



New findings about the spatial and temporal use of the Eastern Atlantic Ocean by large juvenile loggerhead turtles

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ABSTRACT

Aims Effective conservation of threatened or endangered species requires a robust understanding of their spatio-temporal distribution. Although a huge amount is known about the movements of Atlantic adult sea turtles, much less is known about juvenile turtles, and much of the life history model is therefore inferred. We set out to describe the spatio-temporal distribution of juvenile loggerheads turtles found around the Canary Islands.

Location Eastern North Atlantic Ocean.

Methods Between 1999 and 2012, we satellite-tracked 24 healthy large juvenile loggerhead turtles (mean straight carapace length = 47.4 cm, range = 34.6–54.5 cm) captured in the waters around the Canary Islands. We describe their regional distribution, identify high-use areas and create a model for habitat suitability using minimum convex polygons, density rasters and ensemble ecological niche modelling, integrated with physical and biological environmental data.

Results Turtles used a huge oceanic area (2.5 million km²) with particularly high usage around the Canary Islands, Spain, Portugal, Morocco and Western Sahara. In spring and summer, turtles generally moved further north towards the Iberian Peninsula. Ecological niche modelling identified sea surface temperature as the most important contributory variable to the habitat models. We also recorded three juvenile turtles making westward migrations away from the eastern Atlantic Ocean, presumably back towards their original natal beaches near sexual maturity.

Main conclusions The results of the present study provide insight into a significant knowledge gap on the spatio-temporal distribution of large juvenile loggerhead turtles in the eastern Atlantic Ocean. The data highlight that turtles occupy a vast open oceanic area, which hampers the ability of static conservation approaches to afford effective protection. However, ensemble ecological niche modelling highlights key suitable habitat for juvenile loggerhead turtles, which could be used in dynamic conservation protection.

Keywords

Caretta caretta, habitat use, life history, marine vertebrate, satellite tracking, spatial ecology.

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INTRODUCTION

Successful conservation of threatened species may be challenging if their life history is cryptic or poorly understood.

The distribution of many terrestrial species is now relatively well described due to targeted conservation effort and the advent of 'biologging' in which individuals can be tracked using remote telemetry (Block, 2005; Ropert-Coudert *et al.*,

2009; [Hussey *et al.*, 2015](#)). The distribution of oceanic marine species, however, is generally still poorly understood due to the logistical constraints of surveying species at sea ([James *et al.*, 2005](#); [Arendt *et al.*, 2012a](#); [Schofield *et al.*, 2013](#)). It is also challenging to use biologging devices to track very small animals, for example < 50 g body mass (but see [Scott *et al.*, 2014](#)) or to track species that surface too infrequently to transmit location data to overpassing satellites ([Hazen *et al.*, 2012](#)). We arguably know more about marine turtles than we do many other marine vertebrates, possibly because large adult females come ashore in short tractable nesting periods that provide opportunities for study and because it is relatively easy to attach transmitters to their hard carapaces ([Godley *et al.*, 2008](#)). Although we have now tracked adult loggerhead sea turtles on both sides of the Atlantic ([Plotkin & Spotila, 2002](#); [Dodd & Byles, 2003](#); [Hawkes *et al.*, 2006, 2007, 2011](#); [Girard *et al.*, 2009](#); [Arendt *et al.*, 2012a,b](#); [Griffin *et al.*, 2013](#); [Varo-Cruz *et al.*, 2013](#)) and small juvenile turtles from the eastern seaboard of the USA ([Avens *et al.*, 2003](#); [Mansfield *et al.*, 2009](#); [McClellan & Read, 2009](#)), little is known of the larger juvenile turtles thought to be found in eastern Atlantic waters, and much of the juvenile part of the classic life history model for marine turtles is thus still inferred rather than empirically observed.

In the classic sea turtle life cycle, which is based on Atlantic loggerhead sea turtles ([Carr, 1986, 1987](#); [Bolten, 2003](#)), hatchlings leaving nesting beaches in the western Atlantic were thought to become entrained in the Gulf Stream, traveling eastwards to the Azores where they would apparently settle for some years. During this juvenile stage, turtles were thought to travel as passive migrants in currents ([Carr, 1986, 1987](#)), such that a number of juveniles might drift out of the main current, entering the Mediterranean Sea or stranding on northern European beaches ([Witt *et al.*, 2007](#); [Monzón-Argüello *et al.*, 2009](#)). However, recent studies have documented active dispersal of juvenile sea turtles, and suggested that oceanic currents may not necessarily be the primary driver behind juvenile turtle dispersal ([Mansfield & Putman, 2013](#); [Mansfield *et al.*, 2014](#); [Putman & Mansfield, 2015](#)). It appears that the Azores, Madeira and the Canary Islands are key juvenile developmental grounds and that turtles eventually migrate from these areas back to the western Atlantic at larger sizes, settling along the Caribbean and north American coast before breeding some years later within the vicinity of their natal beach ([Bolten, 2003](#)). It has been suggested, however, that this life history model may be more complex, with juveniles potentially making repeated transatlantic crossings ([Carr, 1986](#); [Bolten & Balazs, 1995](#)) or juveniles and adults moving reversibly between both oceanic and neritic waters (see review in [Mansfield & Putman, 2013](#)), with some rookeries in different ocean basins hosting what may be largely oceanic populations of adult turtles ([Hatase *et al.*, 2002](#); [Hawkes *et al.*, 2006](#); [Rees *et al.*, 2010](#)).

