and it appears that it would be better to proceed with the direct attachment methods.

A recent priority-setting exercise for marine turtle conservation highlighted the need to ascertain key foraging areas [57]. In this paper, we have for the first time elaborated the general patterns of post-nesting dispersal for one of the world's major nesting areas for leatherback turtles, highlighting behavioural similarities with conspecifics elsewhere, such as putative migration corridor (Pacific Ocean [58]) and dispersal to coastal mid-latitude habitats (North Atlantic [10]). In addition, we take the novel step of integrating movements of a free-ranging marine megavertebrate species with global-scale data layers of potential threat to contextualize movements with fishing effort and modelled cumulative human impacts. It is clear that this is an area that can be built upon in the future as the magnitude and availability of information (e.g. from vessel-monitoring systems [59] and other metrics describing fishing [33]) increases.

This project was funded by the Large Pelagics Research Center through National Oceanographic and Atmospheric Agency award NA04NMF4550391, the Darwin Initiative (Department of Environment, Food and Rural Affairs; UK) and the Shellshock Campaign (European Association for Zoos and Aquaria). Ethical review of leatherback turtle PTT attachment procedures was undertaken by the University of New Hampshire (USA) IACUC 060501. M.J.W. was in receipt of a Natural Environment Research Council PhD studentship (NER/S/A/2004/12980) and is now supported as a Post-doctoral Research Fellow by the Peninsula Research Institute for Marine Renewable Energy (PRIMaRE), funded by the SouthWest Regional Development Agency (UK). B.J.G. and A.C.B. are funded by the Darwin Initiative and the European Social Fund. We are sincerely grateful to Center National de la Recherche Scientifique et Technologique (CENAREST) and Agence Nationale des Parcs Nationaux (ANPN) for permitting fieldwork within Gabon. Logistical support and field assistance were provided by the Wildlife Conservation Society and the Gabon Sea Turtle Partnership, with funding from the Marine Turtle Conservation Fund (US Fish and Wildlife Service, US Department of the Interior). We extend our thanks to M. Lutcavage, A. Myers and K. Dodge for assistance in the use of the direct attachment methodology. We thank the turtle technicians of the ANPN, Aventures Sans Frontières and the Wildlife Conservation Society, and P. D. Agamboue, M. Ikaran, B. Wilhelms, M. Markovina and F. Hymas for field-site assistance. Global geopolitical spatial data were obtained from the Flanders Marine Institute Maritime Boundaries Geodatabase (v. 5). The author team would like to acknowledge the Trans-Atlantic Leatherback Conservation Initiative (TALCIN), a multi-partner effort coordinated by WWF, for their contribution of satellite tracking data to this manuscript. We sincerely thank two anonymous reviewers, C. McClellan and L. Hawkes, whose comments helped to improve this work.

REFERENCES

1 Hall, M. A., Alverson, D. L. & Metuzals, K. I. 2000 By-catch: problems and solutions. *Mar. Pollut. Bull.* **41**, 204–219. (doi:10.1016/S0025-326X(00)00111-9)

