Research

Modelling the niche for a marine vertebrate: a case study incorporating behavioural plasticity, proximate threats and climate change

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The integration of satellite telemetry, remotely sensed environmental data, and habitat/environmental modelling has provided for a growing understanding of spatial and temporal ecology of species of conservation concern. The Republic of Cape Verde comprises the only substantial rookery for the loggerhead turtle *Caretta caretta* in the eastern Atlantic. A size related dichotomy in adult foraging patterns has previously been revealed for adult sea turtles from this population with a proportion of adults foraging neritically, whilst the majority forage oceanically. Here we describe observed habitat use and employ ecological niche modelling to identify suitable foraging habitats for animals utilising these two distinct behavioural strategies. We also investigate how these predicted habitat niches may alter under the influence of climate change induced oceanic temperature rises. We further contextualise our niche models with fisheries catch data and knowledge of fisheries 'hotspots' to infer threat from fisheries interaction to this population, for animals employing both strategies.

Our analysis revealed repeated use of coincident oceanic habitat, over multiple seasons, by all smaller loggerhead turtles, whilst larger neritic foraging turtles occupied continental shelf waters. Modelled habitat niches were spatially distinct, and under the influence of predicted sea surface temperature rises, there was further spatial divergence of suitable habitats. Analysis of fisheries catch data highlighted that the observed and modelled habitats for oceanic and neritic loggerhead turtles could extensively interact with intensive fisheries activity within oceanic and continental shelf waters of northwest Africa. We suggest that the development and enforcement of sustainable management strategies, specifically multi-national fisheries policy, may begin to address some of these issues; however, these must be flexible and adaptive to accommodate potential range shift for this species.

Continued advancement in marine vertebrate tagging and tracking methodologies have allowed for growing insight into movement patterns and habitat use across a broad spectrum of mobile marine taxa (Hazen et al. 2012). The past decade has seen a proliferation in studies that satellite track marine vertebrates (Hart and Hyrenbach 2009). The integration of telemetry and remotely sensed environmental data, coupled with species/ecological niche modelling has provided for further understanding of spatial and temporal ecology of terrestrial and marine species on both a broad and fine spatial scale (Razgour et al. 2011, Gschweng et al. 2012, Matawa et al. 2012, Pikesley et al. 2013); multi-scale models, that incorporate animal behaviour, may further elucidate behavioural patterns (Lundy et al. 2012). Increased perception of

species spatio-temporal distributions may inform managers about where and when to best place what are often limited resources to achieve effective conservation (Hart et al. 2012). However, designation of conservation recommendations becomes more challenging as animal space use becomes greater, more diverse or more unpredictable (Hamann et al. 2010), necessitating the involvement of a greater number of stake-holders and more dynamic management.

Sea turtles are among the most studied of marine vertebrates, with all seven species having been tracked from multiple sites (Godley et al. 2008, Pendoley et al. 2014); many studies have identified and described hitherto unrecognised foraging patterns, migratory routes and habitat use. Loggerhead sea turtles *Caretta caretta* are perhaps the

best studied species, having been comprehensively studied over several decades through multi-disciplinary approaches including, tagging (Arendt et al. 2012a, Rees et al. 2013), tracking (Rees et al. 2010, Hawkes et al. 2011, Arendt et al. 2012b), genetic (Carreras et al. 2011, Monzón-Argüello et al. 2012) and stable isotope (Eder et al. 2012, Pajuelo et al. 2012, Thomson et al. 2012) studies.

A neritic, coastal model for adult loggerhead sea turtle post-nesting migratory behaviour was established some decades ago (Bolten and Witherington 2003); however, recent tracking (Hatase et al. 2002, Hawkes et al. 2006, McClellan and Read 2007, Mansfield et al. 2009, Rees et al. 2010) has demonstrated that there is considerably more plasticity than previously thought and some loggerhead turtles remain in the oceanic zone as adults, only returning to coastal waters during the breeding season. Dichotomy in adult foraging patterns has been revealed for both female and male loggerheads from the Republic of Cape Verde (Hawkes et al. 2006, Varo-Cruz et al. 2013), maintenance of which may reflect a conditional strategy (Hatase et al. 2013), with smaller turtles utilising oceanic habitats, where they may forage epipelagically around mesoscale fronts (Scales et al. 2014) and larger turtles utilising neritic habitats. Stable isotope analysis suggests that oceanic foragers dominate the Cape Verde adult female population, although neritic foragers may have higher fitness and may be older than oceanic foragers (Eder et al. 2012).

Here we combine data from Hawkes et al. (2006) and Varo-Cruz et al. (2013) together with previously unpublished telemetry data, for both adult male and female loggerhead turtles from Cape Verde to: 1) describe observed habitat use in oceanic and neritic foraging zones over multiple years; 2) model likely suitable foraging habitats using ensemble ecological niche models (EENMs); and 3) identify key environmental drivers of distribution. We also 4) predict how distribution may alter under future climate change scenarios; and 5) integrate available fisheries catch data, apportioned by exclusive economic zones (EEZs), to identify potential bycatch hotspots. Finally, we propose this novel approach, integrating satellite telemetry, ensemble ecological niche modelling and information on anthropogenic threats (fisheries and climate change), has the potential for use in management planning and practice for other widely dispersed species with complex behaviours.