Nevertheless, the lack of data robustly describing the in-water distribution, dispersal and behaviour of juvenile turtles hampers our ability to construct survivorship estimates and to

appropriately target conservation action. In particular, oceanic-stage juvenile turtles between 15 and 63 cm straight carapace length are probably the poorest understood of the life stages ([Mansfield & Putman, 2013](#)) and there have only been 10 turtles tracked to date from the oceanic juvenile loggerhead population in the eastern Atlantic ([McCarthy *et al.*, 2010](#)). Genetic analysis has shown that these individuals come from the USA, Mexico, the Cape Verde Islands and Brazil ([Bolten *et al.*, 1998](#); [Carreras *et al.*, 2006](#); [Monzón-Argüello *et al.*, 2012](#)).

In this study, we set out to describe, for the first time, the spatio-temporal distribution of juvenile loggerheads turtles found around the Canary Islands, a major developmental ground. Specifically, we aimed to (1) describe their regional distribution, (2) identify high-use areas, (3) investigate their diving behaviour, (4) create a model for habitat suitability, based on oceanographic conditions, and (5) add to the life history model for Atlantic loggerhead turtles.

METHODS

Turtles

We captured 24 apparently healthy loggerhead turtles in the waters around the Canary Islands in 1999 ($n = 5$), 2006 ($n = 7$) and 2008–2009 ($n = 12$) using either (1) a modification of the Rodeo technique ([Limpus & Walter, 1980](#)), adapted to deep water and to juvenile loggerhead turtle behaviour, catching them when they were resting and/or breathing at the surface, or (2) a dip net. Both techniques were applied only when sea conditions were suitable, that is calm and with minimal ocean swell. Turtles were measured [straight carapace length from notch to notch, SCLn-n, and curved carapace length from notch to notch, CCLn-n, following [Bolten \(1999\)](#)]. For seven turtles, it was only possible to measure CCLn-n, so we converted their measurements to SCLn-n using morphometric data from 808 loggerhead turtles, which were admitted to the wildlife recovery centre of Gran Canaria (Canary Islands), and from which we had both measurements (equation: $SCLn-n = 0.919 CCLn-n - 1.052$; $R^2 = 0.984$). To contextualize the size of turtles satellite-tracked in this study with the larger regional population around the Canary Islands, we obtained size data for all turtles admitted to the wildlife recovery centre of Gran Canaria for which SCLn-n had been measured ($n = 1195$, admitted between 1998 and 2012; [Fig. 1d](#)). None of the turtles tracked in this study required veterinary treatment. All carapace sizes from here on refer to SCL unless otherwise specifically stated.

Telemetry

We deployed platform transmitter terminals (PTTs) on the 24 healthy captured turtles: Wildlife Computers SDR-T10 ($n = 5$) equipped with time and depth recorders, and Sirtrack KiwiSat 101 ($n = 7$) and 202 ($n = 12$) using two different methods ([Table S1](#)), similar to those described in [Godley *et al.* \(2002\)](#). Although all tracking took place to identify the foraging areas