2 Kimball, L. A. 2005 *The international legal regime of the high seas and the seabed beyond the limits of national*

jurisdiction and options for cooperation for the establishment of marine protected areas (MPAs) in marine areas beyond the limits of national jurisdiction, p. 64. Montreal, Canada: Secretariat of the Convention on Biological Diversity.
3 Lewison, R. L., Freeman, S. A. & Crowder, L. B. 2004 Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol. Lett.* **7**, 221–231. (doi:10.1111/j.1461-0248.2004.00573.x)
4 Boyd, I. L., McCafferty, D. J., Reid, K., Taylor, R. & Walker, T. R. 1998 Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Can. J. Fish. Aquat. Sci.* **55**, 845–852. (doi:10.1139/cjfas-55-4-845)
5 Phillips, R. A., Silk, J. R. D., Croxall, J. P. & Afanasyev, V. 2006 Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biol. Conserv.* **129**, 336–347. (doi:10.1016/j.biocon.2005.10.046)
6 Baumgartner, M. F. & Mate, B. R. 2005 Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Can. J. Fish. Aquat. Sci.* **62**, 527–543. (doi:10.1139/f04-238)
7 Holland, K. N., Wetherbee, B. M., Lowe, C. G. & Meyer, C. G. 1999 Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Mar. Biol.* **134**, 665–673. (doi:10.1007/s002270050582)
8 Eckert, S. A. 2006 High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. *Mar. Biol.* **149**, 1257–1267. (doi:10.1007/s00227-006-0262-z)
9 Ferraroli, S., Georges, J.-Y., Gaspar, P. & Maho, Y. L. 2004 Where leatherback turtles meet fisheries. *Nature* **429**, 521. (doi:10.1038/429521a)
10 Hays, G. C., Houghton, J. D. & Myers, A. E. 2004 Pan-Atlantic leatherback turtle movements. *Nature* **429**, 522. (doi:10.1038/429522a)
11 James, M. C., Ottensmeyer, C. A. & Myers, R. A. 2005 Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195–201. (doi:10.1111/j.1461-0248.2004.00710.x)
12 Benson, S., Dutton, P. H., Hitipeuw, C., Samber, B., Bakarbessy, J. & Parker, D. 2007 Post-nesting migrations of leatherback turtles (*Dermochelys coriacea*) from Jamursba-Medi, Bird's Head Peninsula, Indonesia. *Chelonian Conserv. Biol.* **6**, 150–154. (doi:10.2744/1071-8443(2007)6[150:PMOLTD]2.0.CO;2)
13 Luschi, P., Lutjeharm, J. R. E., Lambardi, R., Mencacci, R., Hughes, G. R. & Hays, G. C. 2006 A review of migratory behaviour of sea turtles off southeastern Africa. *S. Afr. J. Sci.* **102**, 51–58.
14 Shillinger, G. *et al.* 2010 Identification of high-use internesting habitats for eastern Pacific leatherback turtles: role of the environment and implications for conservation. *Endang. Species Res.* **10**, 215–232. (doi:10.3354/esr00251)
15 Shillinger, G. L. *et al.* 2008 Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol.* **6**, 1408–1416. (doi:10.1371/journal.pbio.0060171)
16 McMahon, C. R. & Hays, G. C. 2006 Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob. Change Biol.* **12**, 1–9. (doi:10.1111/j.1365-2486.2006.01174.x)
17 Witt, M. J., Broderick, A. C., Johns, D. J., Martin, C., Penrose, R., Hoogmoed, M. S. & Godley, B. J. 2007 Prey landscapes help identify potential foraging habitats for leatherback turtles in the northeast Atlantic. *Mar. Ecol. Prog. Ser.* **337**, 231–244. (doi:10.3354/meps337231)
18 James, M. C., Davenport, J. & Hays, G. C. 2006 Expanded thermal niche for a diving vertebrate: a leatherback turtle diving into near-freezing water. *J. Exp. Mar. Biol. Ecol.* **335**, 221–226. (doi:10.1016/j.jembe.2006.03.013)
