Multiple approaches and novel techniques to study the spatial ecology of marine vertebrates

Submitted by Stephen Kenneth Pikesley to the University of Exeter
as a thesis for the degree of
Doctor of Philosophy in Biological Sciences
January 2016

I certify that all material in this thesis, which is not my own work, has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Stephen Kenneth Pikesley

Acknowledgements

Without the support of my family this PhD would not have been feasible. Julie, Andrew and Jamie: thank you so much for all your love, understanding and support.

Special thanks to my supervisors; Matthew Witt and Brendan Godley. Firstly, for agreeing to this PhD and secondly, for your advice, guidance and investment of time. Matthew, your ability to patiently, succinctly and clearly describe complex concepts of analysis has been outstanding; I have learnt so much. Brendan, your words of wisdom and 'down to earth' attitude have got me through on more than one occasion. I thank you both most sincerely.

Being a self-funded student has always made for challenges. The requirement to financially support my studies has meant that the need to balance workloads between PhD analysis and contracted hours for the University of Exeter has been demanding. Notwithstanding this, without the part-time work that have been allocated to me over the last few years, this PhD would not have been feasible. So again, I thank Matthew and Brendan for their endeavours to keep me gainfully employed during this period.

Finally, I would like to thank all the fieldworkers involved in the numerous tagging studies that are documented within this thesis. Without the extensive catalogue of data produced by these dedicated researchers the analyses presented here would not have been achievable.

Abstract

To mitigate potential negative impacts to marine vertebrates it is necessary to gain, and build on, knowledge and understanding of their spatial ecology. Aerial and ship based surveys, as well as satellite telemetry data, have allowed for growing insight into habitat use across a broad spectrum of migratory marine species. Furthermore, these data have often enabled characterisation of anthropogenic impacts and identified potential conservation management strategies. This thesis seeks to investigate the spatial ecology of marine vertebrates using sea turtles as a study group. Data for inter-nesting and post-nesting sea turtles are analysed, and where possible, threats investigated. The analyses presented here integrate the use of multiple spatial ecological tools, including aerial surveys, satellite tracking, remote sensing, Geographical Information Systems (GIS) and habitat modelling. Many of the analytical processes employed formulate novel methodologies, as well as build upon and develop existing techniques. For post-nesting turtles, foraging and migratory data are analysed, and observed and modelled habitat niches described. Putative threats from fisheries and climate change are investigated, and where appropriate, contextualised with data describing limits of Marine Protected Areas (MPAs). For inter-nesting turtles, at-sea distributions and coastal density patterns are explored. Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data are used to elucidate shipping densities; spatial patterns of threat from fisheries, and other maritime industries are inferred. Aerial survey data are used to ascertain potential impacts to turtles on nesting beaches. Throughout this thesis spatially explicit areas are identified where concentrated conservation efforts could be applied. Furthermore, many of these analyses highlight that conservation policy must recognise the spatial extent of migratory species, and be flexible and adaptive to accommodate potential range shifts under climate change. Much of the presented analyses assimilate data from multiple sources to provide large datasets; allowing analyses to be made that would be otherwise unfeasible. Finally, this thesis demonstrates the utility of developing and applying novel analytical methodologies to these data to investigate the spatial ecology of marine vertebrates of conservation concern. As such, it is likely that many of the analytical techniques presented here could be adapted and applied to other widely dispersed marine vertebrate species to help inform global conservation planning and practice.

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SSH, NPP and proximity to oceanic frontal activity, using long-term averaged yearly products. These ENMs describe the relative suitability of oceanic habitat, scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability and are represented by monochrome shading as follows: white < 0.5, mid grey 0.5-0.75, dark grey 0.75-0.9 and black > 0.9. Countries are labelled as follows: Gabon (GAB), Republic of Congo (COG), the Democratic Republic of the Congo (COD) and Angola (AGO). Maps drawn to Geographic Coordinate System: WGS 1984.

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Biomod2 modelling parameters
One set of 5000 randomly generated 'pseudo absence' locations (background data), with no minimum or maximum distance to presence locations were generated. All locations that had missing coincident environmental data were removed from the analysis (background data locations that were spatially referenced on land). Total background data locations used in analysis: *n* = 4175.

The algorithm modelling parameters in biomod2 were as follows:
GAM: package = 'mgcv', family = 'binomial', type = 's' (spline based smooth).
MARS: package = 'mda', maximum interaction degree = 2, penalty (cost per degree of freedom) = 2, thresh (forward stepwise stopping threshold) = 0.001, prune = (TRUE).
MaxEnt: Run within biomod2, maximum iterations (for training) = 200, linear/quadratic/product/threshold/ hinge features (the transformation coefficients applied to each environmental variable), default prevalence = 0.5.

Evaluation metrics
AUC (Area under the curve): a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives.
KAPPA (Cohen's Kappa, Heidke skill score) and TSS (True Skill Statistic): measures of accuracy relative to that of random chance.
SR (Success Ratio): the fraction of the true positives that were correct.
Accuracy (fraction correct): the fraction of the predictions (true and false) that were correct.

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Table S5. Ecological Niche Modelling variable importance for 10-fold cross validation.

Relative importance of the contribution of an environmental variable is calculated using a randomisation process. This procedure calculates the correlation between a prediction using all environmental variables and a prediction where the independent variable being assessed is randomly re-ordered. If the correlation is high the variable in question is considered not important for the model and conversely, if low, important. A mean correlation coefficient for each environmental variable is then calculated over multiple runs. This is repeated for each environmental variable. The calculation of the relative importance is made by subtracting these mean correlation coefficient from 1 (Thuiller *et al.* 2009).

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Chapter II

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

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; and neritic EENM with EEZs, where waters deeper than 200 m were excluded.

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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

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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 Figure 1. Maps drawn to Geographic Coordinate System: WGS 1984.

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Table S1. Summary of PTT data for turtles assigned to a foraging strategy, detailing: study ID, foraging strategy, sex, nesting season, data start and end dates, days tracked, PTT manufacturer and model and curved carapace length (CCL) in cm. Turtle IDs: 1-9 (Hawkes *et al.* 2006), 10 &11 (Varo-Cruz *et al.* 2013), 12-22 (unpublished data). All turtles were captured at the nesting beach with the exception of turtle IDs 7, 10 & 11 which were captured at sea. All turtles were released at Boa Vista except turtle ID 7 which was released at Sao Vicente.

Table S2. Ecological Niche Modelling evaluation metrics for 10-fold cross validation (mean and 1SD). Algorithm abbreviations: Generalised Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MaxEnt). Key algorithm modelling parameters and evaluation metric descriptions are detailed at the foot of the table.

Biomod2 modelling parameters
Randomly generated 'pseudo absence' locations (background data), with no minimum or maximum distance to presence locations were generated for each habitat model. All locations that had missing coincident environmental data were removed from the analysis (background data locations that were spatially referenced on land).
The key algorithm modelling parameters in biomod2 were as follows:
GLM: package = 'stats', family= 'binomial'.
MARS: package = 'mda', maximum interaction degree = 2, penalty (cost per degree of freedom) = 2, thresh (forward stepwise stopping threshold) = 0.001, prune = (TRUE).
MaxEnt: Run within biomod2, maximum iterations (for training) = 200, linear/quadratic/product/threshold/ hinge features (the transformation coefficients applied to each environmental variable), default prevalence = 0.5.

Evaluation metrics

AUC (Area under the curve): a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives.

KAPPA (Cohen's Kappa, Heidke skill score) and TSS (True Skill Statistic): measures of accuracy relative to that of random chance.

SR (Success Ratio): the fraction of the true positives that were correct.

Accuracy (fraction correct): the fraction of the predictions (true and false) that were correct.

To compute the threshold value used to transform the probability of presence model output data to binary data for model evaluation metrics based on the comparison of binary data (*e.g.* True Skill Statistic (TSS)), the algorithm calculates the evaluation metric in question (*e.g..* TSS) for a sequence of thresholds from 0 to 1 (100 values). The value that maximises this evaluation metric is then selected as the threshold value used (Thuiller *et al.* 2009).

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Relative importance of the contribution of an environmental variable is calculated using a randomisation process. This procedure calculates the correlation between a prediction using all environmental variables and a prediction where the independent variable being assessed is randomly re-ordered. If the correlation is high the variable in question is considered not important for the model and conversely, if low, important. A mean correlation coefficient for each environmental variable is then calculated over multiple runs. This is repeated for each environmental variable. The calculation of the relative importance is made by subtracting these mean correlation coefficient from 1 (Thuiller *et al.* 2009).

Figure S1. Oceanic loggerhead foraging tracks (*n* =16). Two tracks are drawn in each map part and coloured black and grey respectively. 200 m continental shelf isobath (broken line). Maps drawn to Geographic Coordinate System: WGS 1984.

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Figure S4. Forecast Ensemble Ecological Niche Models (EENMs) projected Long-Term Yearly Averaged (LTYA) Sea Surface Temperature (SST) environmental variable surfaces. Increases of between 0.6º C and 2º C were made 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 + 0.6º C, (c) LTYA SST + 1º C and (d) LTYA SST + 2º C. SST (ºC) are classified into bands and drawn with a blue-yellow-red colour ramp in accordance with the legend detailed in each part. 200 m continental shelf isobath (broken line). Maps drawn to Geographic Coordinate System: WGS 1984.

Chapter III

Mediterranean marine turtle foraging habitats: a test of marine protected areas under climate change

Table 1. Sea area (km^2) of Mediterranean state 12 nautical mile waters coincident with seasonally aggregated green and loggerhead turtle Ensemble Ecological Niche Models (EENMs), with year-round relative suitability ≥ 0.5 (areas with category 2 (red) in Figures 2 and 3), based on present day environmental data, and forecast models. Sea area (km^2) also expressed as a % of total coincident sea area. Net gain or no change in coincidental sea area indicated by + or 0 respectively.

Table 2. Green and loggerhead turtle foraging site centroids, counts (n) and expressed as a percentage of conspecific foraging site centroids coincident with classified and un-classified Marine Protected Areas (MPAs), and proposed United Nations Environment Programme (UNEP) Priority Conservation Areas (PCAs). Total turtles tracked: green turtles *n* = 27, loggerhead turtles *n* = 49. Total foraging sites: green turtles *n* = 29, loggerhead turtles *n* = 54.

[a] MPAs: *n* = 1. Amvrakikos Wetlands, National Park, Greece, IUCN category VI.
[b] MPAs: *n* = 3.
[c] MPAs: *n* = 3.
[d] UNEP PCAs: *n* = 4. Areas; F: Southern Strait of Sicily, G: Northern and Central Adriatic, K: North-eastern Levantine Sea and Rhodes Gyre, L: Nile Delta Region (Figure. 5d).

Table 3. Area (km^2), and percentage, of the total footprint of species-specific aggregated EENMs (relative suitability ≥ 0.5), for present and forecast models, coincident with classified and un-classified Mediterranean Marine Protected Areas (MPAs).

Table 4. Area (km^2), of classified and un-classified protected areas coincident with of the total footprint of species-specific aggregated EENMs (relative suitability ≥ 0.5), for present and forecast models. Areas (km^2) are also

expressed as a % of total area of either; classified areas or un-classified areas. IUCN protected areas are defined by management category: Ia strict nature reserve, Ib wilderness area, II national park, III natural monument or feature, IV habitat/species management area, V protected landscape or seascape and VI protected areas with sustainable use of natural resources (see full IUCN protected area definitions and management categories in Supplementary Material, Table S6).

Figure 1. Post-nesting foraging site centroids (1998 to 2013) (black circles), based on satellite tracked, best daily locations for, (a) green turtles (foraging sites *n* = 29; turtles *n* = 27), (b) loggerhead turtles (foraging sites *n* = 54; turtles *n* = 49). The total number of foraging sites at grouped locations are numbered in bold. Twelve nautical mile limit (broken line). Release locations (grey stars). In part (a) maritime areas are labelled as follows: Mediterranean basins (roman capitals), seas, gulfs and straits (italics). In part (b) countries are identified using their 2 digit sovereign state ISO code (roman capitals) as follows: Spain (ES), France (FR), Italy (IT), Slovenia (SI), Croatia (HR), Bosnia (BA), Montenegro (ME), Albania (Al), Greece (GR), Turkey (TR), Syria (SY), Lebanon (LB), Israel (IL), Egypt (EG), Libya (LY), Tunisia (TN), Algeria (DZ) and Morocco (MA). Islands (bold italics) labelled in full. All parts are drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Figure 2. Aggregated seasonal Ensemble Ecological Niche Models (EENMs) for post-nesting green turtles run with: (a) present day and (b) forecast, environmental data. Parts (c), (d) and (e) are located according to the insets of part (b). Present day models were run with best daily location data, and with the environmental surfaces of depth, slope, euphotic depth, Sea Surface Temperature (SST) thermal niche, net primary productivity (NPP), and SST frontal activity using long-term biannual seasonally aggregated products. Forecast models were run with an increase of 2º C to species-specific biannual SST thermal niche surfaces in accordance with Coupled Model 5 (Intercomparison Project Phase CMIP5) Representative Concentration Pathway (RCP) scenario RCP 8.5 (IPCC 2013). Seasonal EENMs: (i) winter/spring (December - May), and (ii) summer/autumn (June - November) with a relative

suitability ≥ 0.5 were aggregated to form a predictive surface where habitat niches were weighted by the number of seasons in which the predicted area was suitable. These surfaces are drawn in accordance with the figure legend in part (a). Countries, islands and seas are labelled in accordance with Figure 1, 200 m isobath drawn and labelled. Parts (a) and (b) are drawn to the same spatial scale, all other parts are drawn to differing spatial scales. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Figure 3. Aggregated seasonal Ensemble Ecological Niche Models (EENMs) for post-nesting loggerhead turtles run with: (a) present day and (b) forecast, environmental data. Part (c) is located according to the inset of part (b). See Figure 2 for modelling details. Countries, and seas are labelled in accordance with Figure 1, 200 m isobath drawn and labelled. Parts (a) and (b) are drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Figure 4. Combined foraging habitats (relative suitability ≥ 0.5) suitable for both species under: (a) present day and (b) forecast, environmental data. Year-round habitat (red polygons), seasonally dependent habitat (mid grey polygons). Countries are labelled in accordance with Figure 1, 12 nautical mile waters (broken line). Both parts drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Figure 5. Marine Protected Areas (MPAs) within the Mediterranean. (a) Current IUCN classified and un-classified MPAs (blue cross-hatched polygons) (MAPAMED 2014). MPA centroids (black circles) for, (b) IUCN classified and (c) un-classified MPAs. (d) United Nations Environment Programme (UNEP) Priority Conservation Areas (PCAs) (blue hatched polygons). A: Alborán Seamounts, B: Southern Balearic, C: Gulf of Lions shelf and slope, D: Central Tyrrhenian, E: Northern Strait of Sicily, F: Southern Strait of Sicily, G: Northern and Central Adriatic, H: Santa Maria di Leuca, I: North-eastern Ionian, J: Thracian Sea, K: North-eastern Levantine Sea and Rhodes Gyre, L: Nile Delta Region (UNEP 2010). In part (a) countries are labelled in accordance with Figure 1. All parts are drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Table S1. Summary of PTT data for foraging post-nesting female green turtles, detailing: PTT ID, nesting season, release location and date, days tracked, days at foraging site and PTT manufacturer and model. A foraging site was deemed to be an area where an individual turtle remained resident for more than 30 days (Blumenthal *et al.* 2006) and was less than 150 km in diameter. To minimise the potential for pseudo-replication within our data we limited the maximum number of days retained for analysis at any one foraging site to 365 d.
* multiple foraging locations

Table S2. Summary of PTT data for foraging post-nesting female loggerhead turtles, detailing: PTT ID, nesting season, release location and date, days tracked, days at foraging site and PTT manufacturer and model. A foraging site was deemed to be an area where an individual turtle remained resident for more than 30 days (Blumenthal *et al.* 2006) and was less than 150 km in diameter. To minimise the potential for pseudo-replication within our data we limited the maximum number of days retained for analysis at any one foraging site to 365 d.
* multiple foraging locations
NA: data not available

Table S3. Ecological Niche Modelling evaluation metrics for 10-fold cross validation (mean and 1SD). Algorithm abbreviations: Generalised Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MaxEnt). Key algorithm modelling parameters and evaluation metric descriptions are detailed at the foot of the table.

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AUC (Area under the curve): a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives.
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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. This was repeated for each environmental variable. The calculation of the relative importance was made by subtracting these mean correlation coefficients from 1 (Thuiller *et al.* 2009).

Table S5. Loggerhead turtle foraging sites and foraging records apportioned by sex (Schofield *et al.* 2013) coincident with Loggerhead EENM based on present day environmental variables.

Table S6. Summary of IUCN protected area definition and management categories. IUCN defines a protected area as: A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values. The definition is expanded by six management categories (one with a sub-division), summarised below.

Figure S1. Seasonal Ensemble Ecological Niche Models (EENMs) for post-nesting green and loggerhead turtles run with best daily location data, and with the environmental surfaces of depth, slope, euphotic depth, Sea Surface Temperature (SST) thermal niche, net primary productivity (NPP), and SST frontal activity using long-term biannual seasonally aggregated products. Seasonal figure parts: (a,b,c,g,h,i) winter/spring, (d,e,f,j,k,l) summer/autumn. (a,d,g,j) Location data. EENMs run with, (b,e,h,k) present day environmental data, and (c,f,i,l) forecast models with an increase of 2º C to species-specific biannual SST thermal niche surfaces in accordance with Coupled Model 5 (Intercomparison Project Phase CMIP5) Representative Concentration Pathway (RCP) scenario RCP 8.5 (IPCC 2013). The relative suitability of habitats are scaled between 0 and 1 (where 0 represents lowest suitability and 1 highest suitability). Habitats with relative suitability ≥ 0.5 are drawn as red polygons. In part (a) countries and islands are labelled in accordance with Figure 1, 200 m isobath drawn (broken line). All parts are drawn to the same spatial scale. Map drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Figure S2. Discrete loggerhead foraging sites digitised from Schofield *et al.* (2013) (black circles) with present day loggerhead EENM (light blue polygons). Map drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Figure S3. Spatial coincidence of modelled green and loggerhead turtle habitat niche (based on present day and forecast environmental data) with United Nations Environment Programme (UNEP) Priority Conservation Areas (PCAs). Present day (blue), forecast model (red). Countries are labelled in accordance with Figure 1, UNEP PCAs are drawn and labelled in accordance with Figure 5d. 200 m isobath drawn and labelled. Map drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Chapter IV

Here today, here tomorrow: beached timber in Gabon, a persistent threat to nesting sea turtles

Figure 1. Gabon National Parks, Reserves and Rivers. National Parks and Reserves are shown in mid grey, unclassified areas in light grey; PNP: Pongara National Park, UA1: unclassified area 1, WWR: Wonga Wongue Reserve, UA2: unclassified area 2, LNP: Loango National Park, SCR: Sette Cama Reserve, OR: Ouanga Reserve, UA3: unclassified area 3, MNP: Mayumba National Park. The river mouths of the Komo, Ogooué and Nyanga are indicated by solid black lines and labelled in italics. The start and end locations for all surveys are shown as a filled circle and filled triangle respectively. Maps drawn to Geographic Coordinate System: WGS 1984.

Figure 2. Spatial density patterns by latitude. (a) Leatherback turtle nests for 2003 (Witt *et al.* 2009). Beached logs km^{-1} for (b) 2003, (c) 2007 and (d) 2011. Data were standardised to a common spatial resolution of discrete 25 km^{2} squares derived from the 2003 survey. National Parks and Reserves are shown as black bars and unclassified areas as mid grey bars. For abbreviations see Figure 1.

Figure 3. Mean logs km^{-1} (Mean ± SE) for 2003 (dark grey bars), 2007 (mid grey bars) and 2011 (light grey bars). A LME indicated that log densities were not influenced by the main effect of year ($Chi^2_1 = 0.40$, $p = 0.53$) or by any relationship with survey year and area ($Chi^2_8 = 5.38$, $p = 0.72$). There was a significant difference in the density of beached logs recorded among areas ($Chi^2_8 = 77.56$, $p < 0.001$). For abbreviations see Figure 1.