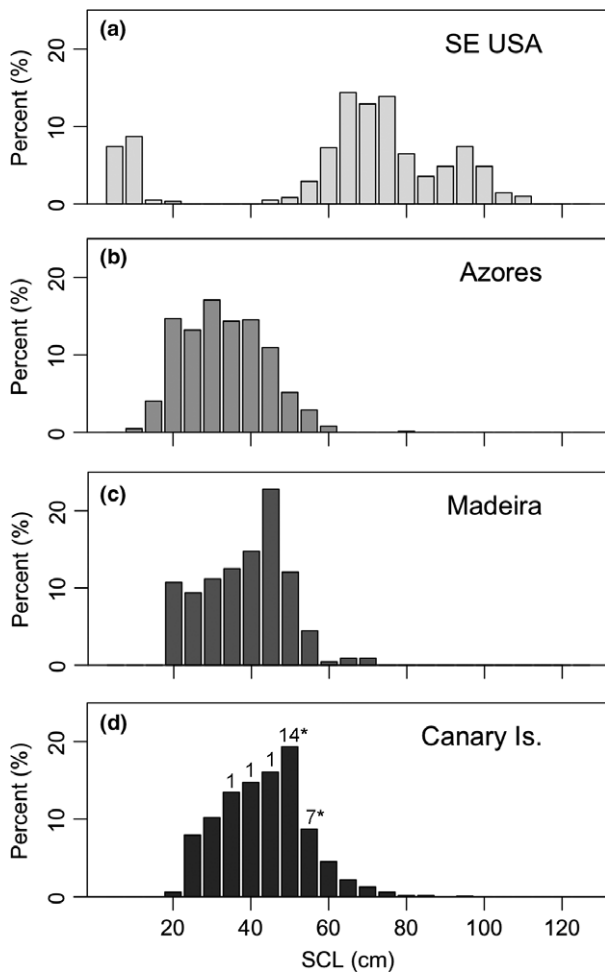


Figure 1 Size-frequency distributions of (a) neritic-stage loggerheads stranded in the south-eastern USA, SCLn-t [$n = 783$, adapted by Bolten & Balazs (1995) from Carr (1987)], (b) oceanic-stage loggerheads captured in waters around the Azores, SCLn-t [$n = 731$, adapted by Bolten & Balazs (1995) from Bolten *et al.* (1993)], (c) oceanic-stage loggerheads captured in waters around Madeira, SCLn-t [$n = 224$, data from Delgado *et al.* (2010)] and (d) loggerheads admitted to the Gran Canaria Wildlife Recovery Center, SCLn-n ($n = 1195$). Numbers above bars in part (d) indicate sizes of individuals tagged in the present study, where number reflects sample size at each size bin. Asterisk shows body sizes for individuals partial or totally crossing the Atlantic Ocean.

and putative threats to juvenile loggerhead turtles, funding was obtained over three separate projects and thus technical aspects, such as duty cycles, varied (Table S1). Turtles were released between 0 and 29 days after capture (13 turtles were released within 1 day of capture, Table S1). Although they were healthy and did not need any treatment, the delay was due to logistical constraints in accessing vessels to return the turtles to sea.

Data handling

Satellite telemetry data were collected using the Argos satellite system (CLS, 2011) and downloaded with the Satellite Track-

ing and Analysis Tool (STAT; Coyne & Godley, 2005). To filter the location data, we first considered that this population has not been previously studied and there are consequently few data to inform on appropriate thresholds of speed and turning angle filters. We therefore used extremely parsimonious filters, retaining location classes 3, 2, 1, A and B, transit speeds slower than 10 km h^{-1} , turning angles $> 30^\circ$ and elevation lower than 0 m, which would remove locations that were clearly erroneous. Previous work using satellite tracking has suggested that mean travel speeds for adult loggerhead turtles are to the order of $1.0\text{--}1.8 \text{ km h}^{-1}$ (Papi *et al.*, 1997), $0.4\text{--}1.4 \text{ km h}^{-1}$ (Renaud & Carpenter, 1994), 2.8 km h^{-1} (Stoneburner, 1982) and $1.0\text{--}3.0 \text{ km h}^{-1}$ (Arendt *et al.*, 2012a) during foraging, although turtles can apparently swim faster than 10 km h^{-1} in short sprint bouts (Renaud & Carpenter, 1994; Stoneburner, 1982) or when swimming within surface currents. Thus, following Arendt *et al.* (2012a) we set a liberal speed filter for this study to reduce the possibility of excluding valid locations. To describe the movements of turtles in the east Atlantic (from now on, referred to as 'regional area'), data corresponding to migrations of three turtles that crossed the ocean (either totally or partially) were excluded from analyses regarding the foraging grounds. The starting point of the migration was fixed arbitrarily from displacement curves and from a visual analysis of the tracks.

To understand space use by turtles, both at an individual and a population level, we calculated home ranges both for each turtle, and as one meta-range for all turtles. The meta-range was intended to provide an estimate of the greatest range of space use by turtles from the study population. Tracking durations were extremely variable between individuals (as is indeed the case for most such studies), and thus, turtles that were tracked for longer durations would likely contribute proportionally more location data to the meta-range. In addition, based on previous tracking of loggerhead turtles (Hawkes *et al.*, 2007; Mansfield *et al.*, 2009), turtles may be expected to show seasonal distribution shifts northwards during summer and thus, turtles that were tracked year-round could potentially contribute a greater spatial range of data than turtles that were tracked for a single season. Therefore, if all turtles had been tracked for longer, it seems plausible that the total meta-range would have been larger and, thus our meta-range is parsimonious. For individual home ranges, we used all filtered raw data per turtle. For the meta-range, we used all filtered raw data from all turtles. To avoid the effect of autocorrelation, we sampled one location per 3 days (because 11 tags were programmed with a duty cycle which permitted transmission only once every 3 days), with a ± 2 -day window: this enabled gaps of 3 days or more to be filled using any other matching data from within 2 days either side of the window. Locations received in the first 7 days after release were also excluded (these tended to be patchy and sporadic), resulting in 1891 filtered locations. All filtering was undertaken in R (R Development Core Team, 2008). Home range areas were estimated using minimum convex polygons (MCP), generated using

custom script in MATLAB (The MathWorks Inc., Natick, MA, USA). To determine 'hotspots' of habitat use, a polygon sampling grid of cells one degree by one degree was overlaid on filtered turtle data, and all spatially coincident locations summed per grid cell to create a density raster. Data were mapped using ArcGIS 10.1 (ESRI, Redlands, California, USA, www.esri.com).

Dive behaviour

The SDR-T10 PTTs ($n = 5$) deployed on turtles recorded dive duration and maximum dive depth for individual dives within 6-h periods and binned the data into 14 depth bins (2–6 m, 6–10, 10–15, 15–20, 20–25, 25–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–100, 100–150 and > 150 m) and 14 duration bins (0–2 min, 2–5, 5–10, 10–20, 20–30, 30–45, 45–60, 60–75, 75–90, 90–105, 105–120, 120–180, 180–240 and > 240 min). The SDR-T10s were configured to register a dive when the turtle descended below 2 m. Median dive duration and median of maximum dive depths were calculated for each turtle per 6-h period. These summary statistics were then carried forward to further analyses, including comparisons in dive behaviour between seasons. Changes in dive depth and duration between seasons (autumn: Sep, Oct, Nov; winter: Dec, Jan, Feb; spring: Mar, Apr, May; summer: Jun, Jul, Aug) were investigated using general linear mixed modelling (glmmPQL in library MASS in R; R Development Core Team, 2008) with lognormal error distribution, controlling for turtle ID as a random effect.