Methods

Satellite tracking data: collection and processing

Platform transmitter terminals (PTTs) were attached to thirty-two adult loggerhead turtles (male = 4, female = 28) within the Cape Verde archipelago over the nesting seasons of 1999 (n = 4), 2004 (n = 10), 2005 (n = 3) and 2006 (n = 15). Method of turtle capture, transmitter type and process of attachment are detailed in Hawkes et al. (2006) and Varo-Cruz et al. (2013). All turtles were released at Boa Vista (Fig. 1) except turtle ID 7 which was released at Sao Vicente (see metadata in Supplementary material Appendix 1, Table A1). Satellite telemetry data were collected using the Argos satellite system (CLS, 2011) and
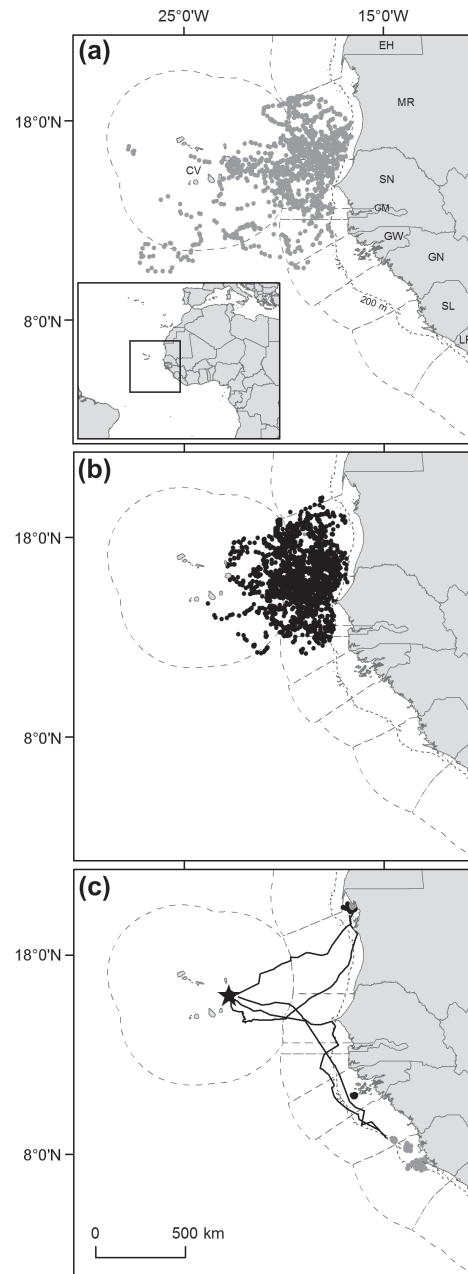

Figure 1. Satellite tracked, post-nesting loggerhead turtle movements, based on non-interpolated best daily locations for, (a) oceanic foragers: previously published data 2004/2005/2006 (n = 8, grey circles), (b) oceanic foragers: unpublished data 2006 (n = 9, black circles) and (c) neritic foragers: previously published data 2004/2005/2006 (n = 4, grey circles), unpublished data 2006 (n = 2, black circles) (see metadata in Supplementary material Appendix 1, Table A1). Black lines represent routes taken to foraging areas. Release location for all turtles (black star). Parts (a), (b) and (c) are drawn to the same spatial scale and are located according to the inset of part (a). 200 m continental shelf isobath (broken line) and EEZ maritime boundaries (broken line polygon). Countries are identified by their 2 digit sovereign state ISO code as follows: Morocco (MA), Madeira (PT), Canary Islands (ES), Western Sahara (EH), Mauritania (MR), Cape Verde (CV), Senegal (SN), Gambia (GM), Guinea-Bissau (GW), Sierra Leone (SL), Guinea-Conakry (GN), Liberia (LR), Ivory Coast (CI), Ghana (GH), Togo (TG), Benin (BJ), Nigeria (NG), Cameroon (CM) and Equatorial Guinea (GQ). Map drawn to Geographic Coordinate System: WGS 1984.

downloaded with the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005). All locations with accuracy class Z and 0 were removed and a speed and azimuth filter applied (Freitas et al. 2008, Witt et al. 2010); filtering was undertaken in R (R Development Core Team; R package: argosfilter (Freitas 2010)). Six PTTs failed to transmit foraging location data. Filtered location data were then reduced to best daily locations (BDLs), which were positions with the highest quality location class recorded during a 24 h period. If more than one location was determined with equal quality within the 24 h period the first received location was retained. These data were used as our response variable in our EENMs (see Habitat modelling). Where daily locations were missing, we interpolated these linearly, in R (R Development Core Team; R package: trip (Sumner 2011)). These data were used to describe observed habitat use and to determine a relative scale of spatial habitat use (see Habitat use).

Location data were imported into the Geographical Information System (GIS) ArcMap 10 (ESRI, Redlands, USA, <www.esri.com>). These data were then assigned to either neritic or oceanic foraging strategies as outlined in Hatase et al. (2002) and Hawkes et al. (2006). As such, neritic foraging turtles made focused migrations to continental shelf waters (as defined by the 200 m isobath) where they remained resident. Oceanic foragers displayed no such tendency and were rarely located within depths < 200 m (Fig. 1 and Supplementary material Appendix 4, Fig. A1).

Habitat use

To describe observed habitat use we used a hexagonal grid (edge to edge distance of 100 km, hexagon area 8660 km²), to sum the total number of individual turtles that had occupied a single grid hexagon for the period of our study. This grid resolution was iteratively determined to provide the optimum cell size, being a balance between too many polygon samples and therefore akin to the original raw data, and too few polygon samples with the density of the locations over-smoothed. Minimum convex polygons (MCPs) were used to determine the total area (km²) occupied by each oceanic and neritic foraging turtle. To enable comparison of spatial use between oceanic and neritic turtles we divided these MCPs by the respective number of interpolated daily locations per turtle to provide a relative scale of spatial habitat use (km² d⁻¹).

Habitat modelling

For our habitat suitability models we adopted an ensemble ecological niche modelling approach (Araújo and New 2007, Rangel and Loyola 2012, Pikesley et al. 2013). We prescribed the modelling area to be within latitudes 35.5°N, 0.5°S, and longitudes 35.5°W, 10.5°E (WGS84) as this extent generously bounded all location data within our study area (sea area: 10.1 million km²).