Figure 4. Threat maps for nesting leatherback turtles. Weighted kernelled distribution of threat indices with a 5 km smoothing factor for (a) Pongara National Park and unclassified area 1 and (b) Sette Cama Reserve. 25%, 50% and 75% polygons of the density distribution are shown with black, mid and light grey fill respectively. National Parks and Reserves are shown in mid grey and unclassified areas in light grey. Maps (a) and (b) are drawn to the same spatial

scale and are located according to the inset of part (a). Maps drawn to Geographic Coordinate System: WGS 1984.

Table S1. Total log counts, distance flown and number of logs km^{-1} for the survey years 2003, 2007 and 2011 assigned to their respective classified or unclassified status.

Table S2. Mean proportion (percentage, standardised for survey effort) of leatherback turtle beach movements impeded by logs, at sites for the nesting seasons 2006/07 to 2010/11 within Pongara National Park, Sette Cama Reserve and Mayumba National Park. Impacts to leatherback turtles were assessed using the following criteria: 0) no impact, 1) nesting was definitely abandoned due to logs, 2) nesting was probably abandoned due to logs, 3) the turtle was blocked by logs but was able to nest above the High Tide Line (HTL), 4) the turtle was blocked by logs but was able to nest below the HTL, 5) the turtle was blocked by logs after nesting, whilst returning to sea.

Chapter V

A novel approach to estimate the distribution, density and at-sea risks of a centrally-placed mobile marine vertebrate

Figure 1. Location data (black circles) for satellite tracked inter-nesting leatherback turtles tracked from, (a) Pongara National Park (*n* = 18) and (b) Mayumba National Park (*n* = 14). Tagging locations (white stars). (c) Modelled leatherback turtle density at-sea October-April. Densities (turtles 100 km^{-2} apportioned by percentiles) are drawn in accordance with the figure legend. 200 m continental shelf isobath (broken line) and EEZ maritime boundaries (broken line polygon). In part (c) coastal National Parks and reserves (mid grey polygons) and the ports of Libreville and Port Gentil are labelled. Mayumba National Park (Marine Protected Area (MPA)), hatched grey polygon. Part (c) is located according to the inset. All parts are drawn to differing spatial scales. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Figure 2. Mean seasonal density of fisheries activity derived from Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data. (a-d) VMS data for leatherback nesting seasons 2010/11 and 2011/12. A speed rule was applied to distinguish fishing from steaming or near-stationery movement (Witt & Godley 2007); only data with speeds ≥ 1 or ≤ 5 knots were retained. (e-h) AIS data for leatherback nesting seasons 2012/13 and 2013/14. A speed rule was applied to remove near-stationery movement; only data with speeds ≥ 1 knot were retained. For each dataset one random location a day for each vessel was extracted. Data were summarised (counts) to a 10 x 10 km resolution raster. Data for the complete nesting season (a,e) were then apportioned into three seasonal groups: (b,f) October and November, (c,g) December to February and (d,h) March and April. Parts (a,b,c,d) and (e,f,g,h) are drawn to differing spatial scales. All other map features are drawn and labelled in accordance with Figure 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Figure 3. Mean seasonal density of vessel activity categorised as, (a-d) oil support vessels, including tankers carrying crude/refined oil and other

petrochemical related products, (e-h) seismic research vessels and (i-l) cargo vessels, derived from Automatic Identification System (AIS) data for leatherback nesting seasons 2012/13 and 2013/14. A speed rule was applied to remove near-stationery movement; only data with speeds ≥ 1 knot were retained. One random location a day for each vessel was extracted. Data were summarised (counts) to a 10 x 10 km resolution raster. Data for the complete nesting season (a,e,i) were then apportioned into three seasonal groups: (b,f,j) October and November, (c,g,k) December to February and (d,h,i) March and April. All parts drawn to the same spatial scale. All other map features are drawn and labelled in accordance with Figure 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Figure 4. Cumulative seasonal shipping densities (a,c,e,g). Vessel density rasters were re-scaled 0-1and summed. Threat index for inter-nesting leatherback turtles (b,d,f,h). Cumulative shipping density rasters were multiplied by leatherback density rasters. To provide for data at the same spatial resolution leatherback turtle at-sea density raster were re-sampled to the same resolution (10 x 10 km) as the VMS and AIS layers using bilinear interpolation. Data for the complete nesting season (a,b) were then apportioned into three seasonal groups: (c,d) October and November, (e,f) December to February and (g,h) March and April. All parts drawn to the same spatial scale. All other map features are drawn and labelled in accordance with Figure 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Table S1. Aerial survey schedule for the Gabonese coast 2002/03 and 2005/06 to 2006/07.

Table S2. Summary of PTT data for female leatherback turtles, detailing: PTT Id., nesting season, release location, deployment date, inter-nesting periods (*n*), PTT manufacturer and model.

Table S3. Summary of output from Wilcoxon test of semi-major, semi-minor and offshore distance for leatherback turtles between the nesting locations of Pongara and Mayumba National Parks.

Author's declaration of contributions to co-authored chapters

All chapters presented in this thesis were written by S.K. Pikesley under the guidance and supervision of M.J. Witt and B.J. Godley. Author's contributions to chapters are detailed below.

Chapter I: On the front line: integrated habitat mapping for olive ridley sea turtles in the southeast Atlantic.

Stephen K. PIKESLEY, Sara M. MAXWELL, Kellie PENDOLEY, Daniel P. COSTA, Michael S. COYNE, Angela FORMIA, Brendan J. GODLEY, Warren KLEIN, Junior MAKANGA-BAHOUNA, Sheryl MARUCA, Solange NGOUESSONO, Richard J. PARNELL, Edgard PEMO-MAKAYA and Matthew J. WITT

Chapter I presents analysis of post-nesting movements of olive ridley turtles. Observed habitat use is described and ecological niche modelling is used to identify regions where environmental variables exist that may be critical in defining post-nesting habitats for this species. Fisheries catch data is integrated to contextualise potential threat from fisheries. I processed SST frontal activity data and carried out all analyses; I was lead author on the manuscript.

The chapter was written under the supervision of M. Witt and B. Godley who provided guidance on data analysis, structure and writing. This chapter was published in Diversity and Distribution in 2013.

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

Stephen K. PIKESLEY, Annette C. BRODERICK, Daniel CEJUDO, Michael S. COYNE, Matthew H. GODFREY, Brendan J. GODLEY, Pedro LOPEZ, Luis Felipe LÓPEZ-JURADO, Sonia Elsy MERINO, Nuria VARO-CRUZ, Matthew J. WITT and Lucy A. HAWKES

This chapter presents analysis of post-nesting loggerhead turtles. Observed habitat use is described and ecological niche modelling is used to identify suitable foraging habitats for animals utilising two distinct behavioural strategies. Forecast models are used to investigate how these predicted habitat niches may alter under the influence of climate change. Fisheries catch data is integrated to contextualise potential threat from fisheries. I processed all raw data, carried out all analyses and was lead author on the manuscript.

The chapter was written under the supervision of M. Witt, L. Hawkes and B. Godley who provided guidance on data analysis, structure and writing.
This chapter was published in Ecography in 2014.

Chapter III: Mediterranean marine turtle foraging habitats: a test of marine protected areas under climate change.

Stephen K. PIKESLEY, Annette C. BRODERICK, Ali Fuat CANBOLAT , Onur CANDAN , Burak A. ÇIÇEK, Wayne J. FULLER, Fiona GLEN, Yaniv LEVY, ALan F. REES, Gil RILOV, Robin T. E. SNAPE, Kimberley STOKES, Iain STOTT, Dan TCHERNOV, Matthew J. WITT, Judith A. ZBINDEN and Brendan J. GODLEY

Chapter III investigates the foraging habitats of green and loggerhead turtles satellite tracked within the Mediterranean basin. Ecological niche models are used to predict present day foraging habitats and forecast models are used to explore how these foraging habitats may alter under the influence of climate change. The spatial efficacy of the extant network of Mediterranean Marine Protected Area (MPAs) is investigated with relation to these habitat niche models. I processed all raw data, carried out all analyses and was lead author on the manuscript.

The chapter was written under the supervision of M. Witt and B. Godley who provided guidance on data analysis, structure and writing.

Chapter IV: Here today, here tomorrow: beached timber in Gabon, a persistent threat to nesting sea turtles.

Stephen K. PIKESLEY, Angela FORMIA, Floriane CARDIEC, Brendan J. GODLEY, Cheryl MILLS, Pierre Didier AGAMBOUE, Eric Augowet BONGUNO, François BOUSSAMBA, William LAURANCE, Brice Didier Koumba MABERT, Gil Avery Mounguengui MOUNGUENGUI, Carine MOUSSOUNDA, Solange NGOUESSONO, Richard J. PARNELL, Guy-Philippe SOUNGUET, Bas VERHAGE, Lee WHITE and Matthew J. WITT

In this chapter multiple year aerial survey data are analysed to determine the temporal persistence and spatial extent of beached timber on the coastal beaches of Gabon, central Africa. This knowledge is then integrated with spatial data on nesting leatherback turtles to ascertain where leatherback turtles are at greatest threat from beached timber. I analysed the aerial survey data to determine the spatial distribution and densities of beached timber as well as undertaking the subsequent threat analysis to nesting leatherback turtles. I was lead author on the manuscript.

The chapter was written under the supervision of M. Witt and B. Godley who provided guidance on data analysis, structure and writing. This chapter was published in Biological Conservation in 2013.

Chapter V: A novel approach to estimate the distribution, density and at-sea risks of a centrally-placed mobile marine vertebrate

Stephen K. PIKESLEY, Pierre Didier AGAMBOUE, Jean Pierre BAYET, Jean Noel BIBANG, Eric Augowet BONGUNO, François BOUSSAMBA, Annette C. BRODERICK, Michael S. COYNE, Philippe Du PLESSIS, François Edgard FAURE, J. Michael FAY, Angela FORMIA, Brendan J. GODLEY, Judicael Regis Kema KEMA, Brice Didier Koumba MABERT, Churley MANFOUMBI, Georges Mba ASSEKO, Kristian METCALFE, Gianna MINTON, Sarah NELMS, Solange NGOUESSONO, Jacob NZEGOUE, Carole OGANDANGA, Franck OTSAGHA, Richard J. PARNELL, Micheline Schummer GNANDJI, Guy-Philippe SOUNGUET, Mesmin WADA, Lee WHITE and Matthew J. WITT

Chapter V builds upon the analysis of threat to nesting leatherback turtles described in Chapter IV. The chapter describes the development of a novel method to model at-sea distribution and densities of inter-nesting leatherback turtles in the coastal waters of Gabon. These modelled distributions are then contextualised with multiple threat layers derived from Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data. I processed all satellite tracking, VMS and AIS data, carried out all analyses and was lead author on the manuscript.

The chapter was written under the supervision of M. Witt and B. Godley who provided guidance on data analysis, structure and writing.

Definitions

AAEAC	Africa Albers Equal Area Conic
AIS	Automatic Identification System
AUC	Area Under the Curve
BDL	Best Daily Location
CBD	Convention for Biological Diversity
CCL	Curved Carapace Length
CECAF	Fishery Committee for the Eastern Central Atlantic
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMIP5	Coupled Model Intercomparison Project Phase 5
DWF	Distant Water Fleet
EENM	Ensemble Ecological Niche Model
EEZ	Exclusive Economic Zone
ENM	Ecological Niche Model
EU	European Union
FAO	Food and Agriculture Organization
GAM	Generalised Additive Model
GDP	Gross Domestic Product
GIS	Geographical Information System
GLM	Generalised Linear Model
GPS	Global Positioning System
HD	High Definition
HTL	High Tide Line
IPCC	Intergovernmental Panel on Climate Change
IQR	Inter-Quartile Range
ITTO	International Tropical Timber Organization
IUCN	International Union for Conservation of Nature
IUU	Illegal, Unreported and Unregulated
KAPPA	Cohen's Kappa (Heidke skill score)
LME	Linear Mixed Effect
LTYA	Long-Term Yearly Averaged
MARS	Multivariate Adaptive Regression Splines
MaxENT	Maximum Entropy

MCP	Minimum Convex Polygon
MedPAN	Mediterranean Protected Areas Network
MGET	Marine Geospatial Ecological Tools
MMSI	Maritime Mobile Service Identity
MODIS	Moderate Resolution Imaging Spectroradiometer
MPA	Marine Protected Area
NPP	Net Primary Production
PCA	Priority Conservation Areas
PTT	Platform transmitter terminal
RCP	Representative Concentration Pathway
RICC	Relative Importance of the Contribution to the model Coefficients
RS	Relative Suitability
RTI	Relative Threat Index
SIED	Single Image Edge Detection
SR	Success Ratio
SSH	Sea Surface Height
SSM	State Space Modelling
SST	Sea Surface Temperature
STAT	Satellite Tracking and Analysis Tool
TSS	True Skill Statistic
UNEP/MAP	United Nations Environment Programme's Mediterranean Action Plan
UTC	Coordinated Universal Time
VMS	Vessel Monitoring System
WGS84	World Geodetic System 1984

Introduction

Human activities are impacting the global marine environment, with the vast majority of maritime ecosystems around the world negatively affected by various drivers of ecological change (Halpern *et al.* 2008). These drivers are disproportionately distributed among regions and ecosystems. Many marine ecosystems with high predicted cumulative impacts are in coastal or continental shelf waters (Halpern *et al*. 2008, 2015); areas where cumulative impacts are also identified as increasing (Halpern *et al.* 2015). Impacts from fisheries (Pauly, Watson & Alder 2005) and climate change (Doney *et al.* 2012; Gattuso *et al.* 2015; Halpern *et al.* 2015) are identified as key stressors. Formulating successful conservation policy to mitigate these impacts, and their associated effects on marine species, requires knowledge and understanding of the spatial ecology of targeted species, particularly when species are highly migratory marine vertebrates (Costa *et al.* 2012). Investigating movement patterns of species within high-use areas, such as foraging grounds or migratory routes, may provide increased insight into the spatial and temporal use of key habitats and help identify potential hotspots of threat. This increased awareness will facilitate the decision process of where and when to place what are often limited resources to achieve maximum benefit (Hart *et al.* 2012). However, effective design, implementation and regulation of protection for mobile marine species can be challenging; especially when the species are far ranging, pelagic and migratory (Hyrenbach, Forney & Dayton 2000) and when habitat use becomes more diverse or more unpredictable (Hamann *et al.* 2010).

Aerial and ship based surveys (*e.g.* Hammond *et al.* 2002; Leeney *et al.* 2012; Scheidat, Verdaat & Aarts 2012; Aerts *et al.* 2013), as well as satellite telemetry data (*e.g.* Shaffer *et al.* 2006; Weng *et al.* 2007; Kappes *et al.* 2010; Hazen *et al.* 2012; Robinson *et al.* 2012) have allowed for growing insight into movement patterns and habitat use across a broad spectrum of migratory marine species including seabirds, marine mammals, and sharks. Furthermore, these data have often enabled characterisation of anthropogenic impacts and/or facilitated definition of management strategies across a similarly broad suite of migratory marine vertebrates including: pinnipeds, elasmobranchs, albatross and pelagic fishes (*e.g.* Matthiopoulos *et al.* 2004; Hobday *et al.* 2011; Zydelis *et al.* 2011; Graham *et al.* 2012).

Sea turtles are a group of air breathing marine vertebrates that have been the subject of both aerial (*e.g.* Houghton *et al.* 2006; Witt *et al.* 2009; Lauriano *et al.* 2011; Fuentes *et al.* 2015) and extensive satellite telemetry research (*e.g.* Hays *et al.* 2003; Godley *et al.* 2008; Hazen *et al.* 2012). The ongoing use of these techniques, coupled with modelling of sea turtle movements has provided insight into their spatial and temporal ecology (Polovina *et al.* 2000; Seminoff *et al.* 2008; Shillinger *et al.* 2008; Hawkes *et al.* 2011; Silva *et al.* 2011; Wingfield *et al.* 2011), as well as identifying potential areas of threat and highlighting focal areas for conservation (Peckham *et al.* 2007; Lauriano *et al.* 2011; Silva *et al.* 2011; Witt *et al.* 2011).

There are seven extant species of sea turtle. Fossil records date the earliest turtle to about 200 million years ago (Spotila 2004) with the extant 'modern' sea turtle appearing some 110 million years ago in the Early Cretaceous Period (Spotila 2004). Of the extant sea turtle species, six belong to the family Cheloniidea (or hard-shell turtles), these are loggerhead (*Caretta caretta*), Kemp's ridley (*Lepidochelys kempii*), olive ridley (*Lepidochelys olivacea*), green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and flat-backed turtles (*Natator depressus*), and one species to the family Dermochelyidae: the leatherback turtle (*Dermochelys coriacea*). The Cheloniidea have a bony plastron (lower shell) and carapace. The carapace, or dorsal (top) shell, is overlain by a series of scutes, which are made of keratin. Leatherback sea turtles have no keratinised scutes but possess a leathery skin overlying a mosaic of thin bony plates connected by soft cartilage (Spotila 2004). Morphologically, sea turtles are considered highly adapted for life in the marine environment (Meylan & Meylan 1999). Features of note include: (i) a streamlined, hydrodynamic efficient carapace shape, (ii) stiff, paddle-shaped limbs with elongated digits, (iii) enlarged and modified lacrimal (tear) glands capable of removing excess salts from body fluids, and (iv) well-developed pectoral muscles attached to a large shoulder girdle to aid propulsion through the water (Meylan & Meylan 1999). Instead of teeth sea turtles possess horny beaks made of keratin, the shape of the beak varies by species and is thought to reflect diet (Spotila 2004). Physiologically, sea turtles have evolved adaptations that allow them to dive to significant depths and remain submerged for extended periods of time, which may result in individuals typically spending 95% of their time underwater (Spotila 2004).

Targeted prey will vary by species and by life-cycle phase (*i.e.* hatchling, juvenile or adult) and foraging niche (*i.e.* benthic or pelagic foragers). There is a paucity of data for the foraging ecology during the early life stages. However, it is suggested that many species of young sea turtles (*e.g.* green, loggerhead, hawksbill and Kemp's ridley) may occupy open ocean pelagic habitats, often in association with floating rafts of sargassum where their diet may be omnivorous (Bjorndal 1997). Adult green sea turtles are primarily benthic herbivores, principally feeding on seagrass, although may also feed on jellyfish, salps and sponges (Bjorndal 1997). Adult hawksbill sea turtles commonly forage benthically over coral or rocky reefs, but may also forage over areas of seagrass. This species likely have a specialised diet comprising of sponges, but may sometimes take other sessile benthic species (Bjorndal 1997). Benthic foraging Kemp's ridley primarily target crab species. Pelagic foraging adult loggerhead and olive ridley sea turtles likely target jellyfish and salps. Whilst in shallower waters, both species may forage opportunistically on benthic species (Bjorndal 1997). Adult leatherbacks will feed throughout the water column taking jellyfish, salps and other gelatinous organisms (Bjorndal 1997).

Sea turtles are globally distributed, inhabiting the Atlantic, Pacific and Indian Oceans, as well as the Mediterranean Sea. Hawksbills are the most tropical of the species, whereas leatherbacks can tolerate colder waters. It is considered that all species of sea turtle (with the exception of Kemp’s ridley and flat-backed turtles) are cosmopolitan in distribution (Meylan & Meylan 1999). With Kemp’s ridley being mainly restricted to the Gulf of Mexico and the eastern seaboard of the United States, and the flat-backed turtle endemic to the Australian continental shelf (Meylan & Meylan 1999). All species are highly migratory and use a wide range of geographic regions and habitats depending on life-cycle phase (*i.e.* hatchling, juvenile or adult). Foraging habitats of many adult sea turtle populations are quite distinct from nesting beach habitats (Bjorndal 1997), however these distributions need not be random, but may be influenced by areas of favourable habitat niche (Hyrenbach, Forney & Dayton 2000). For sea turtles this is likely where habitat is both thermally accessible and prey rich (Witt *et al.* 2007).

On a global scale, the IUCN Red List currently categorises Kemp's ridley, hawksbill and leatherback sea turtles as 'critically endangered', loggerhead and green sea turtles as 'endangered', olive ridley as 'vulnerable', and flat-backed turtles as 'data deficient'. All sea turtle species are listed in Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) prohibiting trade in species between all signatory parties to the convention, alive or dead (Abreu-Grobois & Plotkin 2008). Historically, sea turtles were exploited as a food source by sailors and early settlers in many parts of the world, leading to localised reductions in numbers and some local extinctions (Spotila 2004). In the present, five major threats are identified for sea turtles: fisheries impacts, direct take, coastal development, pollution and pathogens, and global warming. These present-day threats can be categorised as marine or terrestrial.