Habitat modelling

For our habitat suitability models, we adopted an ensemble ecological niche modelling approach (Araújo & New, 2007; Rangel & Loyola, 2012; Pikesley *et al.*, 2013). We prescribed the modelling area to be within a box bounded by N 45–N 4°, and W 35–W 5°, which circumscribed all location data for juvenile loggerhead turtles, excluding migratory tracks. Location data were filtered as described above and used as the response variable in our ecological niche models (ENMs), which were comprised of a generalized additive model 'GAM', multivariate adaptive regression splines 'MARS', generalized linear model 'GLM' and maximum entropy 'Max-Ent' models (see below, Thuiller *et al.*, 2009, 2013). Models were run with and without the inclusion of migratory tracks. Owing to the variability in tracking durations between turtles, data were not available in the same volumes between seasonal quarters of the year, and thus, the predictive power between seasons would be unbalanced. Thus, following Pikesley *et al.* (2015) all filtered location data were combined to form a single aggregated product and used in further analyses. Spatially coincident data describing features of the physical and biological environment most likely to be experienced by the turtles (temperature, depth and proxies for prey availability; sampled for the time period 2006–2011) were prepared using the R package 'raster' (Hijmans & Etten,

2012). These included the following: bathymetry and slope of the seabed (in metres, at 30 arc second grid cell resolution from www.gebco.net), monthly averaged night-time sea surface temperature (SST°C; at 1/24 degree grid cell resolution from MODIS L3; <http://podaac.jpl.nasa.gov>) and net primary production (NPP in mgC m⁻² day⁻¹; at 1/12 degree grid cell resolution from <http://orca.science.oregonstate.edu>). Following Pikesley *et al.* (2013), we used Marine Geospatial Ecological Tools v0.8a49 (MGET; Roberts *et al.*, 2010) to model daily SST oceanic frontal activity for the study area. The MGET software applies the Cayula and Cornillon single image edge detection (SIED) algorithm (Cayula & Cornillon, 1992) to gridded raster products and produces a binary response raster; a minimum frontal edge detection threshold of 0.5°C (SST) was used (Roberts *et al.*, 2010). These daily frontal activity rasters were then aggregated into three yearly rasters with cumulative totals for daily frontal activity; these were in turn averaged into a long-term yearly frontal activity raster. Monthly data for SST and NPP were then averaged into a single overall year and then averaged into long-term yearly averaged products. These long-term yearly products (SST, NPP and SST frontal activity) were then used with the aggregated turtle location data, above in modelling, such that environmental and turtle data were compared at the same temporal scale. Data for SST and NPP were unavailable in 1999 and 2000 so temporally coincident turtle location data for that period were not used in modelling (348 locations excluded). All environmental data were resampled to the coarsest resolution of our environmental data (i.e. 1/12 degree) using bilinear interpolation (which was more than ten times higher than the resolution of the polygon sampling grids used for turtle density analysis, above).

Our response variable was binary: either 'presence' described by our location data (including migratory tracks $n = 580$ locations, excluding migratory tracks $n = 482$ locations) or randomly generated 'pseudo absences' (for which we generated the same number of locations within the modelling area). ENMs were run with the environmental variables of depth and slope, and long-term yearly products for SST, NPP and SST frontal activity. All models were run using 10-fold cross-validation with a 75/25% random split of the location data for calibration, and model testing, respectively. All modelling parameters are detailed in Tables S2 and S3 in Supporting Information. These ENM projected surfaces were then combined to form an ensemble projection (ensemble ecological niche model; from herein described as EENMs) using an un-weighted average across models.

These EENMs described the relative suitability (RS) of foraging habitats, scaled between 0 and 1, where 0 represents lowest suitability and 1 indicates greatest suitability. The relative importance of each environmental variable to the model was calculated using a randomization process and scored using relative importance of the contribution coefficients (RIC) where higher values indicate greater importance (Thuiller *et al.*, 2009). To investigate spatial autocorrelation within model residuals, we calculated Moran's I coefficients

(Dormann *et al.*, 2007) for each of our EENMs. The first iteration of EENMs revealed residual spatial autocorrelation within the data, so we subsampled the location data to reduce the spatial structure within these data. This was achieved using a stepwise percentage reduction in the random sample of these data to iteratively arrive at a subsample of locations (representing 65% of the original location data) where spatial autocorrelation was no longer present in the models' residuals.