We extracted spatially coincident physical and biological environmental data (2004–2009) using R (R Development Core Team; R package: raster (Hijmans and Etten 2012)) from a number of datasets. These data were: a) bathymetric depth (m) (<www.gebco.net>), b) monthly averaged MODIS L3 night-time sea surface temperature (SST:°C) (<http://podaac.jpl.nasa.gov>), c) net primary production (NPP: mg C m⁻² d⁻¹) (<http://orca.science.oregonstate.edu>) and d) sea surface current velocity (m s⁻¹) (<http://hycom.org>). Monthly data, for SST, NPP and surface current velocity were then averaged into long-term yearly averaged (LTYA) products.

We used Marine Geospatial Ecological Tools ver. 0.8a49 (MGET; (Roberts et al. 2010)) to model SST oceanic frontal activity for the study area. To do this we sourced daily MODIS L3 night-time SST (°C) (<http://podaac.jpl.nasa.gov>) to create SST frontal activity rasters for each day between 2004–2009. The MGET software applies the Cayula and Cornillon single image edge detection (SIED) algorithm (Cayula and 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 yearly rasters with cumulative totals for daily frontal activity; these were in turn averaged into a long-term yearly frontal activity raster.

All environmental data surfaces were sampled to a 9×9 km resolution using bilinear interpolation (the coarsest resolution of our environmental data). To test for correlation within these data, coincident environmental data were extracted for a random sub-sample of locations (n = 200) was generated and coincident environmental data extracted for each location. A Spearman's rank correlation test was then calculated for all unique combinations of environmental variables.

We used the generalised linear model (GLM), multivariate adaptive regression splines (MARS) and MaxEnt modelling algorithms within the biomod2 package (R Development Core Team; R package: biomod2 (Thuiller et al. 2013)) to produce ecological niche models (ENMs) to identify favourable oceanic and neritic foraging areas. Our response variables were binary, either 'presence' described by our non-interpolated BDL data apportioned between oceanic and neritic foragers, or randomly generated 'pseudo absences'; these background data characterised the 'available' ecological niche within the study area. ENMs were run with the environmental variables of depth, SST, NPP, SST frontal activity and surface current velocity using LTYA products.

All models were run using 10 fold cross validation with a 75/25% random spilt of the location data for calibration, and model testing respectively. All other modelling parameters are detailed in Supplementary material Appendix 2, Table A2. Model performance was evaluated using five metrics; to evaluate model uncertainties within and between models all evaluation metrics were scaled to the range 0 to 1 (Supplementary material Appendix 2, Table A2). Model evaluation metrics were concordant across models, therefore, we combined our ENMs to form ensemble projections using an un-weighted average across models. These EENMs described the relative suitability (RS) of neritic and oceanic foraging habitats, scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability, 0 represents lowest suitability and 1 indicates greatest suitability. The relative importance of each environmental

variable to the model was calculated using a randomisation process. This procedure calculated the correlation between a prediction using all environmental variables and a prediction where the independent variable being assessed was randomly re-ordered. If the correlation was high the variable in question was considered unimportant for the model and conversely, if low, important. A mean correlation coefficient for each environmental variable was then calculated over multiple runs (Supplementary material Appendix 3, Table A3). This was repeated for each environmental variable (Thuiller et al. 2009). The calculation of the relative importance was made by subtracting these mean correlation coefficients from 1. To investigate spatial autocorrelation within model residuals we calculated Moran's I coefficients (Dormann et al. 2007) for each of our EENMs within ArcMap 10.

To investigate the potential effect of oceanic temperature rise on our EENMs we applied increases of between 0.6°C and 2°C to our LTYA SST environmental data surface. These values represent the minimum and maximum projected global oceanic surface (top 100 m) temperature increases for the end of the 21st century (2081–2100) relative to 1986–2005, based on the Coupled Model Intercomparison Project Phase 5 (CMIP5) Representative Concentration Pathway (RCP) scenarios RCP 2.6 and RCP 8.5 (IPCC 2013).

Fisheries data

To contextualise our observed and modelled areas of habitat use for oceanic and neritic foraging turtles with industrial/commercial fisheries activity within the EEZs of our study area, we sourced spatio-temporally referenced fisheries catch data. First, we downloaded yearly cumulative catch data for all marine fish species (excluding tuna and billfish: e.g. tuna, marlin, swordfish) by Fishery Committee for the Eastern Central Atlantic (CECAF) Major Fishing Area 34 statistical sub-area and division (Supplementary material Appendix 5, Fig. A2) using FishStatJ (FAO 2013a). These data were for all industrial/commercial fisheries gear types (i.e. trawls, purse seine, pole and line). We excluded tuna and billfish species from these data as this database did not apportion tuna and billfish fisheries catch by sub-area or division. Second, we sourced yearly cumulative longline tuna and billfish catch data (1995–2009) by Food and Agriculture Organization of the United Nations (FAO) Major Fishing Area Cell at 5° by 5° resolution for the Eastern Central Atlantic Major Fishing Area 34 (FAO 2013b). These data were for longline fisheries only and excluded catch attributable to other tuna and billfish fisheries gear types such as pole and line or purse seine nets.

We expressed catch data as tonnes km^{-2} per EEZ. As some FAO data cells contained land we first corrected catch data for coincident sea surface area within each cell (FAO cell tonnes km^{-2}). To calculate catch for each EEZ (tonnes km^{-2}/EEZ) we: 1) multiplied FAO cell tonnes km^{-2} by the coincident EEZ area (tonnes per EEZ–FAO cell intersect), 2) as EEZs encompassed multiple FAO data cells we then summed this for all unique EEZs and then, 3) divided the result by total unique EEZ area. This was then compared with the spatial distribution of the turtles' observed and modelled oceanic and neritic habitats.