Terrestrially, sea turtles can be impacted on the nesting beach by way of harvesting of eggs, or direct take of females for consumption (Marco *et al.* 2012; Tanner 2013), or for processing into turtle products such as oil, leather and shell (Islam 2001), or for the medicinal trade (Tanner 2013). Coastal light pollution may discourage females from hauling out at nesting beaches, thereby interfering with clutch deposition (Salmon 2003; Taylor & Cozens 2010; Kamrowski *et al.* 2012). In addition, lights on shore can cause disorientation of hatchlings, causing animals to either crawl in circuitous paths, or on direct paths away from the ocean towards artificial lighting (Salmon 2003). Nesting beaches may also be subject to anthropogenic disturbance (*e.g.* noise, vehicle traffic) as well as habitat alteration and degradation associated with construction work such as beach-side developments or removal of sand (Taylor & Cozens 2010). Modification to nesting beach habitats may also be exacerbated by natural erosion associated with tidal action (Tanner 2013), sea level rise induced by global warming (Katselidis *et al.* 2014), or increase in the frequency of extreme weather events (IUCN 2016). Global warming may also impact natural sex ratios of hatchlings (Hawkes *et al.* 2007) as well as increase the likelihood of disease outbreaks for sea turtles (IUCN 2016).

In the marine environment, sea turtles may be deliberately taken, or incidentally caught as bycatch, by both industrial and artisanal fisheries (Spotila 2004; Lewison *et al.* 2013) with species being impacted by oceanic (Lewison, Freeman & Crowder 2004; Huang 2015) and coastal fisheries (Lum 2006; Alfaro-Shigueto *et al.* 2007; Witt *et al.* 2011). Longlines, gill nets and trawls pose the most likelihood of bycatch mortality. Bottom towed gears may also modify benthic habitats causing changes in food webs, thereby impacting benthic foragers (IUCN 2016). Negative interaction with vessels may result in serious injuries and in some instances death (Nabavi, Zare & Vaghefi 2012; Denkinger *et al.* 2013). Marine pollution, including plastics, discarded fishing gear, petroleum by-products, and other debris directly impact sea turtles through ingestion and entanglement (*e.g.* Follett, Genschel & Hofmann 2014; Schuyler *et al.* 2014; Wilcox *et al.* 2015). Chemical pollutants can weaken sea turtles' immune systems, making them susceptible to pathogens (Camacho *et al.* 2013). Green turtles in particular, can be affected by Fibropapillomatosis which causes tumorous growths around the eyes, neck and mouth. If feeding and vision are restricted this may ultimately result in death of individuals (Jones *et al.* 2015).

Whilst sea turtle populations have suffered severe declines over recent centuries, sea turtles can still play an important role in ocean ecosystems, having major effects on nutrient cycling and community structure in their foraging habitats. If sea turtles are able to attain high population densities, they can represent major grazers and predators in marine habitats (Bjorndal 1997). Green turtles help maintain structure and function of seagrass beds by grazing, thereby increasing seagrass productivity and nutrient content. Without grazing, the resultant loss of productivity can impact local food webs (McClenachan, Jackson & Newman 2006). Hawksbill sea turtles forage on a variety of marine sponges, thereby influencing the composition and distribution of species. In turn, this can have a positive effect on corals, releasing them from competition, as well as affecting overall reef benthic biodiversity (León & Bjorndal 2002). Similarly, as loggerhead turtles are major predators of invertebrates, they may have significant influence on community structure in benthic habitats (Bjorndal 1997). Leatherback turtles are obligate jellyfish foragers (Houghton *et al.* 2006) and are therefore a pivotal predator of jellyfish species (Gibbons & Richardson 2009). Other species of sea turtle will also target jellyfish as prey species (*e.g.* loggerheads and olive ridley). Declines in jellyfish predators could cause large-scale ecosystem changes that would allow jellyfish to thrive. Ultimately, this may negatively impact marine ecosystems (Purcell, Uye & Lo 2007). All sea turtles facilitating nutrient cycling from the marine environment to land by way of defecating or deposition of eggs on nesting beaches (Bjorndal 1997).

Throughout this thesis I investigate spatial patterns of sea turtle distribution whilst incorporating potential factors that may impact these species, during both inter-nesting and post-nesting life-cycle phases. More specifically, the analyses presented within this thesis aim to identify spatially explicit areas that may benefit from focused conservation efforts, for species of conservation concern, where appropriate management strategies could be developed or applied. For post-nesting turtles, foraging and migratory data are analysed and observed and modelled habitat niches described. Putative threats from fisheries and climate change are investigated, and where appropriate, contextualised with data describing the extent of Marine Protected Areas (MPAs). For inter-nesting turtles, at-sea distributions and coastal density patterns are explored. Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data are used to elucidate shipping densities; spatial patterns of threat from fisheries, and other maritime industries, are inferred. Aerial survey data are used to ascertain potential impacts to turtles on nesting beaches.The analyses presented here integrate the use of multiple spatial ecological tools, including aerial surveys, satellite tracking, remote sensing, Geographical Information Systems (GIS) and habitat modelling. Many of the analytical processes employed formulate novel methodologies as well as build upon and refine existing techniques. In particular, throughout this thesis the habitat modelling process is developed and techniques honed to provide for robust analytical methods.

These modelling techniques incorporate spatially coincident data describing features of the physical and biological environment most likely to be of importance in defining sea turtle habitat niche. These data can include environmental surfaces such as sea surface temperature (as a proxy for available thermal niche (Hawkes *et al.* 2007; Witt *et al.* 2007)) and bathymetric depth. Depth may be particularly important when investigating habitat use by benthically foraging sea turtles (*e.g.* green sea turtles), or for defining developmental habitats for juvenile sea turtles, or pelagic foraging habitats for adults (*e.g.* olive ridley) (Hamann *et al.* 2010). Physical and biological parameters that likely act as proxies for prey distribution and abundance will also influence the spatial distribution of sea turtles (Hamann *et al.* 2010). These can include oceanographic currents and eddies, sea surface temperature frontal activity, areas of enhanced net primary productivity, as well as localised features such as seamounts and shelf breaks.

The objective of this thesis was to investigate the spatial ecology of air-breathing marine vertebrates using sea turtles as a study group, with a specific focus on the species of loggerhead (North East Atlantic and Mediterranean), green (Mediterranean), olive ridley and leatherback (Southeast Atlantic) turtles. The IUCN Red List categorises both green and the North East Atlantic loggerhead sea turtles as 'endangered' (Seminoff 2004; Casale & Marco 2015), whilst olive ridley are identified as 'vulnerable' (Abreu-Grobois & Plotkin 2008). The Mediterranean loggerhead subpopulation is classified as of 'least concern', however, this assessment should be considered as entirely conservation-dependent, as the current population status is the result of intense conservation programs (Casale 2015). The Southeast Atlantic leatherback subpopulation is categorised as 'data deficient' and the current population trend is unknown (Tiwari, Wallace & Girondot 2013).

The presented analysis in **Chapter I** describes the observed and modelled post-nesting habitats for female olive ridley (*Lepidochelys olivacea*) sea turtles satellite tracked from two distinct nesting regions of the west coast of central Africa (Gabon and Angola), over multiple nesting seasons using data collected by two independent research groups. Olive ridley sea turtles are considered the most abundant of all sea turtles (Abreu-Grobois & Plotkin 2008). Globally, however, there is a net decline in olive ridley populations (Abreu-Grobois & Plotkin 2008) which is likely attributable to incidental capture (bycatch) in fisheries. The observed and modelled spatial distributions of olive ridley sea turtles are contextualised with tuna and billfish catch data (predominantly longline fisheries gear) to identify areas of potential threat from fisheries. The analysis revealed a considerable overlap of observed post-nesting habitat use for olive ridley turtles within the Angolan Exclusive Economic Zone (EEZ). Ecological niche models highlighted the importance of areas of long-term persistent frontal activity, associated with the continental shelf break, in defining the post-nesting habitat niche for these turtles. Furthermore, the analysis identified the potential for conflict with fisheries in the Angolan EEZ fisheries zones, particularly within the North and Central fisheries zones where both observed and modelled olive ridley spatial distributions, and fisheries catch, were at their greatest. As far as we are aware this is the first time that Ensemble Ecological Niche Modelling (EENM) has been applied to satellite telemetry data for a marine species. As such, this approach allowed for the integration of multiple single-algorithm model predictions and evaluation metrics, that in turn allowed for reduction in potential bias and increased confidence in predictions (Scales *et al.* 2015). This study also represents the largest satellite tracked analysis of olive ridley turtles from the Atlantic to date.

Chapter II investigates previously reported size related dichotomy in post-nesting foraging habitats for adult loggerhead (*Caretta caretta*) sea turtles satellite tracked from Cape Verde (Hawkes *et al.* 2006, Varo-Cruz *et al.* 2013). Tagging studies were carried out over multiple nesting seasons by two independent research groups. In the current study post-nesting data are apportioned by foraging strategy and EENMs are used to identify suitable present-day foraging habitats for oceanic and neritic turtles. Building on the methodology presented in Chapter I, forecast models incorporating projected Long-Term Yearly Averaged (LTYA) Sea Surface Temperature (SST) increases of between 0.6º C and 2º 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) are used to investigate the effect that climate change may have on these habitat niche models. To investigate potential threat from fisheries, observed and modelled present day foraging habitat are contextualised with longline and trawl catch data. Analysis of observed habitat use revealed repeated use of oceanic habitat, over multiple seasons, by all smaller loggerhead turtles, whilst larger neritic turtles occupied continental shelf waters. Ecological niche modelling revealed that modelled present day oceanic and neritic habitat niches were geographically spatially distinct. Forecast models incorporating oceanic temperature rises predicted that there would be a progressive northward shift and overall contraction in oceanic loggerhead turtle habitat niche. Conversely, neritic loggerhead turtle habitat niche were forecast to shift southwards and expand. 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.

In **Chapter III** analysis is made of the post-nesting foraging habitats for two species of sea turtle in the Mediterranean: the green turtle (*Chelonia mydas*) and the loggerhead turtle (*Caretta caretta*), with data being collected by multiple independent research groups over 14 nesting seasons from five nesting locations in the eastern Mediterranean. Both species of sea turtle face multiple threats within the marine and terrestrial environments of the Mediterranean (Casale & Margaritoulis 2010), but because of their high mobility, protection beyond nesting beaches is challenging, and requires more knowledge and new approaches. This chapter builds on the methodology presented in Chapters I and II by seasonally apportioning the satellite telemetry data to provide seasonal habitat models, based on present day and forecast environmental variables, for both green and loggerhead turtles. The spatial overlap between these modelled foraging habitats and the current and speculative Mediterranean MPA network is explored. This analysis revealed shortcomings within the current Mediterranean MPA network that results in a lack of protection within foraging habitats for both species of sea turtle. Nonetheless, adoption of suitably designed IUCN categorised MPAs within site-specific areas identified by this analysis, and by designating current MPAs with appropriate IUCN categories, could provide appreciable gains in protection for both green and loggerhead turtles within the Mediterranean.

The ecological niche modelling described in Chapters I, II and III have the potential to identify likely suitable habitats for species, but lack the ability to determine density of species. As a result, identification of high impact areas with greatest abundance of species within the marine environment, and hence heightened threat, can be subjective. The fourth and fifth chapters seek to develop methods to calculate and identify areas of increased relative threat to sea turtles, whilst at the same time moving the focus of analysis from post-nesting to inter-nesting sea turtle habitats.

Chapter IV investigates the potential negative impacts to nesting leatherback turtles (*Dermochelys coriacea*) in a terrestrial beach environment. Terrestrial threats to sea turtles can manifest themselves in many forms, and be specific to the geographic location of the nesting beach (*e.g.* Salmon 2003; Taylor & Cozens 2010; Kamrowski *et al.* 2012; Marco *et al.* 2012; Tanner 2013; Katselidis *et al.* 2014). An initial assessment by Laurance *et al.* (2008) described the potential for negative interactions between nesting leatherback turtles and beached timber at nesting beaches along the coast of Gabon, central Africa. Chapter IV builds upon this initial assessment with a rigorous and comprehensive statistical analysis of multiple year aerial survey data over a nine year period (February 2003, 2007 and 2011), with the aim of describing the temporal persistence and spatial extent of beached timber. This analysis is coupled with spatial density and distribution data for nesting leatherback turtles, thereby allowing the calculation of a threat index for interaction between nesting leatherbacks and beached timber for the majority of the Gabonese coast. The presented analysis demonstrates that the temporal and spatial extent of beached timber, and hence threat to leatherbacks, described by Laurance *et al.* (2008), is persistent and has the potential to remain so. Furthermore, the analysis demonstrates that the threat posed by beached timber to nesting leatherback turtles is a national issue both within and outside the boundaries of Gabon's National Parks and Reserves.

Multiple modelling techniques exist to build an understanding of habit niches for species in the marine environment (*e.g.* Matthiopoulos *et al.* 2004; Aarts *et al.* 2008; Edrén *et al.* 2010; Pikesley *et al.* 2014). These methods are challenged by the issue of enumerating species densities. In **Chapter V** a novel method is described to model at-sea distribution and densities for inter-nesting leatherback sea-turtles of Gabon, using multiple year aerial survey and satellite telemetry data. These modelled density distributions are contextualised with layers of shipping movements generated from Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data to derive threat layers associated with multiple categories of industrial vessel types. This analysis identifies key at-sea areas in which protection for inter-nesting leatherback turtles urgently needs to be considered. Although the analysis focuses on a single species, many of the associated threats identified (fisheries, seismic activity, general shipping) will apply to other air-breathing mobile marine vertebrates within Gabonese waters. Recently announced proposals to extend Gabon's network of National Parks, including the designation of several new Marine Protected Areas (MPAs) in which commercial fishing will be excluded, may go some way to securing protection for species. However, this analysis highlights that it may be appropriate to consider other categories of threat, as well as seasonality, when finalising MPA boundaries and defining management strategies within these zones.

The ongoing degradation of the global marine environment associated with anthropogenic impacts (Halpern *et al*. 2008, 2015) makes it imperative that we gain and build understanding of the ecology of species in crisis, as well as identify potential sources of threat (Hamann *et al.* 2010). Failure to do so can only hinder development and application of appropriate conservation policy and practice, and ultimately, may result in extinction of species, locally or globally. For sea turtles, this would result in the loss of their valuable services to the ecosystem, which in turn may have downstream deleterious effects to both marine and terrestrial systems.This thesis presents a suite of integrated chapters that investigate sea turtle spatial ecology, together with analysis of potential impacts, and where possible, assessment of protection for this species, using both post-nesting and inter-nesting data. As a result, these studies identify spatially explicit areas where concentrated conservation efforts could be applied to achieve maximum benefits. Many of these analyses highlight that it is imperative that marine conservation policy recognises the spatial extent of highly migratory species with expansive cross-border ranges. Furthermore, this thesis presents evidence to suggest that designation of mitigation measures also needs to be flexible and adaptive to accommodate potential range shift for species under climate change.

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Chapter I: On the front line: integrated habitat mapping for olive ridley sea turtles in the southeast Atlantic

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Published in Diversity and Distributions (2013) Volume 19: 1518-1530

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ABSTRACT

Aim Knowledge and understanding of marine vertebrate spatial ecology are required to identify sources of threat and highlight areas for conservation. Olive ridley sea turtles (*Lepidochelys olivacea*) are in decline in some regions and data for the Eastern Atlantic are sparse. Here, we seek to describe observed, and potential, post-nesting habitats for this species in the southeast Atlantic. We contextualise these with fisheries catch data to identify areas of potential threat from fisheries interaction for this species.

Methods We tracked twenty-one female olive ridley turtles, from two nesting sites, between 2007 and 2010.We used ensemble ecological niche modelling, integrated with knowledge on the physical and biological oceanographic environment, to identify regions where environmental variables exist that may be critical in defining post-nesting habitats for this species. We further integrate fisheries catch data to contextualise potential threat from fisheries.

Results We describe key areas of observed, and potential, olive ridley turtle occurrence at sea, and reveal that there was considerable overlap of these conspecifics, from two distinct nesting regions, within the Angolan Exclusive Economic Zone (EEZ). With the inclusion of fisheries catch data, we highlight areas that have potential for conflict with fishing activities known to result in bycatch.

Main conclusions This study demonstrates that it is imperative that marine conservation policy recognises the spatial extent of highly migratory species with expansive ranges. It also highlights that deficiencies exist in current knowledge of bycatch, both in gear specificity and in catch per unit effort. With integration of Vessel Monitoring System (VMS) data and those on fisheries catch, knowledge and understanding of bycatch may be improved and this will ultimately facilitate development of appropriate management strategies and long-term sustainability of fisheries and their supporting ecosystems.

Keywords: bycatch, ensemble ecological niche modelling, fisheries, ocean fronts, spatial analysis

INTRODUCTION

Successful conservation policy to mitigate anthropogenic impacts to marine vertebrates requires knowledge and understanding of their spatial ecology, particularly when species are highly migratory (Costa *et al.* 2012). Satellite telemetry has been used to determine oceanographic habitat of a number of migratory marine predators including seabirds, marine mammals, and sharks (Shaffer *et al.* 2006; Weng *et al.* 2007; Kappes *et al.* 2010; Robinson *et al.* 2012). Furthermore, satellite telemetry has been applied to successfully characterise anthropogenic impacts and/or define management strategies across a diversity of migratory marine vertebrates, including giant manta rays (*Manta birostris*), grey seals (*Halichoerus grypus*), albatrosses and pelagic fishes (Matthiopoulos *et al.* 2004; Hobday *et al.* 2011; Zydelis *et al.* 2011; Graham *et al.* 2012).

Sea turtles are one marine vertebrate group that has been the subject of extensive satellite telemetry research (Hays *et al.* 2003; Godley *et al.* 2008; Hazen *et al.* 2012). The ongoing use of satellite tracking techniques, coupled with habitat/environmental modelling of sea turtle movements has provided insight into their spatial and temporal ecology (Polovina *et al.* 2000; Seminoff *et al.* 2008; Shillinger *et al.* 2008; Hawkes *et al.* 2011; Silva *et al.* 2011; Wingfield *et al.* 2011), as well as identifying potential areas of threat and highlighting focal areas for conservation (Peckham *et al.* 2007; Silva *et al.* 2011; Witt *et al.* 2011). This increased knowledge has led to a shift away from a generalist migratory model for sea turtle species, to multiple models that recognise post-nesting movements that are flexible (*e.g.* Hawkes *et al.* 2006; Arendt *et al.* 2012a; b), with inter- and intraspecific variability, dichotomous foraging patterns (Schofield *et al.* 2010) and strong relationships between patterns of movements and resources (Plotkin 2010).

Olive ridleys (*Lepidochelys olivacea* Eschscholtz 1829) are considered the most abundant of all sea turtles (Abreu-Grobois & Plotkin 2008), distributed throughout tropical and subtropical oceans, with nesting beaches occurring within tropical waters (excluding the Gulf of Mexico). Globally, however, there is a net decline in olive ridley populations which is likely attributable to incidental capture (bycatch) in fisheries (Abreu-Grobois & Plotkin 2008) . Their associated habitat has been described as both coastal (Marcovaldi 1999; Gopi *et al.*2006) and pelagic (Luschi *et al.* 2003; Abreu-Grobois & Plotkin 2008), with diverse populations occupying different marine habitats (Polovina *et al.* 2004). They are thought to be generalist feeders, targeting prey such as jellyfish, salps, fish, molluscs and crustaceans, with diet varying among geographic regions (Bjorndal 1997).

Olive ridley turtles have demonstrated spatial plasticity in their post-nesting movement strategies within populations (McMahon *et al.* 2007; Whiting *et al.* 2007; Silva *et al.* 2011; Rees *et al.* 2012), as well as in their habitat selection (McMahon *et al.* 2007; Whiting *et al.* 2007; Silva *et al.* 2011). Their migratory movements have also been associated with frontal regions of cold core/warm core eddies (Ram *et al.* 2009). Data for Eastern Atlantic populations of olive ridley turtles are sparse and the status of stocks in this region is unknown due to a lack of long-term quantitative data (Abreu-Grobois & Plotkin 2008).