RESULTS

Size distribution

Mean body size of tracked individuals was 47.4 ± 4.7 cm (mean \pm SD, range = 34.6–54.4 cm, $n = 24$, Table S1). These were generally representative of the modal size distribution of turtles brought to the rehabilitation centre in Gran Canaria between 1998 and 2012 (mean 36.0 ± 11.1 cm SD, range = 13.0–85.2 cm, $n = 1195$ turtles; Fig. 1d) but smaller than loggerheads recorded in USA waters (Bjorndal *et al.*, 2000, 2001; Bolten, 2003; Fig. 1a) and larger than turtles found in the Azores (Bolten & Balazs, 1995; Fig. 1b). Juvenile loggerhead turtles recorded in the waters of Madeira (Fig. 1c) are a similar size to those found in the Canary Islands, but the very largest individuals, likely representing the suggested transitional stage off the coast of Morocco and Western Sahara (Tiwari *et al.*, 2002; Bolten, 2003), occur more frequently in the Canary Islands.

Tracking duration and general movements

Turtles were tracked for 284.8 ± 228.6 days (mean \pm SD; range 24–945 days, $n = 24$), and the mean maximum displacement distance away from release location was 1013.2 ± 944.5 km (range = 197.8–4307.3 km, $n = 24$; Table S1). There was no significant difference in tracking durations between projects, even though the deployment dates, tag types and duty cycles varied (Kruskal–Wallis: $\chi^2 = 0.469$, d.f. = 2, $P = 0.791$). Most turtles ($n = 21$) remained within the larger regional area for the duration of tracking and in spring and summer turtles generally moved further north towards the Iberian Peninsula (Fig. S1). However, three turtles (turtles P, T and U; Table S1) made major movements westwards, which we refer to from here on as 'migrations', across almost the entire Atlantic Ocean. It was not possible to determine from our tracking data if these turtles settled out to the USA or Caribbean coast. One of the tagged turtles (turtle T), after crossing the Atlantic Ocean, was located on land, on the island of St Lucia, Eastern Caribbean, and location data indicated that the turtle was probably on land, potentially having been captured for human consumption.

Regional area

Excluding the migrations made by turtles P, T and U, turtles occupied a total area of just under two and a half million

square kilometres (MCP) from the coast of Portugal (at 39.48 °N) to Mauritania and north of Cape Verde (18.34 °N; Fig. 2a). The longer the turtles were tracked, the greater the resultant MCP area ($R = 0.937$; $P < 0.01$) until the summed MCP area finally plateaued at 96 weeks of tracking (Fig. S2). The majority (96.8%) of locations were in oceanic waters (> 200 m deep), but 12 turtles travelled over neritic waters

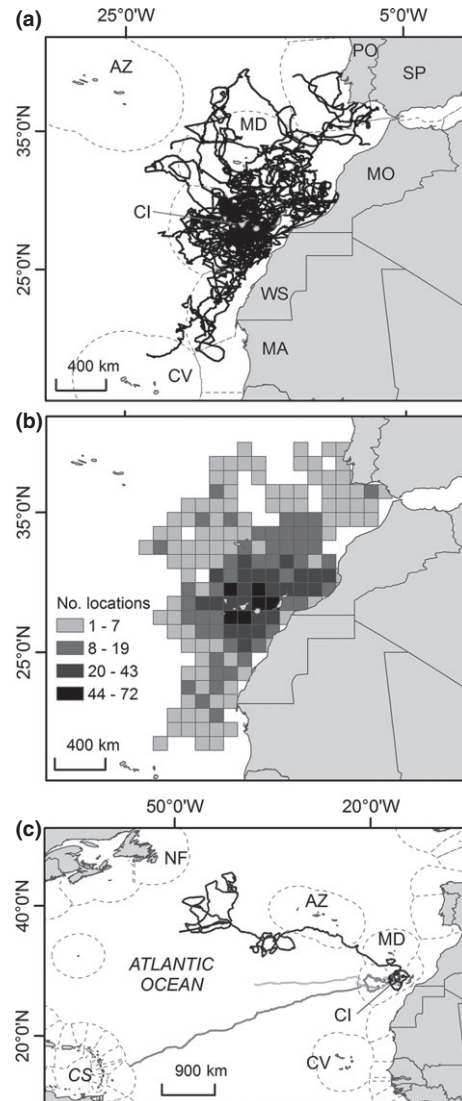


Figure 2 (a) Tracks (excluding migration) of 24 juvenile loggerheads captured and released in the Canary Islands (Spain). (b) Density mapping of juvenile loggerhead movements ($n = 24$) based on one location each 3 days, with a tolerance window of ± 2 days. Locations of the first 7 days were excluded. Raster shows 1-degree grid cells. (c) Tracks of three turtles (P, T and U, see Table S1; light grey, mid grey and black lines, respectively) migrating across the Atlantic Ocean. Broken line polygons show EEZ as CI, Canary Islands (Spain), AZ, Azores (Portugal), MD, Madeira (Portugal), CV, Cape Verde, NF, Newfoundland (Canada) PO, Portugal; SP, Spain; MO, Morocco; WS, Western Sahara; MA, Mauritania and CS, Caribbean Sea (various national jurisdictions). Map drawn to Geographic Coordinate System: WGS 1984.

(< 200 m deep; $n = 60$ locations, representing 3.2% of filtered locations), located off the coast of the Canary Islands, off the south and south-west coast of the Iberian Peninsula, and off the African coast of Morocco, and Western Sahara (Fig. S3, turtles B, D, F, G, J, K, N, O, Q, R, W, X).