Results

Satellite tracking

Twenty-six PTTs transmitted location data for 294 ± 249 d (mean $\pm$ 1SD, range 7–1125) for two male and 24 female loggerhead turtles. Six PTTs failed to transmit foraging location data; reasons may include premature failure of the transmitter or the attachment (Hays et al. 2007). In one case, the PTT failed to transmit after the female turtle was reported as being captured by a fishing boat on her first day of migration (Hawkes unpubl.). We classified 16 turtles as oceanic foragers and five turtles as neritic foragers; only eight oceanic BDLs out of 3269 were located within continental shelf waters (Fig. 1). Four turtles were unassigned to a foraging strategy due to limited transmission durations 22 ± 13 d (mean $\pm$ 1SD, range 7–38). Finally, one male (Supplementary material Appendix 1, Table A1, ID: 10) exhibited a greater degree of plasticity than females (Varo-Cruz et al. 2013), foraging neritically for 3 months (July to October, 2006) and subsequently oceanically (December, 2006 to October, 2007). These data were split and classified neritic/oceanic in subsequent habitat use/modelling analyses.

There was no significant difference in the median tracking durations between foraging strategies (Wilcoxon W = 42, p = 0.90: oceanic n = 16 (female n = 15, male n = 1), median = 286 d; neritic n = 5 (female n = 5), median = 313 d). There was a significant difference in the median curved carapace length (CCL) for female turtles between foraging strategies, with smaller turtles foraging oceanically and larger turtles foraging neritically (Wilcoxon W = 0, p < 0.05: oceanic n = 15, median = 83 cm; neritic n = 5, median 97 cm) (Supplementary material Appendix 1, Table A1). Oceanic loggerheads primarily foraged within the EEZs of Cape Verde, Mauritania, Senegal and Gambia; whereas neritic loggerheads foraged in continental shelf waters within the EEZs of Mauritania, Guinea-Bissau, Guinea-Conakry and Sierra Leone (Fig.1). Data for migration routes to these neritic foraging grounds indicated that turtles were also likely to traverse the EEZs of Cape Verde, Senegal and Gambia. Our telemetry data also indicated that a further two female turtles were captured during the period of this study; both turtles were oceanic turtles returning to Cape Verde. Bycatch for these turtles was established by a marked increase in the frequency and accuracy of daily satellite uplinks 216 and 627 d after deployment, and by analysis of track trajectories that culminated on land where the PTT transmitted from a fixed location for several weeks. All three turtles that were bycaught were captured within Cape Verdean EEZ waters.

Habitat use

Oceanic turtles occupied large diffuse areas of approximately 177 325 km^2 whilst foraging (median; inter-quartile range (IQR): 145 514 to 292 469 km^2), and were predominantly located in water with a median depth of 3278 m (IQR: 2891 to 3629 m) with median distance from shore of 238 km (IQR: 151 to 325 km) (Fig. 1, 2). Neritic turtles remained within the continental shelf waters in median depth of 62 m (IQR: 30 to 94 m) and median 32 km from shore (IQR: 24 to 103 km) (Fig. 1, 2). Foraging patterns for neritic turtles were confined to more distinct areas (median: 499 km^2, IQR: 196 to 1240 km^2). There was some evidence for overlap in habitat use within the
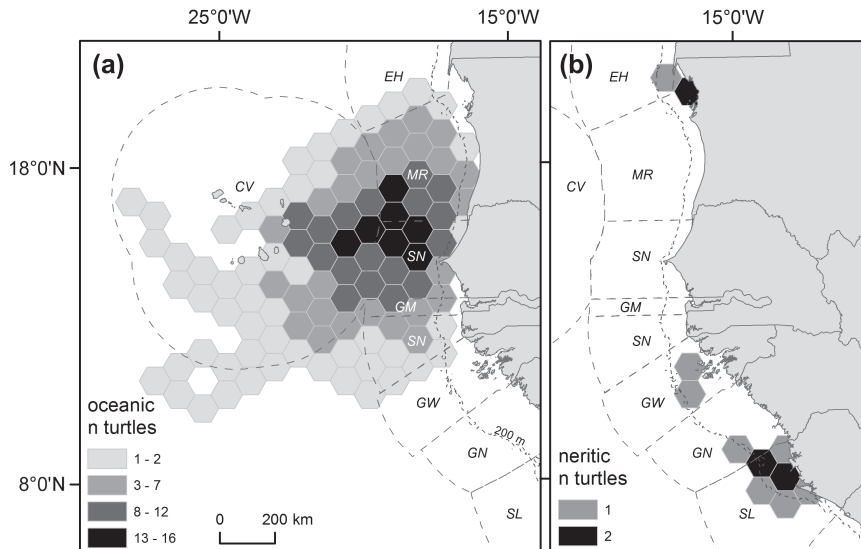
Figure 2. Density mapping of loggerhead turtle post-nesting movements based on interpolated best daily location data summed by hexagonal polygon sampling grid (100 km edge to edge). Sum of individuals occupying a single hexagon polygon for (a) oceanic and (b) neritic foragers. Turtle densities are represented by monochrome shading as detailed in the figure legend. Parts (a) and (b) are drawn to the same spatial scale. Exclusive economic zones (EEZs) are labelled with ISO codes and all other map features are drawn and labelled in accordance with Fig. 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

same year among individuals (19.7 km², n = 2 turtles; 1 male, 1 female). Our relative scale of habitat use indicated that oceanic turtles utilised a far greater sea area on a daily basis (166 km² d⁻¹) than did neritic turtles (5 km² d⁻¹).