Here we describe post-nesting movements of olive ridley turtles from two different nesting regions from the central African Atlantic coast countries of Gabon and Angola. Our aims are to elucidate facets of the life history of this population and to delineate key areas of occurrence. Utilising available physical and biological oceanographic satellite derived environmental data, together with ensemble ecological niche modelling, we highlight areas where environmental conditions for olive ridley turtles may be most favourable and, with the inclusion of fisheries catch data, analyse the potential for conflict with this possible threat.

METHODS

Satellite tracking data: collection and processing

Platform Transmitter Terminals (PTTs) were attached to twenty-eight nesting olive ridley turtles at release sites in southern Gabon and northern Angola. These were Nyafessa (S 3.96, E 11.15; all coordinates given as decimal degrees: WGS 1984) in Mayumba National Park, Gabon (*n* = 18), and Kwanda Island and Sereia Peninsula near the mouth of the Congo River (S 6.07, E 12.22), north of Soyo, Angola (*n* = 10) over the nesting seasons of 2007/08 (Gabon *n* = 5), 2008/09 (Gabon *n* = 13, Angola *n* = 8) and 2009/10 (Angola *n* = 2). PTTs deployed in Gabon were attached in accordance with the method described by Maxwell *et al.* (2011). PTTs deployed in Angola were attached using a combination of thin layers of epoxy adhesive (Power Fast, Powers Fasteners, NY, USA) and fibreglass cloth. Each PTT was positioned on the central anterior portion of the olive ridley turtle carapace, covering approximately the first and second vertebral scutes. PTTs deployed in Gabon, were either KiwiSat 101 (Gabon: *n* = 12, Sirtrack Ltd, Havelck North, New Zealand) or Telonics ST20, Model A1010 (Gabon: *n* = 6, Telonics Inc, Mesa, AZ, USA). PTTs deployed in Angola were KiwiSat (Angola: *n* = 10, Sirtrack Ltd, New Zealand).

Data transmitted by PTTs were collected using the Argos satellite system (CLS 2011) and downloaded with the Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005). All positions with location accuracy class Z and 0 were removed; a speed and azimuth filter was then applied (Freitas *et al.* 2008; Witt *et al.* 2010). All filtering was undertaken in R (R Development Core Team 2008; R package: argosfilter; Freitas 2010). Location data were then reduced to best daily locations, herein after referred to as locations, 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. Where daily locations were missing, we interpolated these linearly, in R (R Development Core Team 2008; R package: trip; Sumner 2011).

PTT derived location data were imported into the Geographical Information System (GIS) ArcView 9.3 (ESRI, Redlands, CA, USA). To facilitate removal of inter-nesting location data we used a 25 km radius buffer (defined by visual assessment of inter-nesting satellite tracking data), extending from each release site, to define the coastal inter-nesting zone for each nesting population of olive ridley turtles. Data within this inter-nesting zone were excluded from this analysis. Seven PTTs (Gabon *n* = 6, Angola *n* = 1), failed to transmit post-nesting movement data, possibly due to premature failure of the transmitter or the attachment (Hays *et al.* 2007). Twenty-one PTTs (Gabon *n* = 12, Angola *n* = 9) transmitted post-nesting movement data for 167 ± 160 days (mean ± 1SD, range 33-686) (Figure 1a,b,c, also see Supplementary Material, Table S1).

Location data, with interpolated positions for missing days, were analysed to determine areas of habitat use. We used a polygon sampling grid of 75 x 75 km grid squares to sum all spatially coincident locations (Figure 2a). The same sampling grid was used to determine the number of individual turtles occupying a grid square (Figure 2b). Non-interpolated locations for all post-nesting movements were analysed to determine monthly latitudinal distributions (Figure 3a), distance from shore (km) (Figure 3b), Sea Surface Temperature (SST °C) (Figure 3c) and depth (m) (Figure 3d) at best daily locations.

Habitat modelling

For our Ecological Niche Models (ENMs), we prescribed the study area to be within latitudes N 1.5º, S 18.5 and longitudes E 0.5º, E 14.0º (sea area: 2.8 million km^2) (Figure 1a). We determined spatially coincident physical and biological environmental data (2008-2010) using Matlab (The MathWorks, Natick, MA, USA) and R (R Development Core Team 2008; R package: raster; Hijmans & Etten 2012). These data were: bathymetric depth (m) (www.gebco.net), and monthly averaged daily SST (°C) (http://podaac.jpl.nasa.gov), Sea Surface Height (SSH) (cm) (http://www.aviso.oceanobs.com), Net Primary Production (NPP) (mg C m^{-2} day^{-1}) (http://orca.science.oregonstate.edu) and distance to persistent frontal activity (km). All data were sampled to a 9 km x 9 km resolution using bilinear interpolation, this being the coarsest resolution of our environmental data. These monthly data, for SST, SSH and NPP, were then averaged into long-term annual products. The resulting data surfaces provided for consistent, near cloud-free, images for the spatial extent of post-nesting movements. To test for correlation within these data a random sample of locations (*n* = 1000) was generated and coincident environmental data extracted for each location. A Spearman's rank correlation test was then calculated for each paired variable.

We used Marine Geospatial Ecological Tools v0.8a43 (MGET; Roberts *et al.* 2010) to detect oceanic frontal activity for the study area. Frontal features can represent significant areas of enhanced primary productivity that in turn may provide areas of increased prey availability for marine vertebrates (Scales *et al.* 2015). The MGET software applies the Cayula and Cornillon (1992) Single Image Edge Detection (SIED) algorithm to gridded SST products and produces a binary response raster; a minimum frontal edge detection threshold of 0.5°C was used. Level 4 Operational SST and Sea Ice Analysis (OSTIA) data were sourced (http://podaac.jpl.nasa.gov). Daily frontal activity rasters were produced for 2008-2010 and these 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. To identify key features while reducing ‘clutter’ from pixels generated by ephemeral frontal activity, we selected the upper 50% of pixel positive day values to represent the occurrence of longer-term persistent frontal activity, from this we then determined a long-term yearly raster of distance to persistent frontal activity for the study area.

For our habitat modelling we adopted an ensemble ecological niche modelling approach (Araújo & New 2007; Rangel & Loyola 2012). We used the Generalised Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS) and MaxEnt modelling algorithms within the biomod2 package (R Development Core Team 2008; R package: biomod2; Thuiller *et al.* 2013) to produce ENMs to identify areas where environmental conditions for olive ridley turtles were most favourable (Figure 4). Our response variable was binary, either 'presence' described by our non-interpolated location data or randomly generated 'pseudo absences'; these background data characterise the 'available' environment parameters within the study area. ENMs were run with the environmental variables of depth, SST, SSH, NPP and proximity to frontal activity, using long-term averaged yearly 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 Table S2.

Model performance was evaluated using five metrics. (1) Area Under (the receiver operating characteristic) Curve (AUC); a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives. (2) Cohen's Kappa (Heidke skill score) (KAPPA) and (3) True Skill Statistic (TSS): a measure of accuracy relative to that of random chance. (4) Success Ratio (SR): the fraction of the true positives that were correct and (5) Accuracy: the fraction of the predictions (true and false) that were correct (Thuiller *et al.* 2009; Thuiller *et al.* 2013). All evaluation metrics were scaled to the range 0 to 1. This enabled us to evaluate model uncertainties within and between models (Supplementary Material, Table S2). As all models performed with similar accuracy, these ENM projected surfaces were then combined to form an ensemble projection using an un-weighted average across models. This ensemble ENM described the relative suitability of oceanic habitat, scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability, 0 represents lowest suitability and 1 indicates greatest suitability (Figure 5a).

The relative importance of the contribution to the model of each environmental variable, 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. This procedure 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.

Fisheries Data

To contextualise our observed and modelled areas of habitat use with fisheries activity, we obtained cumulative tuna and billfish yearly catch data (1995-2009) for the study area (FAO 2012a) by FAO Major Fishing Area Cell (FAO 2012b). As some of these area cells contained land masses we apportioned these data for the cell's coincident sea area (tonnes/km^2); these were then apportioned by the coincident area of the respective Angolan Exclusive Economic Zone (EEZ) fishing zone and by gear type (FAO 2007)

(Figure 6a,b, Supplementary Material, Table S3 & S4). This was then compared with the spatial distribution of the turtles' observed and potential habitat.

RESULTS

Satellite tracking

Post-nesting olive ridley turtles (*n* = 21) were satellite tracked for 112 days (median), 84 to 193 days (d) (inter-quartile range (IQR)) with tracked distances (minimum straight-line) ranging between 694 and 9182 km. There was no significant difference in the median post-nesting tracking durations between release sites (Mann-Whitney, p = 0.943) (Gabon *n* = 12; median 116 d, Angola *n* = 9; median = 111 d). Throughout their post-nesting movements, nineteen olive ridley turtles (Gabon *n* = 12, Angola *n* = 7) occupied oceanic waters, primarily within the 200 nautical mile EEZs of Gabon, Republic of Congo, Democratic Republic of Congo and Angola (Figure 1b,c). The remaining two turtles (Supplementary Material, Table S1, IDs: T and U) both from the Angolan release site (the only turtles tagged during the 2009/10 nesting season) departed the inter-nesting coastal zone in November 2009 and moved into oceanic waters outside the EEZs, with the most northerly tracked turtle's movements being associated with an area of seamounts (Figure 1c). Of the nineteen turtles that occupied oceanic EEZ waters, eighteen made post-nesting movements that progressed in a southerly direction (Gabon *n* = 11, Angola *n* = 7), the remaining turtle (Supplementary Material, Table S1, ID: B) stayed in close proximity to the inter-nesting zone for the period of its PTT transmissions (*n* = 197 days).

Greatest habitat use occurred within approximately 200 km of the coast, off the continental shelf, in depths < 2000 m, with highest densities of olive ridley locations consistently occurring within the Angolan EEZ (Figure 2a,b). Turtles occupied EEZ waters as follows: Angola 77% of all locations, Republic of Congo 9%, Gabon 5%, Democratic Republic of Congo 1% and Equatorial Guinea 1%; 7% of all locations fell outside of EEZ waters.

Analysis of monthly latitudinal distributions showed that there was, in general, a progressive southerly movement in distribution post-nesting (December to February), followed by a slower northerly contraction (March to August) (Figures 3a, Supplementary Material, Figure S1). There was evidence for an offshore expansion in the spatial distribution of turtle locations from the coast for January through to May associated with an increase in depth (Figures

3b,d, Supplementary Material, Figure S1); sea surface temperatures at best daily locations were also at their greatest throughout these months (Figure 3c).

Habitat modelling

Ensemble ecological niche modelling identified that a large majority of Angolan EEZ waters together with a small area of Gabonese/Republic of Congo and Democratic Republic of Congo EEZ waters potentially hosted the most suitable year round environmental conditions for olive ridley turtles. Areas with the highest average probability (> 0.9) that environmental conditions were favourable, predominantly occurred within 150 km of the Angolan coast in depths of 1290 m (638 to 1822 m) (median and inter-quartile range), with much of the area straddling the 1000 m isobath (Figure 5a). Proximity to persistent fronts was the most important contributory variable across all models (Table S5). No one model appreciably outperformed the others on comparison of individual model evaluation scores (Supplementary Material, Table S2). The environmental variables of depth and NPP, as well as SST and SSH, were highly correlated (rho = 0.76, $p < 0.001$ and rho = 0.84, $p < 0.001$ respectively); frontal activity was also associated with shallower depths and areas of higher NPP than was otherwise typically present across the study area (Supplementary Material, Figure S2a,b).

Fisheries Data

Fisheries catch data and associated gear type varied across the Angolan EEZ fisheries zones. Landings were greatest from the northern zone (55% of all landings), compared with central (29%) and southern (16%) zones with purse seine netting accounting for 60% of all landings (40% from the northern zone) compared with 33% for longlines and 7% attributable to all other gear (FAO, 2012a,b) (Figure 6a,b, Supplementary Material, Table S4).

DISCUSSION

As far as we are aware, this is the first time ensemble models have been applied to satellite tracking data for marine species and so some caution should be applied with interpreting results. A range of issues have been identified with the analysis of telemetry data associated with habitat modelling and a number of potential solutions proposed (Aarts *et al.* 2008). We attempted to overcome limitations within our data through a sample size large enough that animal movement converged upon a single foraging region, and by including only a single location per day. Furthermore, with the ensemble model approach, we were able to create a single model that integrated the strengths of multiple models and evaluation metrics simultaneously. Notwithstanding these caveats, the concordance across modelling methodologies adds confidence to our findings and the management recommendations that we make as a result.

East Atlantic olive ridley turtles are understudied (Abreu-Grobois & Plotkin 2008); as a consequence, little knowledge exists for post-nesting migratory behaviour. Post-nesting movement studies from other sites have described plasticity in post-nesting movement strategies within populations (McMahon *et al.* 2007; Whiting *et al.* 2007; Plotkin 2010; Silva *et al.* 2011; Rees *et al.* 2012). These include spatially discordant movements within populations; with individuals displaying local residency and migratory movements (*e.g.* Rees *et al.* 2012), as well as flexibility in habitat use; with sea turtles utilising coastal, continental shelf and deep water habitats (*e.g.* McMahon *et al.* 2007; Whiting *et al.* 2007).

In this study, with the exception of one individual, turtles made expansive migratory movements. Despite occasional movements of up to 200 km offshore, this 'resident' turtle remained in close proximity to the inter-nesting coastal zone, for the 197 days of transmission, generally within 100 km of the nesting beach. Two turtles (the only individuals tagged from the 2009/10 nesting period) migrated to deep and offshore oceanic waters (3000 to 5000 m). The most northerly of these two turtles was tracked west from the inter-nesting beach, and was associated with seamounts. The second turtle made similar southerly movements to those seen for the 2008/9 nesting cohort, but then continued in a south-westerly direction and left the Angolan EEZ. This may represent differences in dispersal strategies between years, as has been shown for loggerhead turtles (Hawkes *et al.* 2006) or specialised foraging strategies of a few individuals as has been seen in other wide-ranging marine species (Maxwell *et al.* 2012), but the sample size is small.

The main assemblage of eighteen turtles made post-nesting movements that progressed in a southerly direction and were focused within the EEZs of Gabon, Congo and Angola. Mapping highlighted significant habitat use by these turtles in waters 200 - 2000 m deep, occurring within 200 km of the coast, with individuals from two distinct nesting sites converging in Angolan waters. Pelagic foraging olive ridley sea turtles will target jellyfish and salps (Bjorndal 1997). It is possible that greater prey availability concentrates these turtles within this region. Ensemble ecological niche modelling indicated that suitable environmental conditions for olive ridleys were most likely to occur within the northern and central section of the Angolan EEZ. The most suitable environmental conditions being closely associated with coastal areas of persistent frontal activity within 150 km of the coast and in depths of approximately 1000 m.

In addition to the long-term persistent frontal activity identified within this study, the coastal waters of the Angolan EEZ benefit from the convergence of the warm Angolan current from the north and the cool Benguela current from the south; this produces the Angola-Benguela front (Peterson & Stramma, 1991). This frontal activity brings associated increased productivity for marine ecosystems and benefits Angolan fisheries. These fisheries are described by three zones; the northern, central and southern fisheries zones (Figure 5c, Supplementary Material, Table S3) (FAO 2007). Longline, purse seine, seine, trawl and gillnet gear types are deployed throughout all fisheries zones (Table S3). The industrial fishery comprises of national and foreign-flagged vessels, which operate through leases or in joint venture with Angolan enterprises. These primarily operate from four ports; Luanda, Porto Amboim, Benguela and Namibe, (Figure 5c) (FAO 2007). In 2002, fisheries in this region had an estimated total catch of 170 000 t (Metric Tonnes) from approximately 200 vessels, mainly using purse-seine and trawl gear types (FAO 2007). However, neither catch nor gear type was distributed evenly across the region. Artisanal fisheries also contribute a significant fisheries effort. In 2002, it was estimated that 3000 to 4500 vessels, operating from 102 regular sites along the length of the coast, landed in excess of 100 000 t (FAO 2007), though significantly, the spatial distribution of these fisheries is almost entirely unknown.

Bycatch is a significant threat to most sea turtle species (Lewison *et al.* 2013). However, there is a paucity of reported data for sea turtle bycatch (Wallace *et al.* 2010). Quantification of impact is hampered by gear specificity and operational characteristics (Casale *et al.* 2007). Bycatch is perceived as the greatest threat to Eastern Atlantic populations of olive ridley turtles (Donlan *et al.* 2010). Olive ridleys elsewhere can be negatively impacted by coastal and offshore trawl (Pandav *et al.* 1997; Gopi *et al.* 2006), purse seine (Abreu-Grobois & Plotkin 2008; Amandè *et al.* 2010) and longline fisheries (Work & Balazs 2002; Polovina *et al.* 2003; Carranza *et al.* 2006). Turtles are also at a high risk of bycatch from small-scale, artisanal fisheries near to nesting or foraging grounds (Parnell *et al.* 2007; Peckham *et al.* 2007; Weir *et al.* 2007; Maxwell *et al.* 2011); olive ridleys have shown flexible inter-nesting behaviour involving extensive travelling distances (Hamel *et al.*2008) which may increase exposure to bycatch.

Given the spatial overlap of olive ridley at-sea distribution and fisheries effort this species is at risk from negative interactions with both small-scale and industrial fisheries once they leave the nesting grounds. This may be particularly so within the northern and central Angolan fisheries zones. Increased knowledge of fishing effort and associated levels of sea turtle bycatch, attributable to gear types within the Angolan EEZ, would help assist the formulation of sustainable and effective bycatch management strategies. Further integration of Vessel Monitoring System (VMS) data (Witt & Godley 2007) together with gear specificity would quantify gear specific fishing effort (*e.g.* Lee *et al.* 2010) and observer-based programmes could provide gear specific bycatch data (Lewison *et al.* 2004; Finkbeiner *et al.* 2011). These measures are likely to increase our understanding of the potential for impact from industrial fisheries. However, impacts from artisanal fisheries are likely to remain under assessed (Lewison *et al.* 2004). This is of considerable concern, as increased understanding of the importance of bycatch, and the spatial distribution of small-scale artisanal fisheries appears to be critical for the management of both catch species and those caught as bycatch (Stewart *et al.* 2010).

Gear modifications and adjustment to fisheries practice may be appropriate to some fisheries (Gilman *et al.* 2009) (Supplementary Material, Table S6). Spatio-temporal gear and effort restrictions may also help mitigate impacts in seasonal olive ridley 'hotspot' areas, as may identification and establishment of appropriately sited Marine Protected Areas (MPAs), however, displacement of fishing effort from these areas may increase bycatch of turtles and/or other species of concern in other areas (Abbott & Haynie 2012). Addressing bycatch in small-scale and artisanal fisheries may be more complex as fishermen are more constrained to regions near to their home, and may be operating on a much smaller profit margin, making gear switches more difficult. Promotion of bycatch release programmes may be an option in some fisheries (Ferraro & Gjertsen 2009), and may be particularly appropriate in smaller scale fisheries. Advancement of ecosystem based fisheries management schemes that promote responsible and sustainable practice may also be a way forward for artisanal fisheries (Casale 2011). The implementation of any measures, must also consider the social and economic impact to the industry, particularly to subsistence artisanal fisheries (Weir *et al.* 2007; Lewison *et al.* 2013).

Olive ridleys nest throughout the west coast of Africa, between Guinea Bissau and Angola, including many of the region's islands (Fretey 2000). This study provides an insight into the understudied post-nesting movements of olive ridley turtles, and represents the largest satellite tracked analysis of olive ridley turtles from the southeast Atlantic to date. While modelling the distribution of a far ranging species from two regions, this analysis highlights the coincident habitat use of olive ridley turtles, in relation to favourable areas. Additional tracking of olive ridleys from other nesting locations may determine the importance of these areas for other southeast Atlantic individuals. Given the variability in the two animals tracked in 2009/10, it is feasible that not all movement patterns have been captured by our study animals and additional years may reveal different strategies and habitats. This study also highlights the potential for conflict with fishing activities. Increased knowledge of gear specific fisheries effort and bycatch, within the Angolan, Congolese, and Gabonese EEZs, would help facilitate an integrated approach, both within and between countries, to formulate a more dynamic and effective conservation policy.