High-use areas

Areas of particularly high usage were located around the Canary Islands, including the exclusive economic zone (EEZ) of Spain and Portugal (Fig. 2b). A density raster also highlighted important areas off the coast of Morocco and Western Sahara, and to a lesser extent, Mauritania.

Diving behaviour

Five turtles were deployed with PTTs that recorded diving behaviour (A–E, Table S1, Fig. 3), from which 94,537 dives were recorded with depth and 91,168 dives were recorded with duration. Turtles made largely shallow dives, with 87.2% of the dives made no deeper than 6 m (Fig. 3a). None of the individuals dived deeper than 150 m (Fig. 3a), and the dives were no longer than 180 min (Fig. 3b). Dive depth and duration were significantly different between all seasons (depth: $\text{glmmPQL } t = 26.9, P < 0.01$, duration $t = 22.4, P < 0.01$; Fig. S6) with turtles making significantly deeper, but shorter dives in autumn and summer, and shallower but longer dives in spring and winter.

Trans-Atlantic migration

Three turtles appeared to depart eastern Atlantic waters and made westward migrations across the Atlantic Ocean (turtles P, T and U) over 148, 101 and 695 days, respectively (Table S1). Two turtles were tracked as far as 4307 and 2065 km in a directed migration across the Atlantic, while the third made looping movements (travelling as far as 3130.6 km away; Fig. 2c). Scaling up from their satellite-derived transit speed, the two turtles that made directed movements would have crossed the entire Atlantic Ocean in 5.6 and 9.1 months, respectively. The third turtle would have taken much longer (43 months), but it is unclear whether its looping movements might have been directed towards westward migration as opposed to general oceanic foraging movements.

Model

Ensemble ecological niche modelling identified that the EEZs (Fig. 2) around the Canary Islands (Spain), the south-west of the Iberian Peninsula, Morocco and Western Sahara, hosted the most suitable year-round environmental conditions for juvenile loggerhead turtles. This was also reflected in all the individual GAM, MARS, GLM and MaxEnt models that comprised the ensemble (Fig. S4 and Fig. S5). This area also extended to the north-west and included Madeira and the Azores (Fig. 4). Areas with the highest habitat suitability

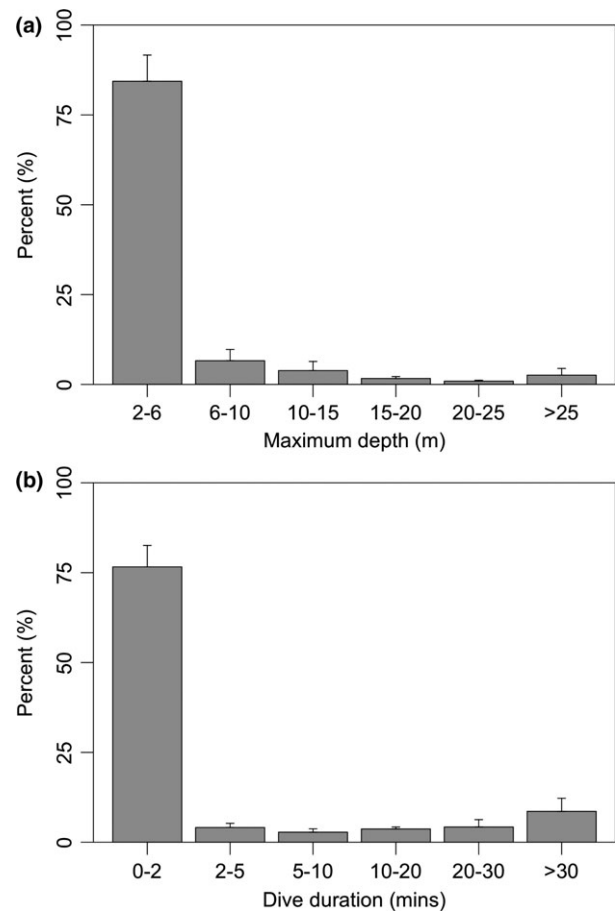


Figure 3 Frequency histograms of dives showing (a) maximum depth (metres) and (b) dive duration (minutes) for five turtles with dive recording transmitters (turtles A–E, Table S1).

($RS > 0.8$) predominantly occurred off the coast of Western Sahara and Morocco (Fig. 4b). With the inclusion of migratory tracks, there was negligible change in the overall footprint of the EENMs (oceanic sea area excluding migratory tracks ($RS \geq 0.5$) 2.4 million km^2 ; oceanic sea area inclusive of migratory tracks ($RS \geq 0.5$) 2.6 million km^2 (Fig. 4c). The most important contributory variable to both EENMs was SST with mean relative importance of the contribution coefficients (RIC) of 0.77 and 0.89 for EENMs excluding and including migratory tracks, respectively (Table S3). The second most important contributory variable across EENMs was NPP (RIC 0.16 and 0.04, respectively). Moran's I coefficients indicated that there was no spatial autocorrelation within our models' residuals (EENM excluding migratory tracks: $z = 1.69, P = 0.09$; EENM inclusive of migratory tracks: $z = 0.55, P = 0.58$).