Habitat modelling

Our oceanic EENM (RS ≥ 0.5 sea area 788 577 km²) overlapped with 51% of the total oceanic area (water deeper than 200 m) within the EEZs of Cape Verde, Western Sahara, Mauritania, Senegal and Gambia (Fig. 3). EEZs in order of greatest overlap (coincident coverage) of oceanic EENM are shown in Table 1. Turtles occupied the entire area that the model deemed suitable. Sea surface temperature and NPP were the most important contributory variables to these ENMs (Supplementary material Appendix 3, Table A3) with mean relative importance of the contribution to the model coefficients (RICC) of 0.47 (SST) and 0.28 (NPP) respectively. Ocean depth was the least important contributory variable (RICC 0.00). There was no significant correlation between SST and NPP.

Our neritic EENM (RS ≥ 0.5 sea area 197 371 km²) overlapped with 52% of west African continental shelf waters from Western Sahara to Equatorial Guinea (Fig. 3). EEZs in order of greatest coincident coverage of neritic EENM are shown in Table 1. The EENM identified neritic foraging areas that were not being utilised by our tracked neritic foraging turtles; however, these areas were not continuous. Depth and NPP were the most important contributory variables to these ENMs (Supplementary material Appendix 3, Table A3) with mean RICCs of 0.40 (depth) and 0.36 (NPP) respectively. Sea surface temperature was the third most important contributory variable (RICC 0.16). Within the study area NPP was greatest within continental shelf waters (Supplementary material Appendix 6, Fig. A3). Moran's I coefficients indicated that there was no spatial autocorrelation within our models' residuals (oceanic EENM:

z = 1.11, p = 0.27; neritic EENM: z = 1.37, p = 0.17). There was minimal overlap between oceanic and neritic EENMs; 1752 km² (0.2% of combined oceanic and neritic sea areas).

Forecast models incorporating oceanic temperature increases of 0.6°C, 1°C and 2°C, indicated that there would be a progressive northward shift in the niche suitable for oceanic turtles with an associated reduction in suitable habitat with a RS ≥ 0.5 (Fig. 4). Forecast sea areas that would remain suitable for oceanic loggerhead turtles, decreased by 6% (EENM + 0.6°C), 11% (EENM + 1°C) and 20% (EENM + 2°C) respectively. Conversely, forecast models indicated that the niche suitable for neritic turtles would expand to the south within the confines of the 200 m isobath to provide a near continuous corridor of suitable coastal waters habitat to the south of west Africa. Forecast neritic sea areas increased by 40% (EENM + 0.6°C), 57% (EENM + 1°C) and 72% (EENM + 2°C) respectively. There was minimal overlap between oceanic and neritic forecast EENMs within the EEZs of Mauritania and Senegal across all modelling scenarios; EENM + 0.6°C: 0.5% of combined oceanic and neritic sea areas, EENM + 1°C: 0.7% and EENM + 2°C: 1 %.

Fisheries data

Catch data for all species (excluding tunas) was greatest throughout the coastal EEZs of Morocco to Guinea-Bissau. Longline tuna fisheries catch varied across EEZs but was greatest in the EEZs of Western Sahara, Cape Verde, Mauritania, Sierra Leone, Guinea-Conakry, and Liberia (Fig. 5).

Observed and modelled oceanic loggerhead turtle habitats were coincident with greatest longline fisheries catch data within the EEZs of Western Sahara, Cape Verde and Mauritania, and with all other gear types within the coastal EEZs of Western Sahara, Mauritania, Senegal, Gambia and Guinea-Bissau.
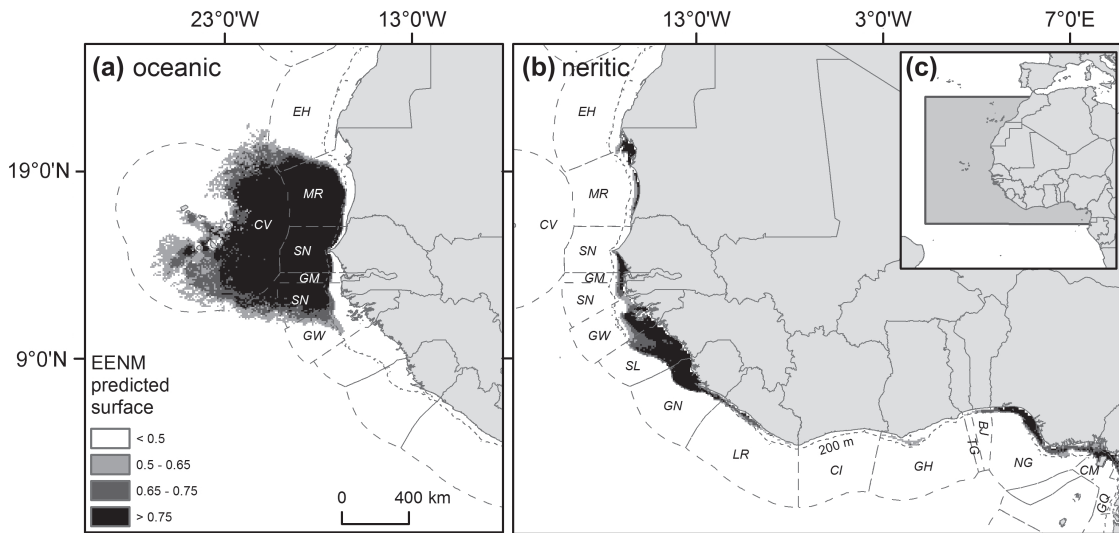
Figure 3. Ensemble ecological niche models (EENMs) for post-nesting loggerhead turtles run with non-interpolated best daily location data, and with the environmental variables of depth, SST, NPP, sea surface current velocity and SST oceanic frontal activity using long-term yearly averaged (LTYA) products for, (a) oceanic foragers (n = 17), and (b) neritic foragers (n = 6). Parts (a) and (b) are drawn to the same spatial scale. The inset (c) of part (b) shows the location and extent of our EENMs. The relative suitability of habitats are scaled between 0 and 1 (where 0.5 represents areas of typical habitat suitability, 0 represents lowest suitability and 1 highest suitability), are represented by monochrome shading as detailed in the figure legend. All other map features are drawn and labelled in accordance with Fig. 1. Map drawn to Geographic Coordinate System: WGS 1984.