19 Reina, R. D., Spotila, J. R., Paladino, F. V. & Dunham, A. E. 2009 Changed reproductive schedule of eastern Pacific leatherback turtles *Dermochelys coriacea* following the 1997–1998 El Niño to La Niña transition. *Endang. Species Res.* **7**, 155–161. (doi:10.3354/esr00098)
20 Saba, V. S., Santidrian-Tomillo, P., Reina, R. D., Spotila, J. R., Musick, J. A., Evans, D. A. & Paladino, F. V. 2007 The effect of the El Niño Southern Oscillation on the reproductive frequency of eastern Pacific leatherback turtles. *J. Appl. Ecol.* **44**, 395–404. (doi:10.1111/j.1365-2664.2007.01276.x)
21 Spotila, J. R., Reina, R. D., Steyermark, A. C., Plotkin, P. T. & Paladino, F. V. 2000 Pacific leatherback turtles face extinction. *Nature* **405**, 529–530. (doi:10.1038/35014729)
22 Troëng, S., Harrison, E., Evans, D., de Haro, A. & Vargas, E. 2007 Leatherback turtle nesting trends and threats at Tortuguero, Costa Rica. *Chelonian Conserv. Biol.* **6**, 117–122. (doi:10.2744/1071-8443(2007)6[117:LTNTAT]2.0.CO;2)
23 Dutton, D. L., Dutton, P. H., Chaloupka, M. & Boulon, R. H. 2005 Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biol. Conserv.* **126**, 186–194. (doi:10.1016/j.biocon.2005.05.013)
24 Girondot, M., Godfrey, M. H., Ponge, L. & Rivalan, P. 2007 Modeling approaches to quantify leatherback nesting tends in French Guiana and Suriname. *Chelonian Conserv. Biol.* **6**, 37–46. (doi:10.2744/1071-8443(2007)6[37:MATQLN]2.0.CO;2)
25 McGowan, A. *et al.* 2008 Down but not out: marine turtles of the British Virgin Islands. *Anim. Conserv.* **11**, 92–103. (doi:10.1111/j.1469-1795.2007.00152.x)
26 Witt, M. J. *et al.* 2009 Aerial surveying of the world's largest leatherback turtle rookery: a more effective methodology for large-scale monitoring. *Biol. Conserv.* **142**, 1719–1727. (doi:10.1016/j.biocon.2009.03.009)
27 Georges, J. Y. *et al.* 2007 Meta-analysis of movements in Atlantic leatherback turtles during the nesting season: conservation implications. *Mar. Ecol. Prog. Ser.* **338**, 225–232. (doi:10.3354/meps338225)
28 Witt, M. J., Broderick, A. C., Coyne, M., Formia, A., Ngouessono, S., Parnell, R. J., Sounguet, G.-P. & Godley, B. J. 2008 Satellite tracking highlights difficulties in the design of effective protected areas for leatherback turtles during the internesting period. *Oryx* **42**, 296–300. (doi:10.1017/S0030605308006947)
29 Billes, A., Fretey, J., Verhage, B., Huijbregts, B., Giffoni, B., Prosdocimi, L., Albareda, D. A., Georges, J.-Y. & Tiwari, M. 2006 First evidence of leatherback movement from Africa to South America. *Mar. Turtle Newsl.* **111**, 13–14.
30 Lopez-Mendilaharsu, M., Rocha, C. F. D., Miller, P., Domingo, A. & Prosdocimi, L. 2009 Insights on leatherback turtle movements and high use areas in the southwest Atlantic Ocean. *J. Exp. Mar. Biol. Ecol.* **378**, 31–39. (doi:10.1016/j.jembe.2009.07.010)
31 Worm, B. *et al.* 2009 Rebuilding global fisheries. *Science* **325**, 578–585. (doi:10.1126/science.1173146)
32 Carranza, A., Domingo, A. & Estrades, A. 2006 Pelagic longlines: a threat to sea turtles in the Equatorial Eastern Atlantic. *Biol. Conserv.* **131**, 52–57. (doi:10.1016/j.biocon.2006.02.003)
33 Wallace, B. P. *et al.* 2010 Global patterns of marine turtle bycatch. *Conserv. Lett.* **xx**, 1–12.