DISCUSSION

Informing knowledge gaps

The results of the present study provide data informing the knowledge gap on the spatio-temporal distribution and

diving behaviour of large juvenile loggerhead turtles transitioning back to western Atlantic nesting grounds. It appears that prior to their return, juvenile loggerhead sea turtles inhabit east Atlantic waters over vast areas throughout the EEZs of Spain, Portugal, Morocco, Western Sahara, Mauritania, Cape Verde and in International waters, remaining in oceanic habitats and making short, shallow dives (generally < 6 m in depth). It is not clear what ecological parameter might 'trigger' the return westward, but our results provide evidence, for the first time, that it may happen at approximately 50 cm carapace length. In the present study, there were seven turtles larger than 50 cm that were *not* recorded migrating westward (see also McCarthy *et al.*, 2010), which might suggest that there are additional factors, such as body condition, that might also govern when migration begins and remain to be investigated. We also highlight that there was no discernible difference in the transmission duration and movement patterns of turtles that were held at the recovery centre of Gran Canaria prior to release.

The waters near the coast of Morocco and Western Sahara have been suggested by Tiwari *et al.* (2002) to be a transitional area for large juvenile loggerheads. The present study, along with McCarthy *et al.* (2010), has provided evidence that large juvenile loggerhead turtles are found in both coastal neritic waters and offshore oceanic waters in this area. Loggerhead turtles have been recorded in both neritic and oceanic waters of the Canary Islands (R. Herrero; R. Herrera pers. comms.) so it seems possible that a habitat shift may be present in some individuals. Future work into the plasticity of oceanic and neritic habitat use by loggerhead turtles in the eastern Atlantic could use stable isotopes to

assess the prevalence of each strategy, as well as providing insight into the diet of juvenile sea turtles in Canary Island waters (Cardona *et al.*, 2009; Vander Zanden *et al.*, 2010).

Habitat suitability

Our analysis suggests that there is a broad longitudinal band of suitable habitat for juvenile loggerhead turtles that crosses the Atlantic Ocean north of the Canary Islands and the south of the Azores. Although this area was only occupied by one turtle that crossed the Atlantic in a relatively undirected migration, it suggests it may be an important area for future survey effort to locate juvenile turtles. Other studies of marine taxa (Block *et al.*, 2011) and, indeed, other marine turtle populations (Pendoley *et al.*, 2014) have proposed core migratory corridors for protection, although recent work has highlighted that static protected areas may be inadequate for effective conservation of mobile resources (and resource users) and that the future of successful ocean management is more likely through dynamic protected areas based on real-time biological, oceanographic and socio-economic data (Maxwell *et al.*, 2015). Areas of highest habitat suitability were located off the coast of Western Sahara, Morocco, around the Canary Islands (Spain) and the south-west of the Iberian Peninsula (Portugal and Spain), and thus, conservation action in the waters of these nations may have the greatest impact on population recovery. It would be challenging to propose boundaries for an area that would encompass the majority of large juvenile loggerhead turtle movements because it is clear that such an area would be huge. However, this area also intersects with medium to high impact from

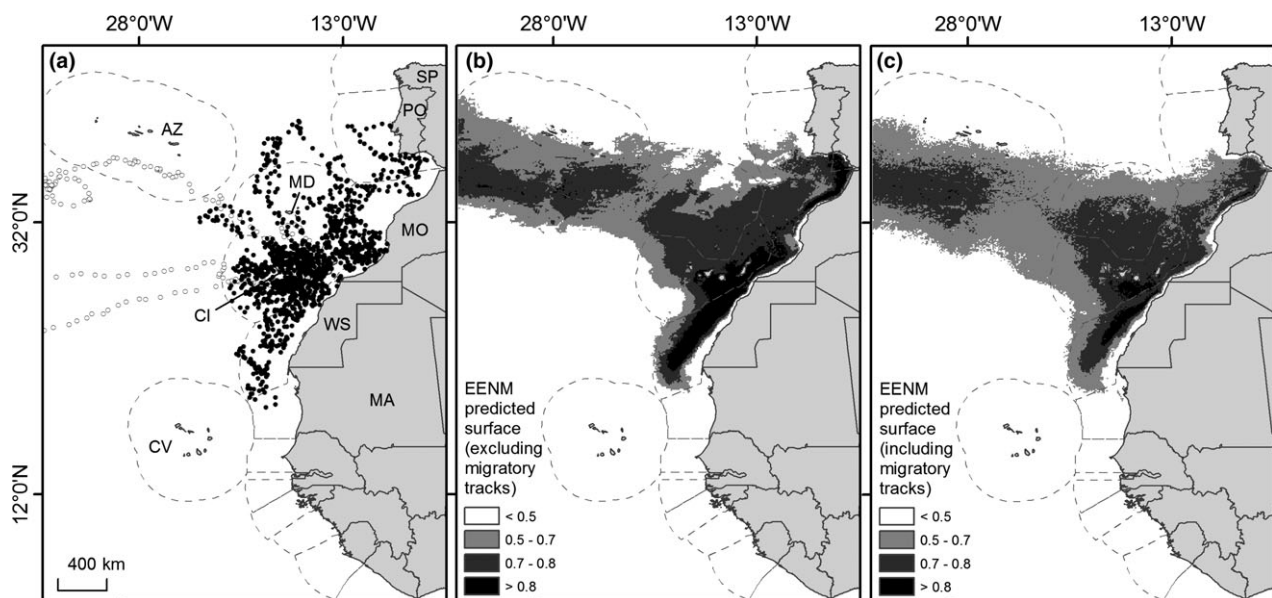


Figure 4 Maps showing: (a) filtered juvenile loggerhead location data for non-migratory (black dots) and migratory (grey dots) behaviour; (b, c) results of ensemble ecological niche modelling (EENM), where darker shading represents areas of most suitable habitat and lighter shading least suitable habitat, (b) excluding migratory tracks; and (c) including migratory tracks. All parts are drawn to the same scale, EEZs are shown as grey dashed lines. Map drawn to Geographic Coordinate System: WGS 1984.