Observed neritic loggerhead turtle habitats were coincident with greatest longline fisheries within the EEZs of Mauritania, Guinea-Bissau, Sierra Leone and Guinea-Conakry, and with all other gear types within coastal EEZs of Mauritania, Guinea-Bissau and Sierra Leone. Modelled neritic loggerhead turtle habitats were coincident with greatest catch from all other gears throughout the coastal EEZs of Mauritania to Sierra Leone.

Table 1. Exclusive economic zones (EEZs) in order of greatest overlap of: oceanic ensemble ecological niche model (EENM) with EEZs, where waters shallower than 200 m were excluded; an neritic ecological niche model (EENM) with EEZs, where waters deeper than 200 m were excluded.

Habitat model	Country EEZ	Proportion of EEZ (%)
Oceanic EENM		
	Gambia	100
	Senegal	99
	Mauritania	95
	Cape Verde	51
	Guinea Bissau	22
	Western Sahara	9
Neritic EENM		
	Guinea	96
	Sierra Leone	94
	Cameroon	78
	Nigeria	75
	Guinea Bissau	64
	Gambia	61
	Benin	54
	Mauritania	49
	Liberia	47
	Senegal	42
	Equatorial Guinea	40
	Ghana	17
	Togo	13
	Western Sahara	1
	Ivory Coast	0

Discussion

The Republic of Cape Verde hosts a globally significant rookery of loggerhead turtles and the only substantial rookery in the eastern Atlantic (Marco et al. 2012), which is genetically distinct from other Atlantic and Mediterranean units (Monzón-Argüello et al. 2010).

Our modelling and analysis revealed that smaller, oceanic adult loggerhead turtles from the Cape Verde islands forage across almost the entire extent of suitable habitat while larger, neritic turtles foraged within discrete areas, which comprised only a limited portion of total suitable habitat. However, neritic turtle sample size was small and spatial/temporal patterns may not be representative of the wider population. There was no overlap in observed habitat use between foraging strategies, and minimal overlap between predicted oceanic and neritic niche models. Neritic turtles foraged exclusively within continental shelf waters bounded by the 200 m isobath; depth was the most important contributory variable to our neritic EENM. Analysis of oceanic foraging movements showed the opposite; turtles were only located 8 out of 3269 times over waters shallower than 200 m (Supplementary material Appendix 4, Fig. A1).

The driver(s) behind the apparent size/age related foraging dichotomy of adult Cape Verdean loggerhead turtles have still not been elucidated. Eder et al. (2012) suggest that there may be an ontogenetic shift of use to neritic habitats with age, with this shift due to a higher accumulated probability of detecting continental shelf waters with time. Hatase et al. (2013) additionally suggests that a conditional strategy may maintain this dichotomy, where individual turtles can switch between selected habitats i.e. oceanic vs neritic, in response to differing environmental conditions. Dive data collected by Hawkes et al. (2006) indicate that larger Cape Verdean neritic turtles likely perform deeper and longer dives than smaller oceanics turtles, this being consistent with what is
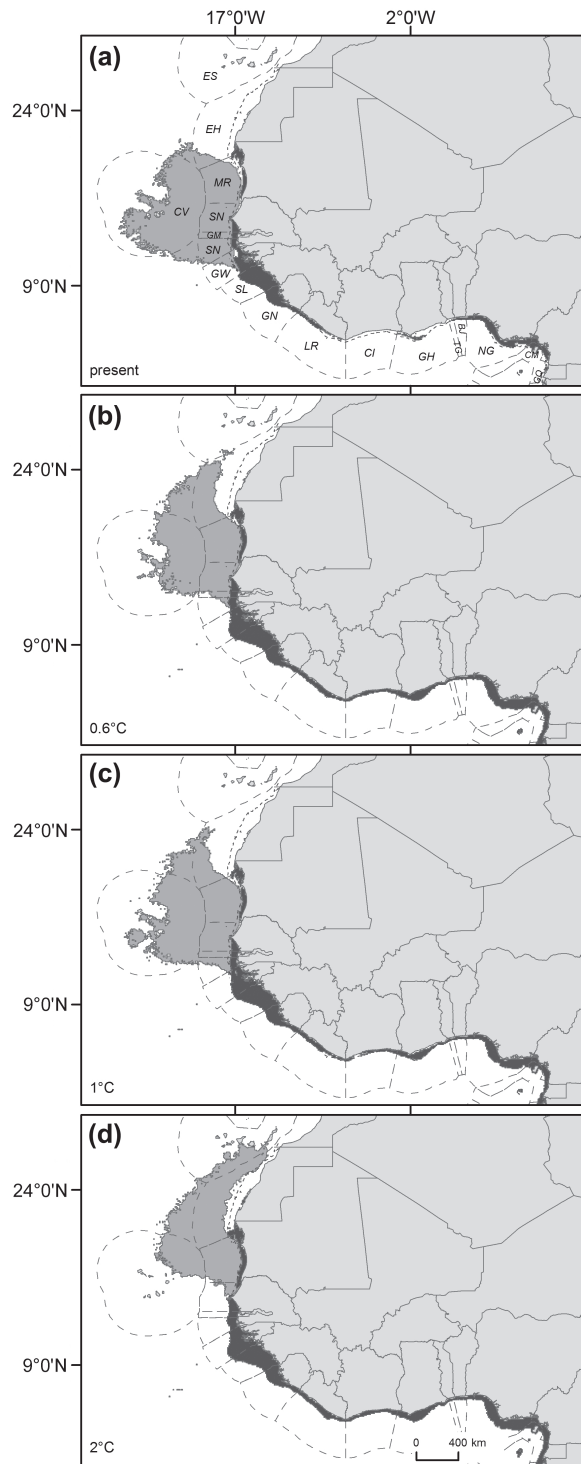
Figure 4. Forecast ensemble ecological niche models (EENMs). Oceanic and neritic EENMs (Fig. 3) were run with projected long-term yearly averaged (LTYA) sea surface temperature (SST) increases of between 0.6°C and 2°C in accordance with coupled model intercomparison project phase 5 (CMIP5) representative concentration pathway (RCP) scenarios RCP 2.6 to RCP 8.5 (IPCC 2013). (a) Existing conditions, (b) LTYA SST + 0.6°C, (c) LTYA SST + 1°C and (c) LTYA SST + 2°C. Habitats with a relative suitability ≧ 0.5 for foraging loggerhead turtles are drawn as filled polygons as follows: oceanic turtles (mid grey), neritic turtles (dark grey). All parts are drawn to the same spatial scale. All other map features are drawn and labelled in accordance with Fig. 1. Map drawn to Geographic Coordinate System: WGS 1984.