ACKNOWLEDGEMENTS

This study was supported by the Darwin Initiative and NERC. Gabonese tracking work was supported by the Disney Worldwide Conservation Fund (STO-08-01) and the Tagging of Pacific Predators Project, with additional support from the Darwin Initiative, Centre for the Dynamics and Evolution of the Land-Sea Interface, Friends of Long Marine Laboratory, Society for the Study of Amphibians and Reptiles, the Marilyn Davis Memorial Scholarship, the UCSC Graduate Student Association, Square’s Landscaping and Kitchen Gardens, Inc. SMM was supported by fellowships from the National Science Foundation, University of California Santa Cruz, Achievement Awards for College Scientists and Steve Blank. Sea turtle nest monitoring in Gabon was coordinated through the Gabon Sea Turtle Partnership, with funding from the Marine Turtle Conservation Fund (United States Fish and Wildlife Service, U.S. Department of the Interior). We thank A. Mavoungou Djimbi Alain, S. Zassi, E. Ibouanga Amos, L. Schonkneckt and M. Markovina for field support and Wildlife Conservation Society staff, especially Q. Makaya Pambou, for logistical support. Angolan tracking work was funded by the Angola LNG project (Kwanda Base, Soyo) with logistical support provided by Chevron USA. The authors acknowledge the constructive input from three anonymous referees, the Editor-in-Chief and the Associate Editor.

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Biosketch

Stephen K. Pikesley is a marine ecologist, whose work focuses on the integration and use of spatial ecological tools, including satellite tracking, remote sensing, GIS and habitat modelling to help identify and gain insight, into marine vertebrate spatial and temporal patterns and trends. This work constituted part of his doctoral thesis with MJW and BJG at the University of Exeter, working in the Marine Turtle Research Group (MTRG). Further information about the MTRG can be found at: http://www.seaturtle.org.uk/mtrg/.

Statement of author contributions

This work is the result of a major collaborative effort: SMM, KP, DPC, MSC, AF, BJG, WK, SM, SN, RJP, designed the experiments; SMM, KP, DPC, MSC, WK, JM-B, EP-M, collected data; SKP, MJW and BJG analysed the data, developed the manuscript and led the writing with contributions from all authors.

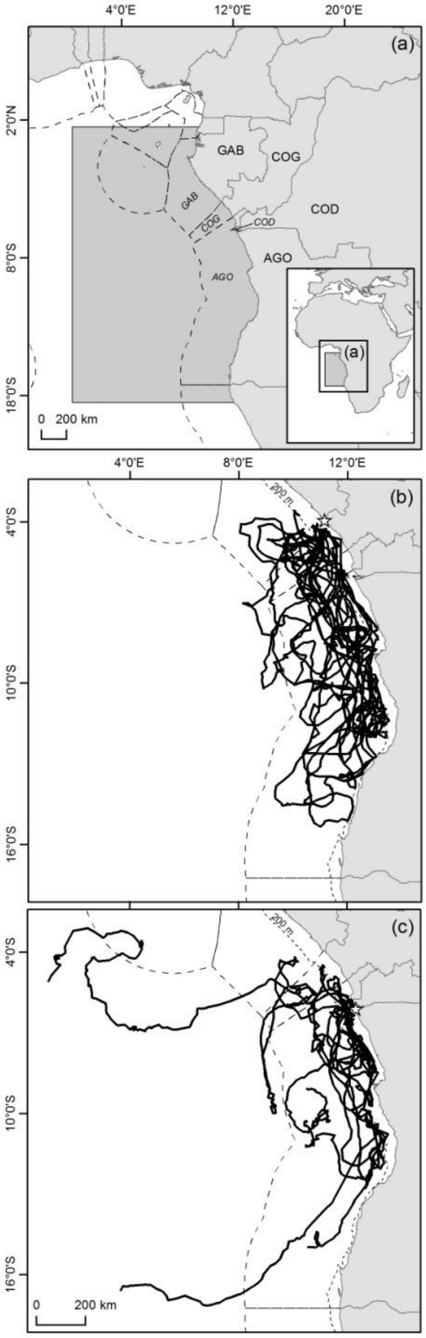

Figure 1. Study area (a). Post-nesting movements based on best daily locations for satellite tracked olive ridley turtles released from (b) Gabon (*n* = 12) and (c) Angola (*n* = 9). Release locations (open stars), 200 m continental shelf isobath (broken line). Parts (b) and (c) are drawn to the same spatial scale. EEZ maritime boundaries (broken line polygon used throughout all maps). Countries and EEZs are labelled as follows: Gabon (GAB), Republic of Congo (COG), the Democratic Republic of the Congo (COD) and Angola (AGO). Maps drawn to Geographic Coordinate System: WGS 1984.

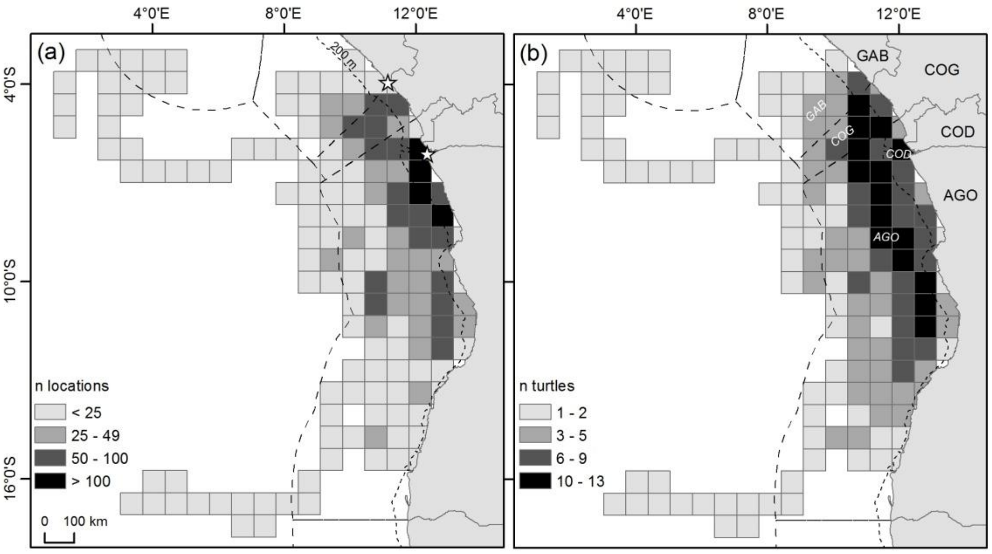

Figure 2. Density mapping of olive ridley post-nesting movements (*n* = 21) based on interpolated best daily location data. Polygon sampling grid (75 x 75 km) of (a) the sum of spatially coincident olive ridley locations and (b) the sum of individuals occupying a grid square. Map features are drawn and labelled in accordance with Figure 1. Maps drawn to Geographic Coordinate System: WGS 1984.

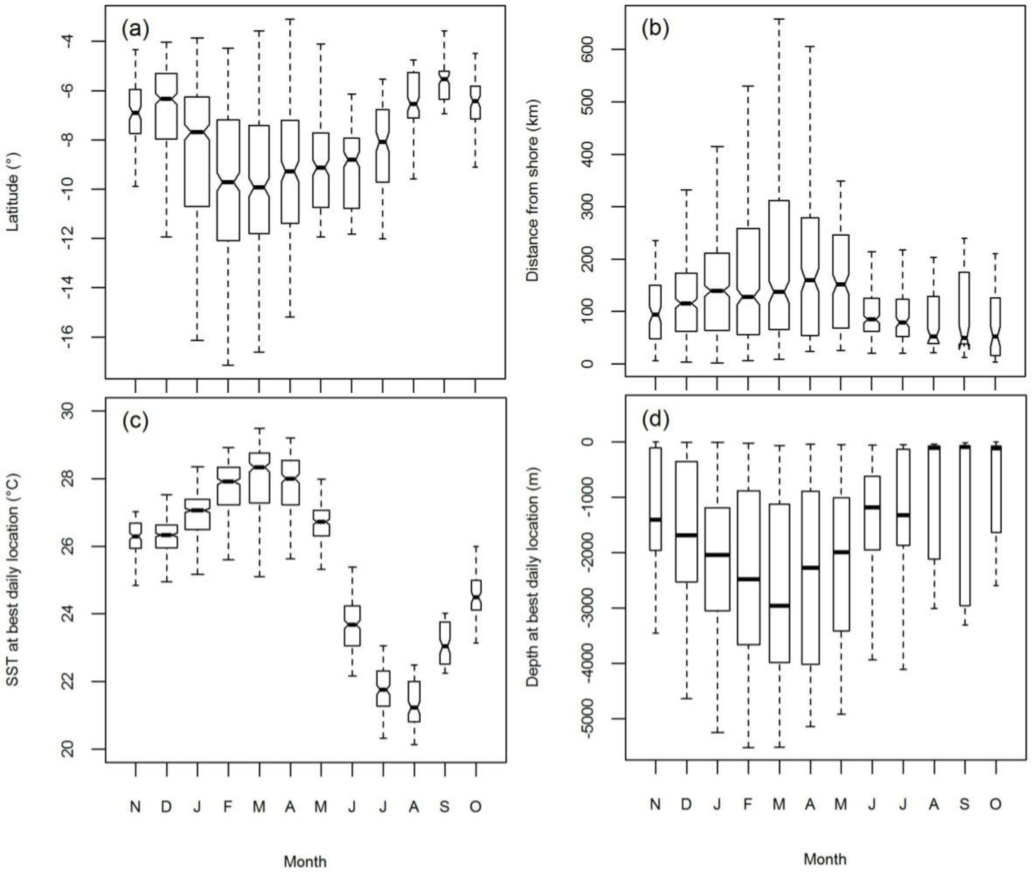

Figure 3. Median and inter-quartile ranges for (a) latitudinal distribution (°), (b) distance from shore (m), (c) monthly SST (°C) (3 year mean) and (d) depth (m). Data were derived from non-interpolated, best daily locations, excluding locations within 25 km inter-nesting zone. Box widths are proportional to the square-roots of the number of observations in the box, outliers are not drawn. Month order was determined by the start of turtle post-nesting activity.

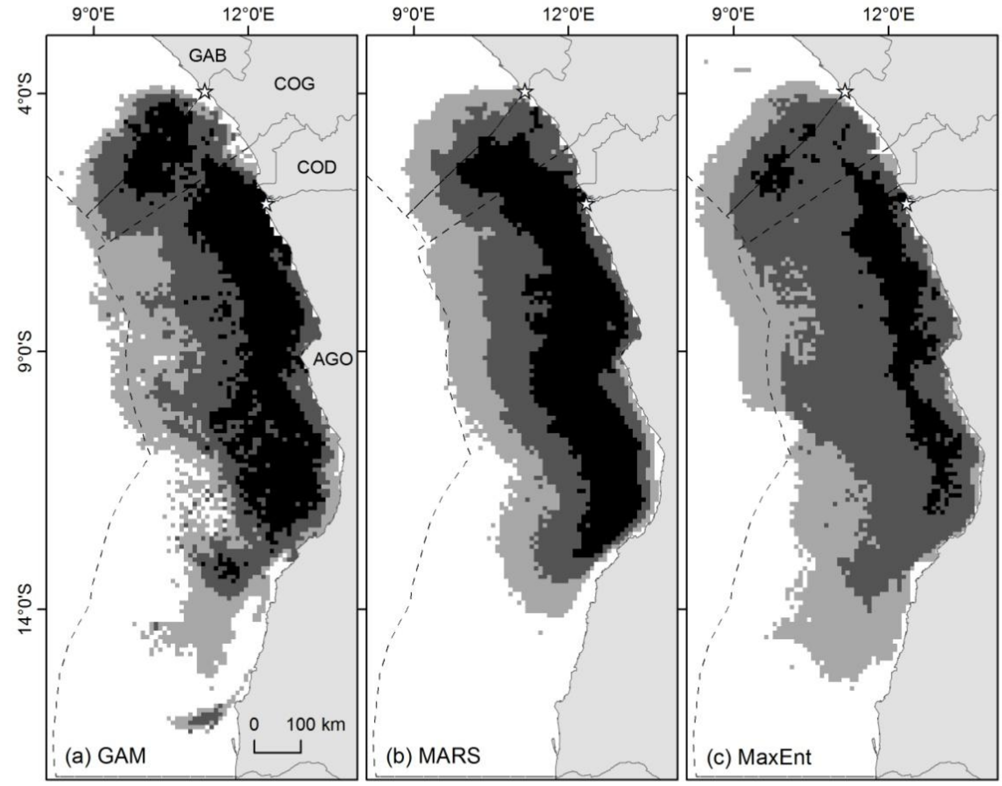

Figure 4. Ecological Niche Models using the (a) Generalised Additive Model (GAM), (b) Multivariate Adaptive Regression Splines (MARS) and (c) MaxEnt modelling algorithms within the biomod2 package (R Development Core Team 2008; R package: biomod2; Thuiller *et al.* 2013). ENMs were run with non-interpolated location data and with the environmental variables of depth, SST, SSH, NPP and proximity to oceanic frontal activity, using long-term averaged yearly products. These ENMs describe the relative suitability of oceanic habitat, scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability and are represented by monochrome shading as follows: white < 0.5, mid grey 0.5-0.75, dark grey 0.75-0.9 and black > 0.9. Countries are labelled as follows: Gabon (GAB), Republic of Congo (COG), the Democratic Republic of the Congo (COD) and Angola (AGO). Maps drawn to Geographic Coordinate System: WGS 1984.

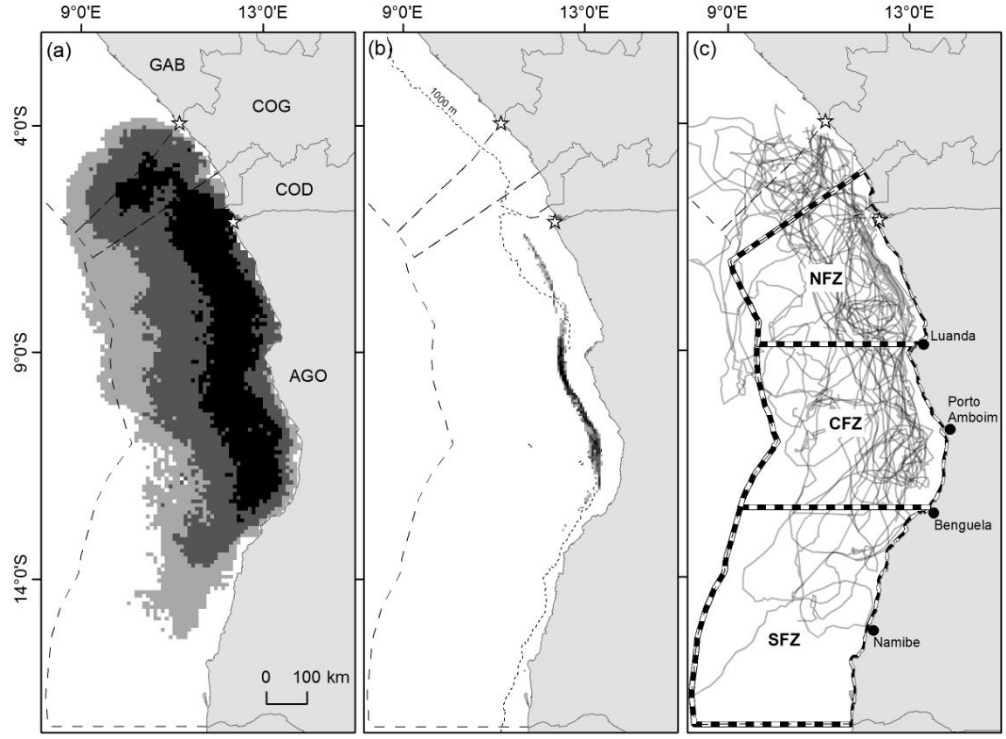

Figure 5. (a) Ensemble ecological niche model for post-nesting movements based on best daily locations for olive ridley turtles (*n* = 21), depth and the long term yearly environmental variables of SST, SSH, NPP and proximity to oceanic frontal activity. The relative suitability of oceanic habitat is scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability, 0 represents lowest suitability and 1 highest suitability, is represented by monochrome shading as follows: white < 0.5, mid grey 0.5-0.75, dark grey 0.75-0.9 and black > 0.9. (b) Shows the location and spatial extent of longer-term persistent oceanic frontal activity, the 1000 m isobath is represented as a broken line. (c) Cumulative yearly post-nesting movements based on best daily locations satellite tracking data for all olive ridley turtles (*n* = 21) with key fishing ports labelled. The northern (NFZ), central (CFZ) and southern (SFZ) Angolan fisheries zones are shown as polygons with heavy weight broken black lines. Maps drawn to Geographic Coordinate System: WGS 1984.

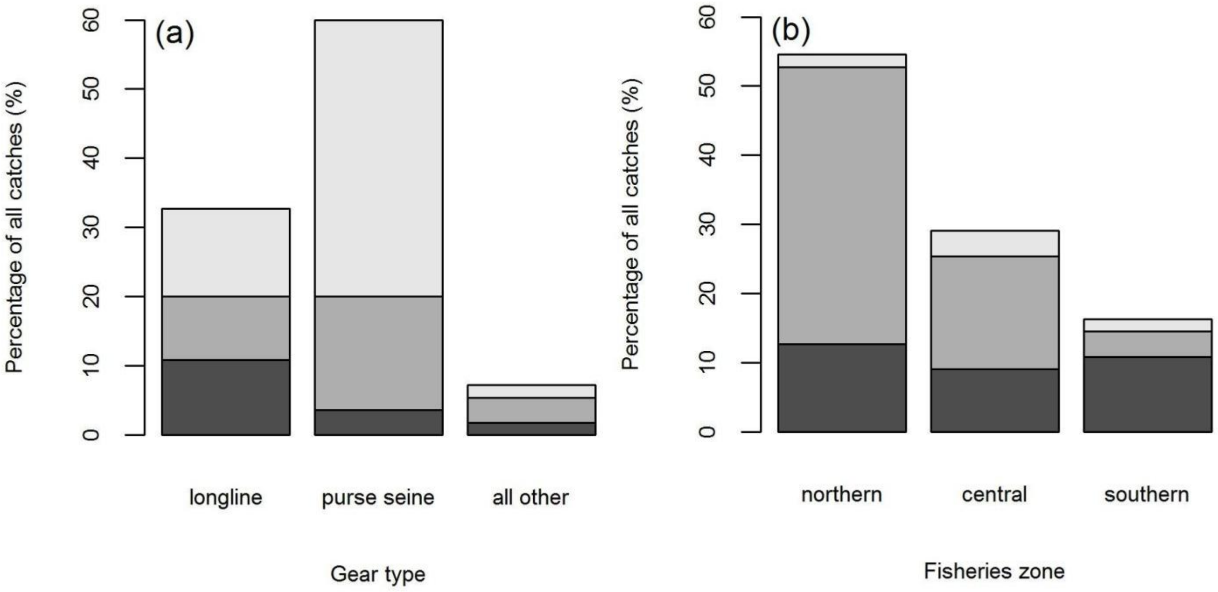

Figure 6. Cumulative tuna and billfish catch data (1995-2009) by Fishing Area Cell at 5º by 5º resolution, apportioned by the cell's coincident sea area, as a percentage of all data, by (a) gear type and fisheries zone, Angolan EEZ fisheries zones identified as: northern (light grey), central (mid grey) and southern (dark grey), and b y (b) Angolan EEZ fisheries zone and gear type, gear type is identified as: longline (dark grey), purse seine (mid grey) and all other gear type (light grey).

Table S1. Summary of PTT data detailing nesting season, release site, and data start and end dates. Post-nesting periods, including track durations, are identified together with post-nesting turtle IDs and habitat classifications.