anthropogenic activities (Halpern *et al.*, 2008, 2015), so it is clear that it is an important area that requires further conservation and legislative consideration.

Distribution, movements and dives

In the present study, we may also have documented some of the first migrations by juvenile loggerhead turtles from transitional development grounds back to natal waters, but with a limited sample size, it is important to interpret the results cautiously. From the present study, it is unclear whether their movements were influenced by prevailing currents, or whether they were directed migrations or indirect trips in which turtles forage en route. While two turtles made apparently directed migrations westwards across the Atlantic, a third took a much more meandering route across the Atlantic heading towards the northern USA and Newfoundland, where the presence of loggerhead turtles as incidental captures by fisheries has been reported (Witzell, 1999; LaCasella *et al.*, 2013). Unfortunately, it is not possible to determine from the present dataset whether these individuals would have settled to neritic habitat in the western Atlantic.

Link with other populations and conservation

Juvenile loggerhead sea turtles are found throughout much of the east Atlantic (Bjorndal *et al.*, 2000) and Mediterranean Sea (Carreras *et al.*, 2006). These juveniles are thought to belong to different nesting populations from the west and east North Atlantic, presumably migrating between the two sides of the Atlantic (Bolten *et al.*, 1998; Monzón-Argüello *et al.*, 2009). The North Atlantic has a high level of fisheries activity, and incidental captures of sea turtles are well described (Bolten, 2003; Watson *et al.*, 2005; Service, 2008; LaCasella *et al.*, 2013). While significant progress has been made to reduce by-catch in some fisheries in the north-west Atlantic, the eastern Atlantic lags behind (Conant *et al.*, 2009) and in the case of the Canary Islands, there is a lack of information regarding incidental captures. Thus, in order to effectively conserve this complex network of rookeries and foraging grounds, it will be necessary to assess the current levels of anthropogenic threat, evaluate conservation measures currently in place, and design and implement efficient measures for the whole area. It remains extremely intractable to effectively protect the huge area over which turtles in the present study were located and political and economic provisions for management of threats to marine turtles in this area of the world seem unlikely to be put in place, at least in the short term (see also Blumenthal *et al.*, 2006; Hawkes *et al.*, 2006). It is therefore vital that nations in the eastern Atlantic in which we have demonstrated habitat use by marine turtles are encouraged as much as possible to ratify international marine conservation treaties and included in international plans to reduce as much as possible fisheries by-catch.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Density rasters showing juvenile loggerhead distribution by seasons based on one location each 3 days, with a tolerance window of ± 2 days, grid cells are coloured denoting the number of locations received in each cell.

Figure S2 (a) Boxplots showing proportion of maximum minimum convex polygon for all filtered location data from juvenile loggerhead turtles ($n = 24$) at weekly intervals after release.

Figure S3 (a) Maps showing the regional movements of juvenile loggerhead turtles as filtered locations (dots). (b) Maps showing the regional movements of juvenile loggerhead turtles as filtered locations (dots).

Figure S4 Box plots of (a) maximum depth median values and (b) dive duration median values, for autumn (Sep, Oct, Nov), winter (Dec, Jan, Feb), spring (Mar, Apr, May), summer (Jun, Jul, Aug).

Figure S5 Ecological Niche Models excluding migratory location data using the (a) Generalised Additive Model (GAM), (b) Multivariate Adaptive Regression Splines (MARS), (c) Generalised Linear Model (GLM) and (d) MaxEnt modelling algorithms within the BIOMOD2 package [R Development Core Team, 2008; R package: biomod2; (Thuiller *et al.*, 2013)].

Figure S6 Ecological Niche Models including migratory location data using the (a) Generalised Additive Model (GAM), (b) Multivariate Adaptive Regression Splines (MARS), (c) Generalised Linear Model (GLM) and (d) MaxEnt modelling algorithms within the BIOMOD2 package [R Development Core Team, 2008; R package: biomod2; (Thuiller *et al.*, 2013)].

Table S1 Summary data for 24 juvenile loggerheads captured around the Canary Islands (Spain) and satellite-tracked for the present study.

Table S2 Ecological Niche Modelling evaluation metrics for 10-fold cross-validation (mean and 1 SD).

Table S3 Ecological Niche Modelling variable importance for 10-fold cross-validation.

BIOSKETCH

Nuria Varo-Cruz is a post-doctoral researcher at the Cetacean and Marine Research Institute of the Canary Islands (CEAMAR) and at ADS Biodiversidad, Spain. Her work focuses on spatial ecology and threats to marine vertebrates, with a particular emphasis on satellite telemetry and at-sea surveying.

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