known for other species (Mori 2002). This increased body size may therefore confer a greater ability to forage on benthic species (Hawkes et al. 2006). Regardless of the drivers behind the dichotomy it is clear from our modelling that depth is critical in defining the location of suitable foraging habitats for neritic turtles, and that selection of these habitats may be associated with increased diving capacity.

Sea surface temperature can be critical in defining the ecological niche of loggerhead turtles (Polovina et al. 2004, Hawkes et al. 2007). Our forecast oceanic EENMs indicated that under temperature rises of between 0.6°C and 2°C there would be a progressive northward shift and overall contraction in oceanic loggerhead turtle habitat niche. Conversely, our forecast neritic EENMs indicated that neritic loggerhead turtle habitat niche would shift southwards, primarily within the confines of the 200 m isobath, and expand. For neritic turtles this may eventually facilitate the creation of a near continuous corridor of suitable coastal waters habitat along the west African coast. It is likely that the presence of the southward flowing Canary Current to the north of our study area (Supplementary material Appendix 7, Fig. A4), with associated coastal cold upwellings (Marchesiello et al. 2004), restricts the northward shift in forecast neritic habitat and the east/west extent of the forecast oceanic habitat. In addition to these shifts in habitat niche, an increase in temperature may also impact hatching success (Pike 2014). Given the geographic isolation of the Cape Verdean rookery, and the philopatric nature of the species, this may further negatively impact Cape Verdean loggerheads.

Our forecast EENMs do not take into account any potential changes to other contributory variable within our models, or cumulative impacts. For example; equatorial trade winds lead to the offshore transport of surface water and subsequent upwelling of cold, nutrient rich waters along the west African coast (Marchesiello et al. 2004). Evidence exists for climate change induced strengthening of alongshore wind stress that may lead to intensification of these upwellings (Bakun 1990, McGregor et al. 2007). This may lead to an in situ increase of NPP, along continental shelf waters and the shelf break, which may favour turtles that forage within these areas. Conversely, given that SST is an important contributory variable to our EENM, intensification of cold coastal upwellings along the west African coast, coupled with warming of equatorial oceanic waters, may further contract thermally suitable habitats for both oceanic and neritic loggerhead turtles. Our forecast SST surfaces do not allow for meso-scale (10s to 100s of km) nuances across their surface. Ocean warming, on a global scale, is greatest near the surface; the upper 75 m warmed, on average, by 0.11°C (0.09 to 0.13°C) per decade over the period 1971 to 2010. Tropical and Northern Hemisphere subtropical regions are projected to experience greatest oceanic surface warming (IPCC 2013). Our forecast models apply generic minimum and maximum projected global oceanic surface (top 100 m) temperature increases of between 0.6°C and 2°C, based on CMIP5 RCP scenarios (IPCC 2013), uniformly across our study area. However, while our approach of handling one aspect of climate change forcing is heuristic, it does provide insight on how distribution patterns may alter under various climate change pathways/scenarios.
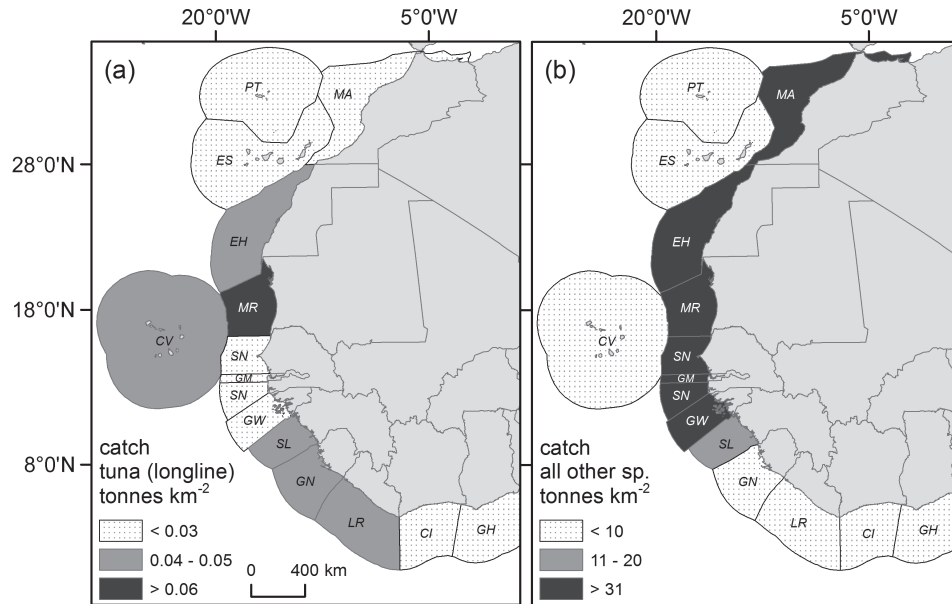
Figure 5. Cumulative fisheries catch data (1995–2009). (a) Cumulative longline tuna and billfish catch data, and (b) cumulative catch data for all marine species (excluding tuna and billfish) expressed as tonnes km⁻² per EEZ. All data are drawn as filled polygons with a low (white/light grey stipple) to high (dark grey) monochrome shaded ramp in accordance with the legend detailed in each part. Parts (a) and (b) are drawn to the same spatial resolution. All other map features are drawn and labelled in accordance with Fig. 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Loggerhead turtles in Cape Verde, which are protected by law (Loureiro 2008), face multiple terrestrial threats and impacts such as deliberate take (Marco et al. 2012), disturbance and loss of nesting beach habitat (Taylor and Cozens 2010), and are likely impacted by fisheries bycatch within near-shore waters (López-Jurado et al. 2003). Within the study period three female loggerhead turtles were positively identified as being captured (12% of our study animals), all three turtles were caught within the EEZ of Cape Verde. Bycatch is a considerable threat to loggerhead sea turtles (Lewison et al. 2004a, b) and is primarily associated with longline, trawl and gillnet fisheries (Lewison et al. 2004a).