Release site	**ID**	**Post-nesting classification**	**Nesting season**	**PTT attachment date**	**Post-nesting start date**	**Last received position**	**Post-nesting tracking duration (days)**	**Post-nesting tracking distance (km)**
Gabon	A	oceanic (within EEZ)	2007/08	30/10/2007	30/11/2007	10/01/2008	41	1206
Gabon	B	coastal	2008/09	23/10/2008	07/01/2009	07/05/2009	120	787
Gabon	C	oceanic (within EEZ)	2008/09	12/11/2008	04/12/2008	29/06/2009	207	3362
Gabon	D	oceanic (within EEZ)	2008/09	13/11/2008	03/12/2008	20/09/2009	291	6261
Gabon	E	oceanic (within EEZ)	2008/09	14/11/2008	18/11/2008	10/03/2009	112	1985
Gabon	F	oceanic (within EEZ)	2008/09	14/11/2008	05/12/2008	16/08/2009	254	4582
Gabon	G	oceanic (within EEZ)	2008/09	15/11/2008	12/12/2008	01/02/2009	51	1337
Gabon	H	oceanic (within EEZ)	2008/09	15/11/2008	10/12/2008	04/03/2009	84	1149
Gabon	I	oceanic (within EEZ)	2008/09	16/11/2008	14/12/2008	16/01/2009	33	694
Gabon	J	oceanic (within EEZ)	2008/09	19/12/2008	23/01/2009	27/02/2009	35	730
Gabon	K	oceanic (within EEZ)	2008/09	19/11/2008	28/12/2008	09/07/2009	193	3505
Gabon	L	oceanic (within EEZ)	2008/09	19/11/2008	05/12/2008	14/04/2010	495	9182
Angola	M	oceanic (within EEZ)	2008/09	19/11/2008	22/12/2008	24/03/2009	92	1537
Angola	N	oceanic (within EEZ)	2008/09	21/11/2008	30/11/2008	24/01/2009	55	904
Angola	O	oceanic (within EEZ)	2008/09	26/11/2008	29/12/2008	05/07/2009	188	2416
Angola	P	oceanic (within EEZ)	2008/09	03/12/2008	04/12/2008	13/03/2009	98	1305
Angola	Q	oceanic (within EEZ)	2008/09	03/12/2008	28/12/2008	19/04/2009	111	2199
Angola	R	oceanic (within EEZ)	2008/09	14/12/2008	24/12/2008	10/11/2010	686	6880
Angola	S	oceanic (within EEZ)	2008/09	11/01/2009	13/01/2009	07/04/2009	84	2769
Angola	T	oceanic (outside EEZ)	2009/10	05/05/2009	07/11/2009	01/03/2010	114	2710
Angola	U	oceanic (outside EEZ)	2009/10	05/05/2009	22/11/2009	13/05/2010	172	1572

Table S2. Ecological Niche Modelling evaluation metrics for 10-fold cross validation. Algorithm abbreviations: Generalized Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MaxEnt). Key algorithm modelling parameters and evaluation metric descriptions are detailed at the foot of the table.

Evaluation metric	**Run**	**Modelling algorithm**			**Run**	**Modelling algorithm**		
		GAM	**MARS**	**MaxEnt**		**GAM**	**MARS**	**MaxEnt**
AUC	***1***	0.95	0.95	0.95	***6***	0.95	0.95	0.95
KAPPA		0.78	0.78	0.78		0.78	0.76	0.78
TSS		0.79	0.80	0.79		0.79	0.78	0.79
SR		0.98	1.00	0.97		0.99	0.96	1.00
Accuracy		0.89	0.89	0.89		0.89	0.88	0.89
AUC	***2***	0.95	0.95	0.95	***7***	0.96	0.95	0.95
KAPPA		0.79	0.80	0.79		0.81	0.80	0.80
TSS		0.80	0.81	0.81		0.82	0.81	0.81
SR		0.99	0.94	0.97		1.00	0.98	0.98
Accuracy		0.89	0.90	0.89		0.90	0.90	0.90
AUC	***3***	0.96	0.96	0.95	***8***	0.95	0.95	0.95
KAPPA		0.79	0.79	0.80		0.79	0.77	0.78
TSS		0.81	0.81	0.81		0.80	0.78	0.79
SR		1.00	0.98	1.00		0.97	0.97	0.97
Accuracy		0.90	0.90	0.90		0.90	0.89	0.89
AUC	***4***	0.96	0.96	0.95	***9***	0.95	0.95	0.95
KAPPA		0.80	0.81	0.79		0.79	0.79	0.79
TSS		0.81	0.82	0.80		0.80	0.81	0.80
SR		1.00	0.99	0.99		1.00	0.98	0.98
Accuracy		0.90	0.91	0.90		0.90	0.90	0.90
AUC	***5***	0.95	0.95	0.95	***10***	0.95	0.94	0.95
KAPPA		0.78	0.76	0.78		0.77	0.78	0.78
TSS		0.79	0.78	0.79		0.79	0.80	0.79
SR		0.99	0.96	1.00		1.00	0.97	0.99
Accuracy		0.89	0.88	0.89		0.89	0.89	0.89

Biomod2 modelling parameters

One set of 5000 randomly generated 'pseudo absence' locations (background data), with no minimum or maximum distance to presence locations were generated. All locations that had missing coincident environmental data were removed from the analysis (background data locations that were spatially referenced on land). Total background data locations used in analysis: *n* = 4175.

The algorithm modelling parameters in biomod2 were as follows:

GAM: package = 'mgcv', family = 'binomial', type = 's' (spline based smooth).

MARS: package = 'mda', maximum interaction degree = 2, penalty (cost per degree of freedom) = 2, thresh (forward stepwise stopping threshold) = 0.001, prune = (TRUE).

MaxEnt: Run within biomod2, maximum iterations (for training) = 200, linear/quadratic/product/threshold/ hinge features (the transformation coefficients applied to each environmental variable), default prevalence = 0.5.

Evaluation metrics

AUC (Area under the curve): a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives.

KAPPA (Cohen's Kappa, Heidke skill score) and TSS (True Skill Statistic): measures of accuracy relative to that of random chance.

SR (Success Ratio): the fraction of the true positives that were correct.

Accuracy (fraction correct): the fraction of the predictions (true and false) that were correct.

Table S3. Summary of Angolan marine fisheries gear types and fisheries zones (FAO 2007).

Fishery	Fishing gear	Fisheries zone
Pelagic	Trawl, seine	Whole coast, but mostly southern zone
	Purse seine	Whole coast, but mostly central and northern zones
	Longline	Whole coast
Demersal	Trawl, gillnet	Whole coast
Crustaceans	Trawl	Central zone
	Trap	Central and southern zones

Approximate latitudinal banding of fisheries zones:
Northern zone: Cabinda to Luanda (S 5° to S 9.25°)
Central zone: Luanda to Benguela/Lobito (S 9.25° to S 13°)
Southern zone: Benguela/Lobito to the Cunene River (S 13° to S 17.25°)

Table S4. Cumulative tuna and billfish catch data (1995-2009) by FAO Major Fishing Area Cell (FAO 2012a; 2012b) at 5º by 5º resolution. These data were apportioned for the cell's coincident sea area, by fisheries zone and gear type. Source data: http://www.fao.org/figis/geoserver/tunaatlas/

	Cumulative tuna and billfish catches by fisheries gear (1995-2009)							
	longline		**purse seine**		**other gear**		**all gear**	
Fisheries zone	**tonnes/ km^2**	**% of total**	**tonnes/ km^2**	**% of total**	**tonnes/ km^2**	**% of total**	**tonnes/ km^2**	**% by zone**
Northern	0.07	12.7	0.22	40.0	0.01	1.8	0.30	55
Central	0.05	9.1	0.09	16.3	0.02	3.6	0.16	29
Southern	0.06	10.9	0.02	3.6	0.01	1.8	0.09	16
						Total all gear	0.55	

Table S5. Ecological Niche Modelling variable importance for 10-fold cross validation.

Model	Run	Depth	Dist. to front	NPP	SSH	SST	Run	Depth	Dist. to front	NPP	SSH	SST
GAM	***1***	0.03	0.44	0.05	0.20	0.29	***6***	0.03	0.44	0.05	0.20	0.29
MARS		0.00	0.54	0.15	0.20	0.11		0.00	0.56	0.11	0.17	0.15
MaxEnt		0.04	0.44	0.18	0.17	0.18		0.06	0.44	0.17	0.15	0.18
mean var. imp.		0.02	0.47	0.13	0.19	0.19		0.03	0.48	0.11	0.18	0.21
GAM	***2***	0.03	0.44	0.05	0.20	0.29	***7***	0.03	0.44	0.05	0.20	0.29
MARS		0.00	0.40	0.22	0.25	0.13		0.00	0.50	0.19	0.20	0.11
MaxEnt		0.06	0.42	0.18	0.16	0.18		0.05	0.45	0.18	0.16	0.17
mean var. imp.		0.03	0.42	0.15	0.20	0.20		0.02	0.46	0.14	0.18	0.19
GAM	***3***	0.03	0.44	0.05	0.20	0.29	***8***	0.03	0.44	0.05	0.20	0.29
MARS		0.00	0.54	0.13	0.18	0.15		0.00	0.50	0.24	0.22	0.04
MaxEnt		0.06	0.43	0.18	0.15	0.18		0.04	0.42	0.19	0.16	0.19
mean var. imp.		0.03	0.47	0.12	0.18	0.21		0.02	0.45	0.16	0.19	0.17
GAM	***4***	0.03	0.44	0.05	0.19	0.30	***9***	0.03	0.44	0.05	0.19	0.29
MARS		0.00	0.53	0.13	0.18	0.15		0.00	0.50	0.13	0.28	0.09
MaxEnt		0.05	0.43	0.18	0.16	0.18		0.05	0.41	0.19	0.17	0.18
mean var. imp.		0.03	0.47	0.12	0.18	0.21		0.03	0.45	0.12	0.21	0.19
GAM	***5***	0.03	0.44	0.05	0.20	0.29	***10***	0.03	0.44	0.05	0.20	0.29
MARS		0.01	0.53	0.17	0.21	0.08		0.00	0.52	0.19	0.19	0.10
MaxEnt		0.06	0.44	0.17	0.15	0.18		0.06	0.42	0.18	0.16	0.19
mean var. imp.		0.03	0.47	0.13	0.19	0.18		0.03	0.46	0.14	0.18	0.19
mean of means variable importance								**0.027**	**0.461**	**0.131**	**0.188**	**0.193**
standard deviation of the mean								**0.003**	**0.016**	**0.014**	**0.012**	**0.011**

Relative importance of the contribution of an environmental variable is calculated using a randomisation process. This procedure calculates the correlation between a prediction using all environmental variables and a prediction where the independent variable being assessed is randomly re-ordered. If the correlation is high the variable in question is considered not important for the model and conversely, if low, important. A mean correlation coefficient for each environmental variable is then calculated over multiple runs. This is repeated for each environmental variable. The calculation of the relative importance is made by subtracting these mean correlation coefficient from 1 (Thuiller *et al.* 2009).

Table S6. Gear modifications and adjustment to fisheries practice to reduce turtle bycatch (Gilman *et al.* 2009).

Fishery	Principal mitigation measures
Pelagic longlines and bottom set longlines	Use circle hooks
	Set hooks deeper avoiding the upper water column*
	Reduce gear soak time
	Use fish as bait, not squid
	Single hook bait, do not thread hook through the bait
Purse seine	Avoid encircling turtles
	Monitor Fish Aggregating Devices (FADs)
	Recover FADs when not in use
	Modify FADs to reduce/eliminate entanglement risk
Trawl	Use Turtle Excluder Devices (TEDs)
Set gillnets and drifting gillnets	Set nets perpendicular to the shore to reduce interactions with nesting females
	Set nets deeper, avoid the upper water column
	Use low profile nets
	Eliminate the use of 'tie-down' ropes

* There is the potential for the interaction rate to be much lower with deeper set nets, although the mortality rate for those turtles that are caught is higher

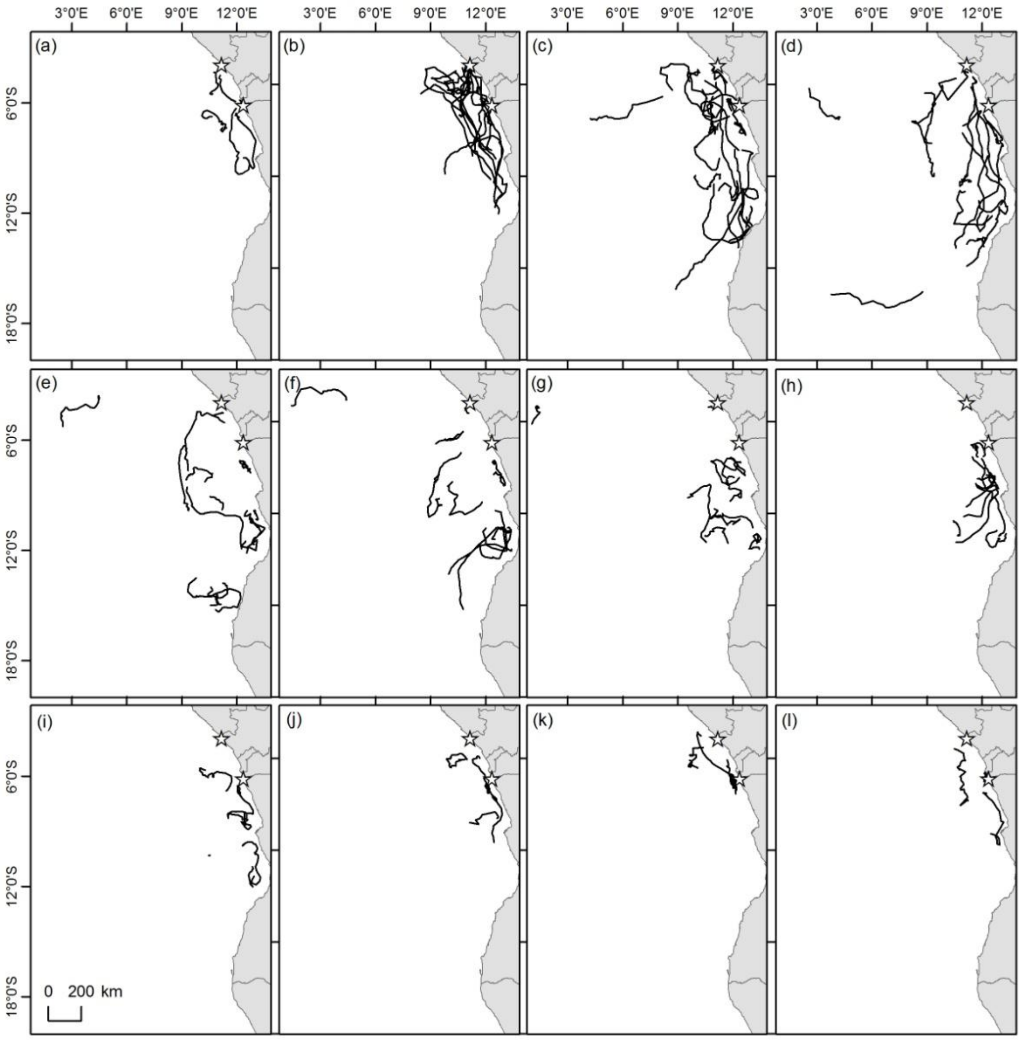

Figure S1. Monthly satellite tracked post-nesting movements for olive ridley turtles derived from non-interpolated, best daily locations. Months are ordered from November (a: top left) to October (l: bottom right). Month order was determined by the start of turtle post-nesting activity. The release sites for tagged turtles are shown as open stars. Maps drawn to Geographic Coordinate System: WGS 1984.

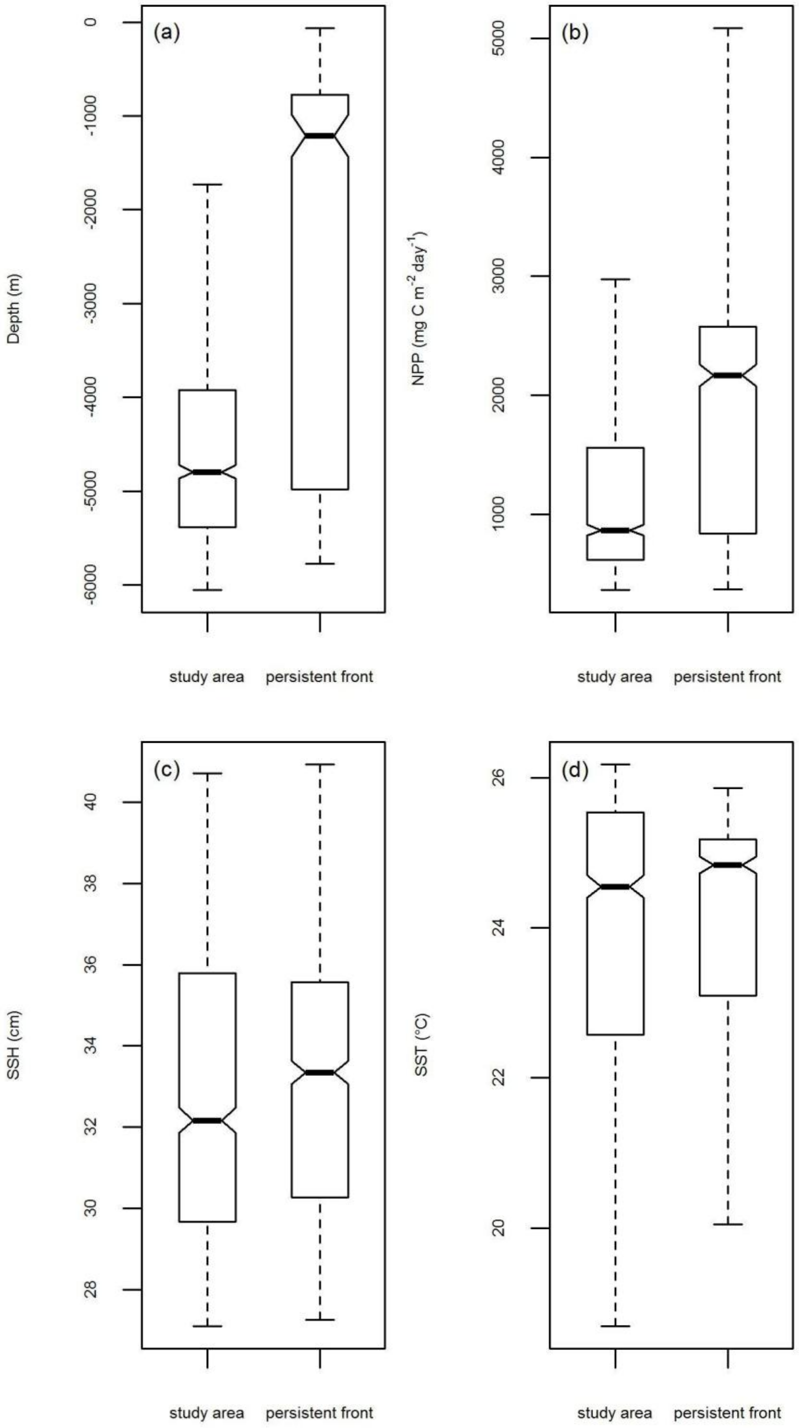

Figure S2. Median and inter-quartile ranges for (a) depth (m), (b) NPP (mg C m^{-2} day^{-1}), (c) SSH (cm) and (d) SST (°C) for areas of persistent frontal activity (sample *n* = 887) and the entire study area (sample *n* = 1000).

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

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Published in Ecography (2014) DOI: 10.1111/ecog.01245

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ABSTRACT

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.

Keywords: bycatch, climate change, ensemble ecological niche modelling, fisheries, foraging, spatial analysis

INTRODUCTION

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 & 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 (*e.g.* 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 a group of marine vertebrates that have been extensively satellite tracked, 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* Linnaeus 1758) are perhaps the best studied species, having been comprehensively researched over several decades through multi-disciplinary approaches including, flipper 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 & Witherington 2003); however, recent tracking (Hatase *et al.* 2002, Hawkes *et al.* 2006, McClellan & 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 (depths > 200 m) 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). This may reflect a conditional strategy (Hatase *et al.* 2013), with smaller turtles utilising oceanic habitats, where they may forage epipelagically around mesoscale fronts, exploiting profitable foraging opportunities resulting from physical aggregation of prey (Scales *et al.* 2015), and larger turtles utilising neritic habitats (although the driver behind this strategy is unknown). 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: (i) describe observed habitat use in oceanic and neritic foraging zones over multiple years; (ii) model likely suitable foraging habitats using Ensemble Ecological Niche Models (EENMs); (iii) identify key environmental drivers of distribution and (iv) predict how distribution may alter under future climate change scenarios. Finaly, (v) we integrate available longline and trawl fisheries catch data, apportioned by Exclusive Economic Zones (EEZs), to identify areas that have potential for conflict with fishing activities known to pose a significant threat (bycatch) to sea turtles (Lewison *et al.* 2013). 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 (Figure 1) except turtle ID 7 which was released at Sao Vicente (see metadata in Supplementary Material, Table S1). Satellite telemetry data were collected using the Argos satellite system (CLS 2011) and downloaded with the Satellite Tracking and Analysis Tool (STAT) (Coyne & 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 2008; R package: argosfilter (Freitas 2010)). Six PTTs failed to transmit 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 2008; 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 http://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 (Figure 1 & Supplementary Material, Figure S1).