34 Eckert, S. A. & Eckert, K. L. 1986 Harnessing leatherbacks. *Mar. Turtle Newsl.* **37**, 1–3.
35 Fossette, S., Corbel, H., Gaspar, P., Maho, Y. L. & Georges, J.-Y. 2008 An alternative technique for the long-term satellite tracking of leatherback turtles. *Endang. Species Res.* **4**, 33–41. (doi:10.3354/esr00039)
36 CLS. 2008 *Argos user's manual*. See http://www.argos-system.org/documents/userarea/argos_manual_en.pdf.
37 Coyne, M. S. & Godley, B. J. 2005 Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Mar. Ecol. Prog. Ser.* **301**, 1–7. (doi:10.3354/meps301001)
38 Witt, M. J. *et al.* 2010 Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Anim. Behav.* **80**, 571–581. (doi:10.1016/j.anbehav.2010.05.022)
39 Tremblay, Y. *et al.* 2006 Interpolation of animal tracking data in a fluid environment. *J. Exp. Biol.* **209**, 128–140. (doi:10.1242/jeb.01970)
40 Halpern, B. S. *et al.* 2008 A global map of human impact on marine ecosystems. *Science* **319**, 948–952. (doi:10.1126/science.1149345)
41 Crawley, M. J. 2007 *The R book*. Chichester, UK: John Wiley & Sons Ltd.
42 Boulon, R., Dutton, P. & McDonald, D. 1996 Leatherback turtles (*Dermochelys coriacea*) on St. Croix US Virgin Islands: fifteen years of conservation. *Chelonian Conserv. Biol.* **2**, 141–147.
43 Kotas, J. E., dos Santos, S., Azevedo, V. G., Gallo, B. M. G. & Barata, P. C. R. 2004 Incidental capture of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles by the pelagic longline fishery off southern Brazil. *Fish. Bull.* **102**, 393–399.
44 James, M. C., Myers, R. A. & Ottensmeyer, C. A. 2005 Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc. R. Soc. B* **272**, 1547–1555. (doi:10.1098/rspb.2005.3110)
45 Saba, V. S., Spotila, J. R., Chavez, F. P. & Musick, J. A. 2008 Bottom-up and climatic forcing on the worldwide population of leatherback turtles. *Ecology* **89**, 1414–1427. (doi:10.1890/07-0364.1)
46 Lynam, C. P., Gibbons, M. J., Axelsen, B. A., Sparks, C. A. J., Coetzee, J., Heywood, B. G. & Brierley, A. S. 2006 Jellyfish overtake fish in a heavily fished ecosystem. *Curr. Biol.* **16**, 492–493. (doi:10.1016/j.cub.2006.06.018)
47 Heath, M. R. 2008 Comment on 'A global map of human impact on marine ecosystems'. *Science* **321**, 1446b. (doi:10.1126/science.1157390)
48 Lewison, R. L. & Crowder, L. B. 2007 Putting longline bycatch of sea turtles into perspective. *Conserv. Biol.* **21**, 79–86. (doi:10.1111/j.1523-1739.2006.00592.x)
49 Gilman, E. *et al.* 2010 Mitigating sea turtle by-catch in coastal passive net fisheries. *Fish Fish.* **11**, 57–88. (doi:10.1111/j.1467-2979.2009.00342.x)
50 Saba, V. S., Shillinger, G. L., Swithenbank, A. M., Block, B. A., Spotila, J. R., Musick, J. A. & Paladino, F. V. 2008 An oceanographic context for the foraging ecology of eastern Pacific leatherback turtles: consequences of ENSO. *Deep Sea Res. Part I: Oceanogr. Res. Papers* **55**, 646–660. (doi:10.1016/j.dsr.2008.02.006)
51 Hays, G. C., Houghton, J. D., Isaacs, C., Kin, R. S., Lloyds, C. & Lovell, P. 2004 First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Anim. Behav.* **67**, 733–743. (doi:10.1016/j.anbehav.2003.08.011)
52 Dutton, P. H., Bowen, B. W., Owens, D. W., Barragan, A. & Davis, S. K. 1999 Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). *J. Zool.* **248**, 397–409. (doi:10.1111/j.1469-7998.1999.tb01038.x)
53 Barata, P. C. R. & Fabiano, F. F. C. 2002 Evidence for Leatherback Sea Turtle (*Dermochelys coriacea*) nesting in Arraial do Cabo, State of Rio de Janeiro, and a review of occasional leatherback nests in Brazil. *Mar. Turtle Newsl.* **96**, 13–16.
54 Tomás, J., Godley, B., Castroviejo, J. & Raga, J. 2010 Bioko: critically important nesting habitat for sea turtles of West Africa. *Biodiversity Conserv.* **19**, 2699–2714. (doi:10.1007/s10531-010-9868-z)
55 Broderick, A. C., Godley, B. J. & Hays, G. C. 2001 Trophic status drives interannual variability in nesting numbers of marine turtles. *Proc. R. Soc. Lond. B* **268**, 1481–1487. (doi:10.1098/rspb.2001.1695)
56 Troëng, S. *et al.* 2006 Report on long-term transmitter harness retention by a leatherback turtle. *Marine Turtle Newsl.* **111**, 6–7.
57 Hamann, M. *et al.* 2010 Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endang. Species Res.* **11**, 245–269. (doi:10.3354/esr00279)
58 Morreale, S. J., Standora, E. A., Spotila, J. R. & Paladino, F. V. 1996 Migration corridor for sea turtles. *Nature* **384**, 319–320. (doi:10.1038/384319a0)
59 Witt, M. J. & Godley, B. J. 2007 A step towards seascape scale conservation: using vessel monitoring systems (VMS) to map fishing activity. *PLoS ONE* **2**, e1111. (doi:10.1371/journal.pone.0001111)
60 Feldman, G. C. & McClain, C. R. 2010 Ocean color web. *Modis Aqua Reprocessing, version 2009* (eds N. Kuring & S. W. Bailey). NASA Goddard Space Flight Center. See http://oceancolor.gsfc.nasa.gov.