Analysis of fisheries catch data highlighted that oceanic and neritic loggerhead turtles' observed and modelled habitats could significantly interact with fisheries. The central south Atlantic (including the Cape Verde archipelago) represents a hotspot of pelagic longline effort from the industrial fishing fleets of China, Equatorial Guinea and some Central American fleets (Lewison et al. 2004b). However, there is a paucity of reported data for sea turtle bycatch (Wallace et al. 2010), with significant data gaps around Africa (Wallace et al. 2013), particularly for longline fisheries. Trawl fisheries of the northwest African continental shelf waters have been identified as having significant bycatch rates of pelagic megafauna, including sea turtles (Zeeberg et al. 2006). This area is described as being amongst the most intensively fished in the world; subject to near year round exploitation from European and international industrial fisheries, this being orchestrated through international access agreements and private arrangements (Zeeberg et al. 2006). Given the spatial overlap of both our oceanic and neritic EENMs and foraging patterns with known areas of intense industrial longline and trawl fisheries activity, it is clear that both oceanic and neritic loggerhead turtles are at risk of bycatch from industrial fisheries.

In addition to bycatch from industrial fisheries, loggerhead turtles are also at risk from small scale artisanal fisheries using a variety of gear types as has been reported elsewhere (Carreras et al. 2004, Peckham et al. 2007, Echwikhi et al. 2010). Assessment of risk posed from artisanal fisheries is difficult due to a lack of data. However, given that neritic foraging turtles exploit shallow near-shore coastal waters, and that artisanal fisheries may employ both longline, trawl gear and gillnets, this could result in these fisheries sustaining a high loggerhead turtle bycatch rate (Peckham et al. 2007). Turtle bycatch can vary depending on many confounding factors such as gear specificity, seasonality or other bio-geographic factors (Álvarez de Quevedo et al. 2010, Báez et al. 2010, Casale 2011). Nonetheless, measures to improve knowledge of industrial fisheries effort and sea turtle bycatch rates may enable quantification of threat and may also identify the most appropriate mitigation measures; although, artisanal fisheries will potentially remain under assessed.

Given the expansive range that our study animals occupied, over multiple EEZs, the problem of enforcement of independent states' fisheries management policies is immense. Many west African coastal countries sell fisheries access agreements to Distant Water Fleets (DWFs). These DWFs have traditionally been dominated by European, US and Japanese fisheries (Gagern and van den Bergh 2013). Within sub-Saharan west Africa coastal countries traditional EU access agreements have been neither environmentally, economically nor socially sustainable, thereby promoting excessive pressure on resources and damaging the marine ecosystems (Kaczynski and Fluharty 2002). European, US and Japanese fisheries have, in part, gradually moved towards responsible fishing practice. However, these DWFs are now being displaced by a rise in other Asian DWFs that can be associated with non-transparent fishing agreements and illegal, unreported and unregulated

(IUU) fishing infringements (Gagern and van den Bergh 2013), which in turn, likely result in underestimation of fisheries pressure (Belhabib et al. 2014). This shift in fisheries market will only hinder development and enforcement of sustainable fisheries policies that recognise the threat of bycatch to marine megafauna. The potential modifications to suitable foraging habitats under global climate change further exacerbates management policy, and highlights the need for flexibility to accommodate potential range shift in species.

This study provides an insight into the migration and habitat use of loggerhead turtles from Cape Verde in both open oceanic and neritic coastal waters of the central eastern Atlantic. Our analyses clearly discriminated habitat use for these two foraging strategies, and highlighted the importance of distinct key environmental drivers in delineating these habitat preferences within a dynamic and diverse environment. Modelled habitat niches were spatially differentiated, and under the influence of predicted sea surface temperature rises, there was further spatial divergence of suitable habitats. Although oceanic and neritic habitat niches may be distinct, loggerhead turtles face homogenous threats. Notwithstanding national conservation management policy, Cape Verdean loggerhead turtles face multiple anthropogenic threats on land and at sea (López-Jurado et al. 2003, Lewison et al. 2004a, Taylor and Cozens 2010, Marco et al. 2012). Increased knowledge of gear specific fisheries effort and bycatch, within nation states' EEZs, would help facilitate an integrated approach, to formulate dynamic and effective conservation policy that begins to address the issue of bycatch. However, future conservation management strategies must be flexible and adaptive to accommodate potential range shift in species. Finally, this study demonstrates the utility of an analytical framework in robustly defining the ecological and environmental niche, of a marine vertebrate of conservation concern, that has the potential to be applied to conservation management planning and practice for other widely dispersed species with complex behaviours.

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