Habitat use

To describe observed habitat use we used a hexagonal grid (edge to edge distance of 100 km, hexagon area 8660 km^2), 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 (km^2) 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 (km^2 day^{-1}).

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 latitudes N 35.5º, S 0.5º, and longitudes W 35.5º, E 10.5º (WGS84) as this extent generously bounded all location data within our study area (sea area: 10.1 million km^2).

We extracted spatially coincident physical and biological environmental data (2004-2009) using R (R Development Core Team 2008; R package: raster (Hijmans & 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} day^{-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 v0.8a49 (MGET; (Roberts *et al.* 2010) to model SST oceanic frontal activity for the study area. Frontal features can represent significant areas of enhanced primary productivity that in turn may provide areas of increased prey availability for marine vertebrates (Scales *et al.* 2015). 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 & 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 x 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). 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 2008; 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 Table S2 (in Supplementary Material). 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, Table S2). 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, Table S3). 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 0.6º C and 2º 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

Bycatch is a significant threat to most sea turtle species (Lewison *et al.* 2013). Therefore, 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, Figure S2) 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 5º by 5º 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 days (mean ± 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, pers. obs.). 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 (Figure 1). Four turtles were unassigned to a foraging strategy due to limited transmission durations 22 ± 13 days (mean ± 1SD, range 7 - 38). Finally, one male (Supplementary Material, Table S1, ID: 10) exhibited a greater degree of plasticity than females (Varo-Cruz *et al.* 2013), foraging neritically for three 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, Table S1). 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 (Figure1). 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 days 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) (Figures 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) (Figures 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 same year among individuals (19.7 km^2, 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 km^2 day^{-1}) than did neritic turtles (5 km^2 day^{-1}).

Habitat modelling

Our oceanic EENM (RS ≥ 0.5 sea area 788 577 km^2) 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 (Figure 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, Table S3) 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 km^2) overlapped with 52% of West African continental shelf waters from Western Sahara to Equatorial

Guinea (Figure 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 used 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, Table S3) 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, Figure S3). 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 km^2 (0.2% of combined oceanic and neritic sea areas).

Forecast models incorporating oceanic temperature increases of 0.6º C, 1º C and 2º 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 (Figure 4). Forecast sea areas that would remain suitable for oceanic loggerhead turtles, decreased by 6% (EENM + 0.6º C), 11% (EENM + 1º C) and 20% (EENM + 2º 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 + 0.6º C), 57% (EENM + 1º C) and 72% (EENM + 2º C) respectively. There was minimal overlap between oceanic and neritic forecast EENMs within the EEZs of Mauritania and Senegal across all modelling scenarios; EENM + 0.6º C: 0.5% of combined oceanic and neritic sea areas, EENM + 1º C: 0.7% and EENM + 2º 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, Guinea-Conakry, Sierra Leone, and Liberia (Figure 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 (*i.e.* trawls, purse seine, pole and line) within the coastal EEZs of Western Sahara, Mauritania, Senegal, Gambia and Guinea-Bissau.

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.

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, Figure S1).

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) suggested 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 suggested 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) indicated that larger Cape Verdean neritic turtles likely perform deeper and longer dives than smaller oceanic turtles, this being consistent with what is known for other species (Mori 2002). In pelagic waters foraging loggerhead turtles likely target jellyfish and salps, whilst in shallower, neritic waters, they may forage opportunistically on benthic species (Bjorndal 1997).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 0.6º C and 2º 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, Figure S4), 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 (10's to 100's 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 0.11º 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 0.6º C and 2º 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.

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 & 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 (Báez *et al.* 2010, Álvarez de Quevedo *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 & 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 & 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 & 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 & 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.

ACKNOWLEDGEMENTS

We thank the staff, students and volunteers of Cabo Verde Natura 2000, British Chelonia Group, Marine Conservation Society, Natural Environmental Research Council, People's Trust for Endangered Species, SeaWorld Busch Gardens, and Seaturtle.org. Additional support was provided by the Large Pelagics Research Centre at the University of New Hampshire through National Oceanographic and Atmospheric Agency award NA04NMF4550391. The authors acknowledge the constructive input from the Subject Editor.

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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; and neritic 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

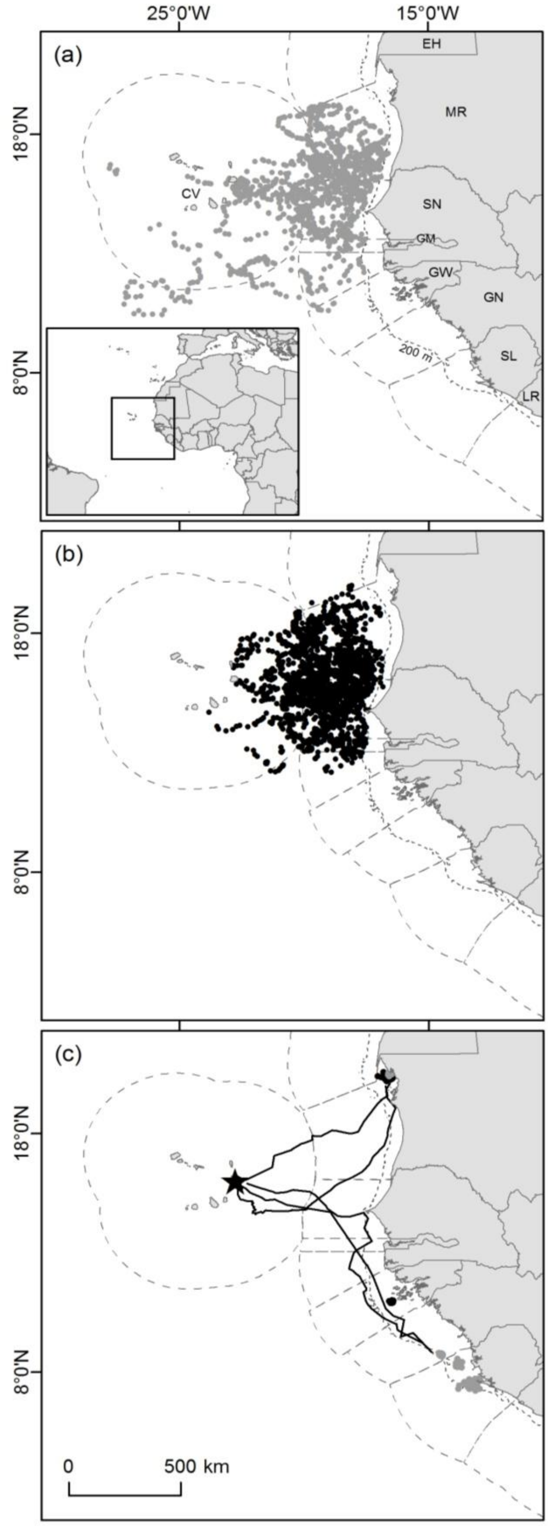

Figure 1. Satellite tracked, post-nesting loggerhead turtle movements, based on non-interpolated best daily locations for, (a) oceanic foragers: previously published data 2004/05/06 (*n* = 8, grey circles), (b) oceanic foragers: unpublished data 2006 (*n* = 9, black circles) and (c) neritic foragers: previously published data 2004/05/06 (*n* = 4, grey circles), unpublished data 2006 (*n* = 2, black circles) (see metadata in Supplementary Material, Table S1). 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). Maps drawn to Geographic Coordinate System: WGS 1984.

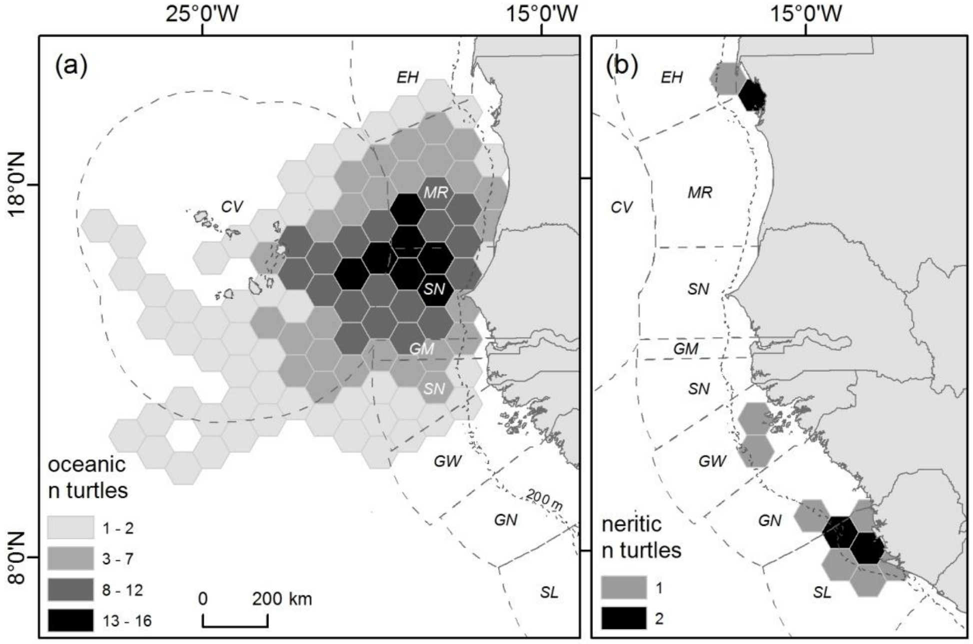

Figure 2. Density mapping of loggerhead turtle post-nesting movements based on interpolated best daily location data summed by hexagonal polygon sampling grid (100 km edge to edge). Sum of individuals occupying a single hexagon polygon for (a) oceanic and (b) neritic foragers. Turtle densities are represented 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 Figure 1. Maps drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

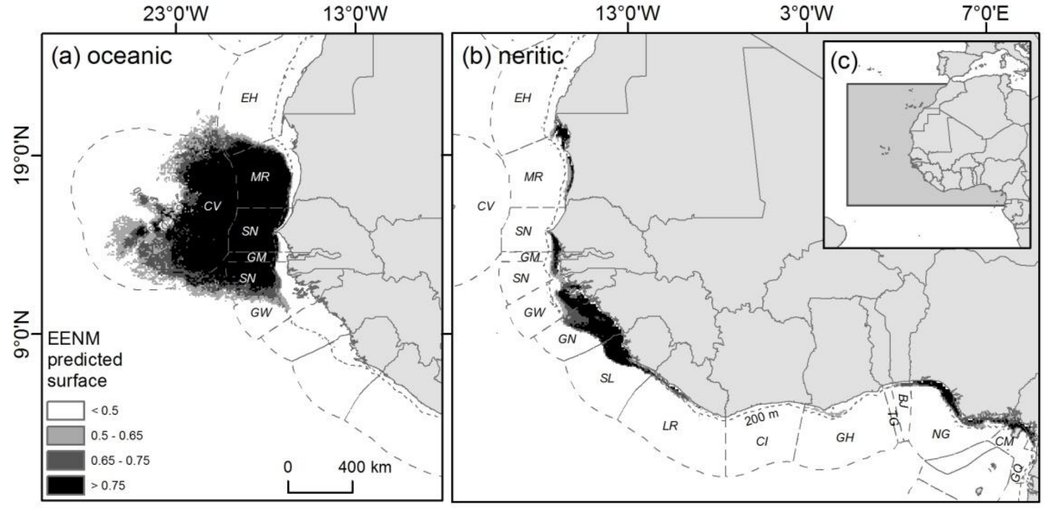

Figure 3. Ensemble Ecological Niche Models (EENMs) for post-nesting loggerhead turtles run with non-interpolated best daily location data, and with the environmental variables of depth, SST, NPP, sea surface current velocity and SST oceanic frontal activity using Long-Term Yearly Averaged (LTYA) products 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 Figure 1. Maps drawn to Geographic Coordinate System: WGS 1984.

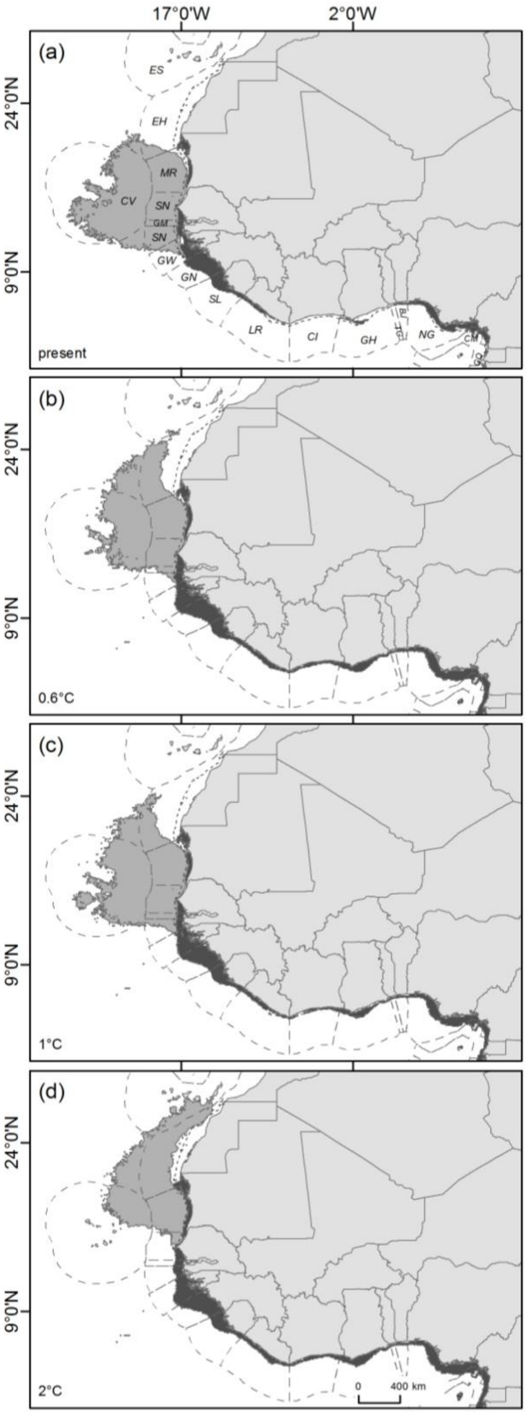

Figure 4. Forecast Ensemble Ecological Niche Models (EENMs). Oceanic and neritic EENMs (Figure 3) were run with projected Long-Term Yearly Averaged (LTYA) Sea Surface Temperature (SST) increases of between 0.6º C and 2º C in accordance with Coupled Model Intercomparison Project Phase 5 (CMIP5) Representative Concentration Pathway (RCP) scenarios RCP 2.6 to RCP 8.5 (IPCC 2013): (a) existing conditions, (b) LTYA SST + 0.6º C, (c) LTYA SST + 1º C and (d) LTYA SST + 2º 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 Figure 1. Maps drawn to Geographic Coordinate System: WGS 1984.

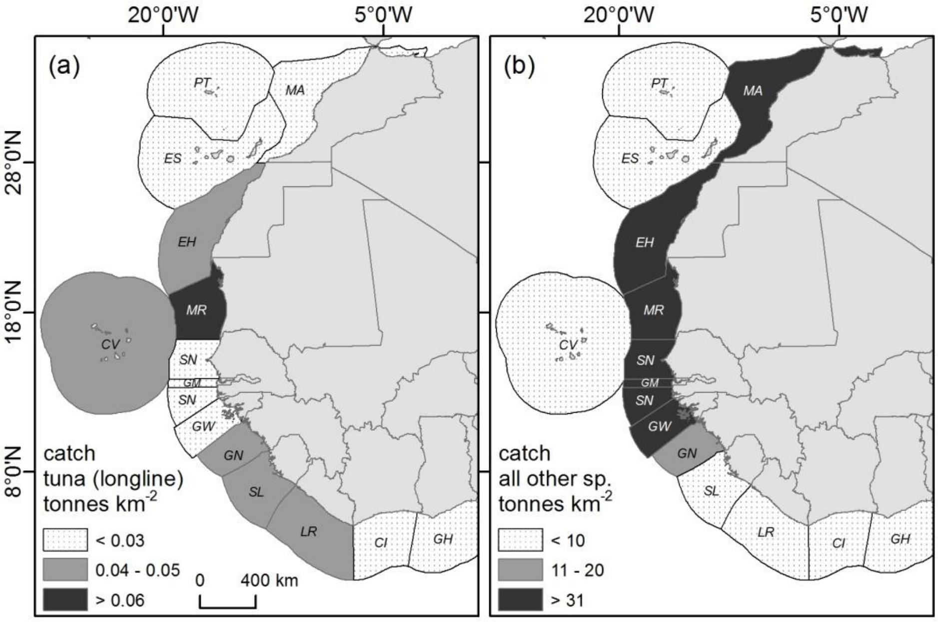

Figure 5. Cumulative fisheries catch data (1995-2009). (a) Cumulative longline tuna and billfish catch data, and (b) cumulative catch data for all marine species (excluding tuna and billfish) expressed as tonnes km^{-2} per EEZ. All data are drawn as filled polygons with a low (white/light grey stipple) 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 scale. All other map features are drawn and labelled in accordance with Figure 1. Maps drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Table S1. Summary of PTT data for turtles assigned to a foraging strategy, detailing: study ID, foraging strategy, sex, nesting season, data start and end dates, days tracked, PTT manufacturer and model and curved carapace length (CCL) in cm. Turtle IDs: 1-9 (Hawkes *et al.* 2006), 10 &11 (Varo-Cruz *et al.* 2013), 12-22 (unpublished data). All turtles were captured at the nesting beach with the exception of turtle IDs 7, 10 & 11 which were captured at sea. All turtles were released at Boa Vista except turtle ID 7 which was released at Sao Vicente.

ID	**Strategy**	**Sex**	**Nesting season**	**Start**	**End**	**Days tracked**	**PTT manufacturer & model**	**CCL**
1	oceanic	F	2004	2004-08-16	2004-11-06	83	SMRU: SRDL	84
2	oceanic	F		2004-09-13	2005-04-23	223	Sirtrack Ltd: kiwisat 101	76
3	oceanic	F		2004-09-17	2006-06-05	627	Sirtrack Ltd: kiwisat 101	72
4	oceanic	F		2004-09-23	2005-07-09	290	Sirtrack Ltd: kiwisat 101	74
5	neritic	F		2004-10-06	2005-04-27	204	Sirtrack Ltd: kiwisat 101	99
6	neritic	F		2004-10-16	2005-08-24	313	Sirtrack Ltd: kiwisat 101	98
7	oceanic	F		2004-10-24	2005-02-23	123	Telonics: ST-14	79
8	oceanic	F	2005	2005-08-22	2006-03-10	201	Sirtrack Ltd: kiwisat 101	86
9	neritic	F		2005-10-26	2006-09-19	329	SMRU: SRDL	95
10	oceanic/neritic	M	2006	2006-05-15	2007-11-01	536	Sirtrack Ltd: kiwisat 101	92
11	oceanic	M		2006-07-20	2007-05-01	286	Sirtrack Ltd: kiwisat 101	87
12	oceanic	F		2006-08-29	2007-04-01	216	SMRU: SRDL	74
13	oceanic	F		2006-08-30	2008-04-03	583	Sirtrack Ltd: kiwisat 101	82
14	oceanic	F		2006-08-31	2007-06-11	285	SMRU: SRDL	90
15	oceanic	F		2006-09-03	2007-08-22	354	SMRU: SRDL	86
16	oceanic	F		2006-09-05	2008-03-23	566	Sirtrack Ltd: kiwisat 101	NA
17	oceanic	F		2006-09-06	2007-07-14	312	Sirtrack Ltd: kiwisat 101	88
18	oceanic	F		2006-09-11	2009-10-09	1125	Sirtrack Ltd: kiwisat 101	89
19	oceanic	F		2006-09-14	2007-01-12	121	SMRU: SRDL	76
20	neritic	F		2006-09-20	2008-01-19	487	Sirtrack Ltd: kiwisat 101	91
21	oceanic	F		2006-10-04	2007-05-07	216	Sirtrack Ltd: kiwisat 101	81
22	neritic	F		2006-10-07	2006-12-19	74	Sirtrack Ltd: kiwisat 101	97

Table S2. Ecological Niche Modelling evaluation metrics for 10-fold cross validation (mean and 1SD). Algorithm abbreviations: Generalised Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MaxEnt). Key algorithm modelling parameters and evaluation metric descriptions are detailed at the foot of the table.

	Oceanic foragers					**Neritic foragers**				
Evaluation metric	**Modelling algorithm**					**Modelling algorithm**				
	GLM	**MARS**	**MaxEnt**	**mean**	**sd**	**GLM**	**MARS**	**MaxEnt**	**mean**	**sd**
AUC	0.987	0.986	0.987	0.987	0.001	0.991	0.994	0.995	0.993	0.002
KAPPA	0.913	0.920	0.910	0.914	0.005	0.976	0.981	0.983	0.980	0.004
TSS	0.920	0.924	0.912	0.919	0.006	0.977	0.981	0.983	0.980	0.003
SR	0.994	0.995	0.999	0.996	0.003	0.984	0.993	0.996	0.991	0.006
Accuracy	0.969	0.971	0.968	0.969	0.002	0.988	0.991	0.992	0.990	0.002

Biomod2 modelling parameters

Randomly generated 'pseudo absence' locations (background data), with no minimum or maximum distance to presence locations were generated for each habitat model. All locations that had missing coincident environmental data were removed from the analysis (background data locations that were spatially referenced on land).

The key algorithm modelling parameters in biomod2 were as follows:

GLM: package = 'stats', family= 'binomial'.

MARS: package = 'mda', maximum interaction degree = 2, penalty (cost per degree of freedom) = 2, thresh (forward stepwise stopping threshold) = 0.001, prune = (TRUE).

MaxEnt: Run within biomod2, maximum iterations (for training) = 200, linear/quadratic/product/threshold/ hinge features (the transformation coefficients applied to each environmental variable), default prevalence = 0.5.

Evaluation metrics

AUC (Area under the curve): a measure of the ratio of true positives out of the positives vs. the ratio of false ositives out of the negatives.

KAPPA (Cohen's Kappa, Heidke skill score) and TSS (True Skill Statistic): measures of accuracy relative to that of random chance.

SR (Success Ratio): the fraction of the true positives that were correct.

Accuracy (fraction correct): the fraction of the predictions (true and false) that were correct.

To compute the threshold value used to transform the probability of presence model output data to binary data for model evaluation metrics based on the comparison of binary data (*e.g.* True Skill Statistic (TSS)), the algorithm calculates the evaluation metric in question (*e.g.* TSS) for a sequence of thresholds from 0 to 1 (100 values). The value that maximises this evaluation metric is then selected as the threshold value used (Thuiller *et al.* 2009).

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

	Oceanic foragers					**Neritic foragers**					
Modelling algorithm	**Environmental variable**					**Environmental variable**					
	Current	**Depth**	**NPP**	**SST front activity**	**SST**	**Current**	**Depth**	**NPP**	**SST front activity**	**SST**	
GLM	0.18	0.00	0.05	0.25	0.51	0.00	0.48	0.28	0.02	0.22	mean
	0.07	0.00	0.05	0.09	0.05	0.00	0.05	0.02	0.03	0.01	sd
MARS	0.06	0.01	0.50	0.02	0.42	0.19	0.29	0.30	0.00	0.21	mean
	0.05	0.01	0.07	0.06	0.06	0.06	0.05	0.04	0.00	0.01	sd
MAXENT	0.11	0.00	0.30	0.10	0.49	0.00	0.45	0.47	0.00	0.07	mean
	0.01	0.00	0.03	0.03	0.02	0.00	0.02	0.01	0.00	0.02	sd
mean of means	0.12	0.00	0.28	0.12	0.47	0.06	0.41	0.35	0.01	0.17	

Relative importance of the contribution of an environmental variable is calculated using a randomisation process. This procedure calculates the correlation between a prediction using all environmental variables and a prediction where the independent variable being assessed is randomly re-ordered. If the correlation is high the variable in question is considered not important for the model and conversely, if low, important. A mean correlation coefficient for each environmental variable is then calculated over multiple runs. This is repeated for each environmental variable. The calculation of the relative importance is made by subtracting these mean correlation coefficient from 1 (Thuiller *et al.* 2009).

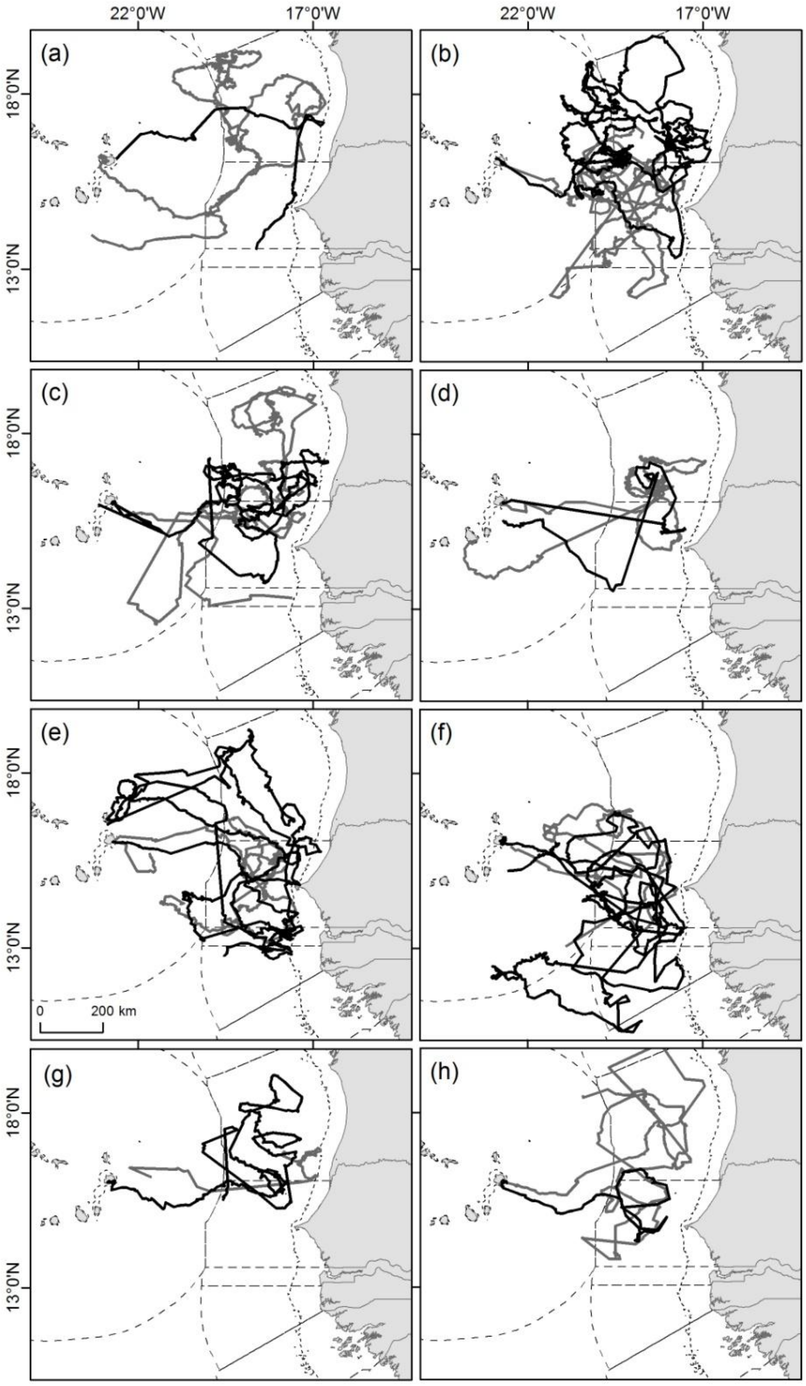

Figure S1. Oceanic loggerhead foraging tracks (*n* =16). Two tracks are drawn in each map part and coloured black and grey respectively. 200 m continental shelf isobath (broken line). Maps drawn to Geographic Coordinate System: WGS 1984.

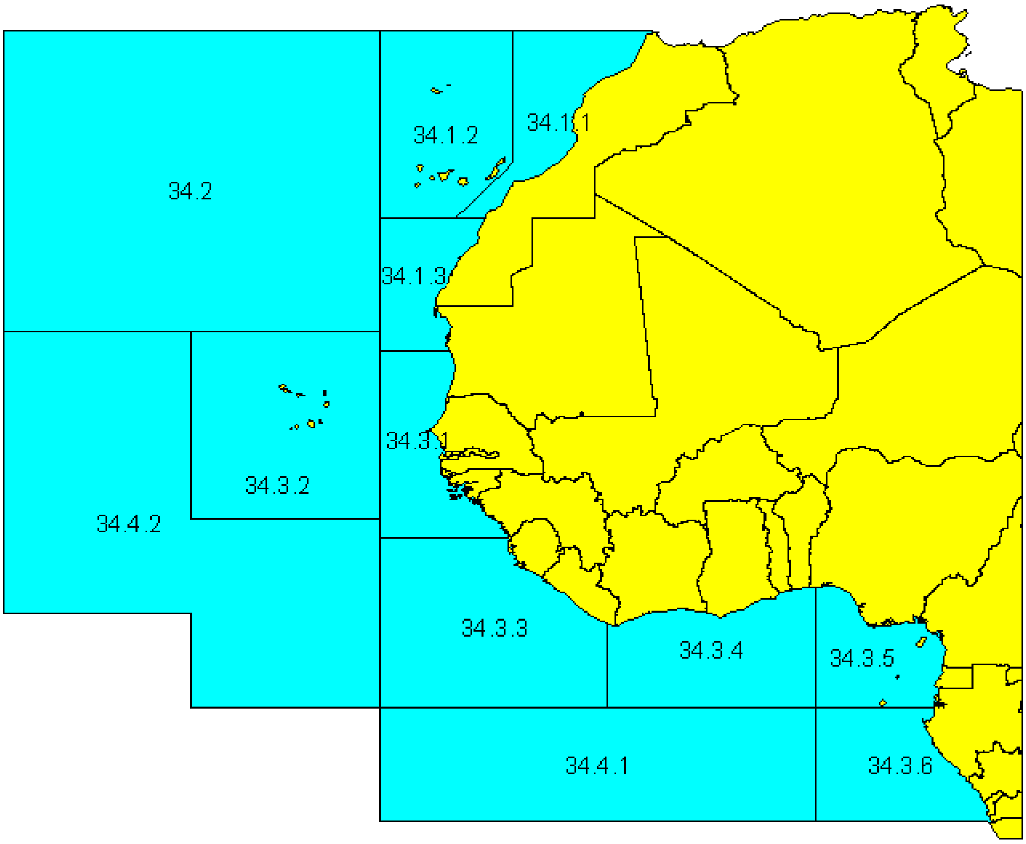

Figure S2. Fishery Committee for the Eastern Central Atlantic (CECAF) Major Fishing Area 34 statistical sub-areas and divisions (FAO 2013a).

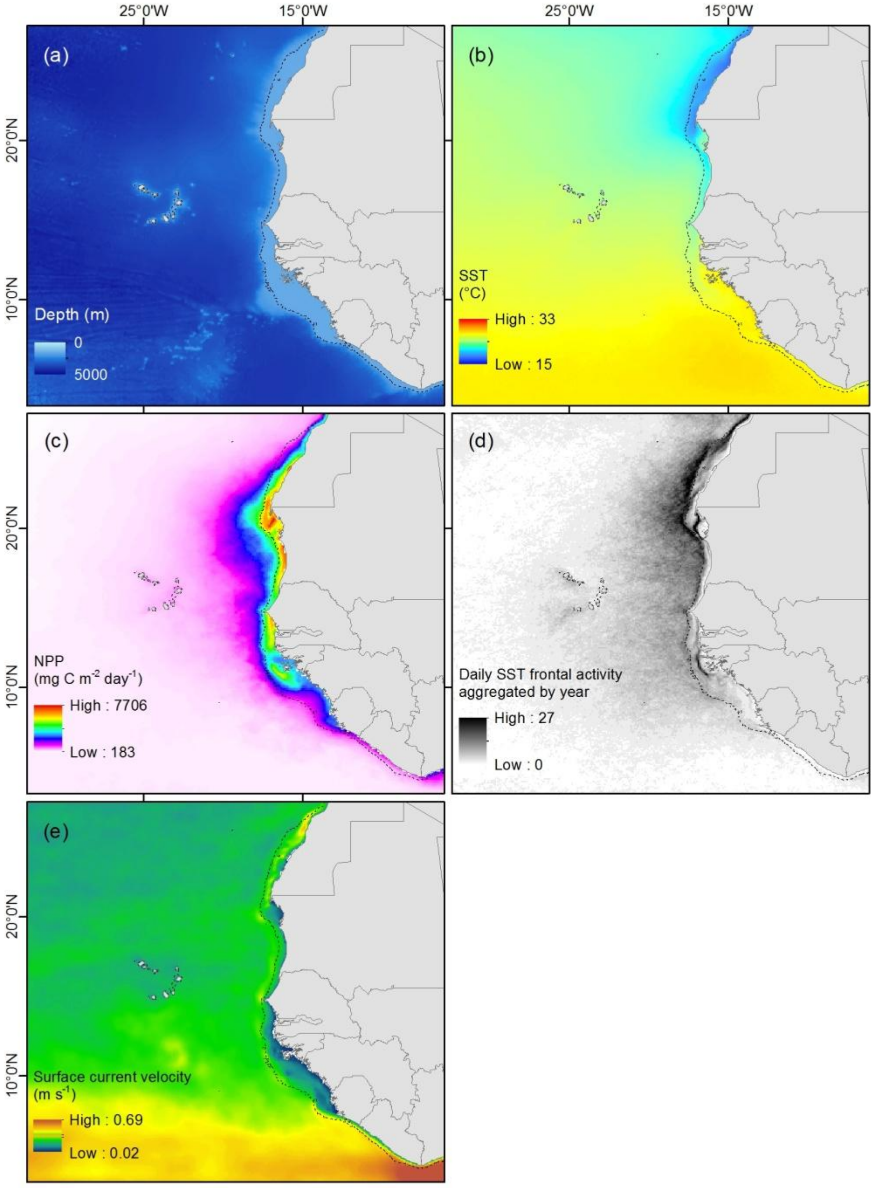

Figure S3. Ecological Niche Model (ENM) environmental variables. (a) Bathymetric depth (m), (b) Sea Surface Temperature (SST: °C), (c) Net Primary Production (NPP: mg C m^{-2} day^{-1}), (d) daily SST frontal activity and (e) sea surface current velocity (m s^{-1}). All environmental data surfaces were sampled to a 9 km x 9 km resolution using bilinear interpolation. Surfaces (b), (c) and (e) are Long-Term Yearly Averaged (LTYA) products. 200 m continental shelf isobath (broken line). Maps drawn to Geographic Coordinate System: WGS 1984.

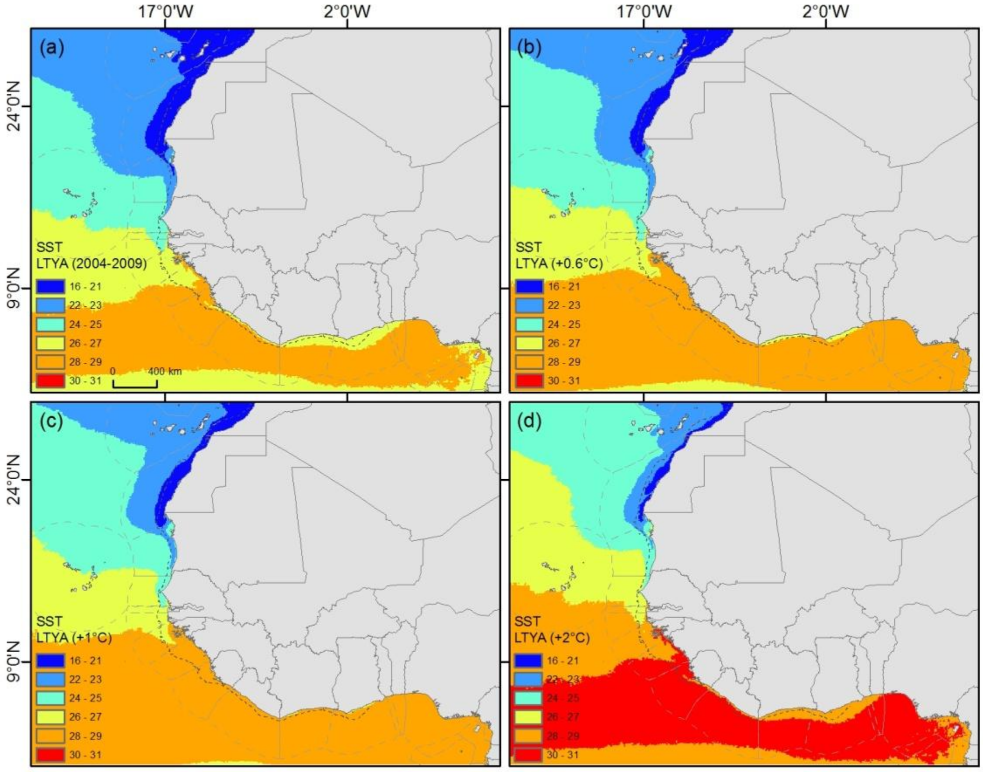

Figure S4. Forecast Ensemble Ecological Niche Models (EENMs) projected Long-Term Yearly Averaged (LTYA) Sea Surface Temperature (SST) environmental variable surfaces. Increases of between 0.6º C and 2º C were made in accordance with Coupled Model Intercomparison Project Phase 5 (CMIP5) Representative Concentration Pathway (RCP) scenarios RCP 2.6 to RCP 8.5 (IPCC 2013). (a) existing conditions, (b) LTYA SST + 0.6º C, (c) LTYA SST + 1º C and (d) LTYA SST + 2º C. SST (ºC) are classified into bands and drawn with a blue-yellow-red colour ramp in accordance with the legend detailed in each part. 200 m continental shelf isobath (broken line). Maps drawn to Geographic Coordinate System: WGS 1984.

Chapter III: **Mediterranean marine turtle foraging habitats: a test of marine protected areas under climate change**

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ABSTRACT

The Mediterranean Sea is an area of high biodiversity that is identified as being under threat from multiple cumulative impacts. The Convention for Biological Diversity calls for 10% of coastal and marine ecosystems to be protected by 2020 through an integrated network of Marine Protected Areas (MPAs); currently only 4.6% of the Mediterranean Sea is protected. Here we identify and describe observed and modelled foraging habitats for two species of sea turtle within the Mediterranean Sea; the green turtle (*Chelonia mydas*) and the loggerhead turtle (*Caretta caretta*), and investigate the spatial overlap between these habitats and current and speculative MPAs. We investigate how these spatial overlaps may alter under the influence of climate change induced sea surface temperature rise. Our analysis reveals inadequacies within the current Mediterranean MPA network that result in a lack of protection within foraging habitats for both species of sea turtle. Appreciable gains in protection for both species could be made with the adoption of new suitably designed IUCN categorised MPAs within site-specific areas identified in this study, and by designating existing MPAs with appropriate IUCN categories. However, comprehensive protection may only be afforded to these species if consideration is also given to protecting key breeding and migratory habitats. To be holistic, we suggest that the Mediterranean MPA network needs to protect multiple species with variable residency and migratory spatial patterns , and to be suitably flexible to accommodate potential range shifts as the Mediterranean basins warm with future climate change.

Keywords: climate change, ensemble ecological niche modelling, foraging habitats, Marine Protected Areas, sea turtles, strategic planning, spatial analysis

INTRODUCTION

The marine environment is under threat from human activities, with a large proportion of the world's ecosystems negatively impacted by multiple stressors (Halpern *et al.* 2008, 2015) including fisheries (Pauly, Watson & Alder 2005) and climate change (Doney *et al.* 2012; Gattuso *et al.* 2015; Halpern *et al.* 2015). These drivers are disproportionately distributed among regions and ecosystems. Many marine areas with highest predicted cumulative impacts are in continental shelf and coastal waters (Halpern *et al.* 2008, 2015); areas where cumulative impacts are also identified as generally increasing (Halpern *et al.* 2015).

Biodiversity loss may be greatest in enclosed basins, such as the Mediterranean Sea (Costello *et al.* 2010), due to cumulative impacts being concentrated in a relatively small region with limited water exchange. The Mediterranean Sea is identified as experiencing high cumulative impact from both land and ocean based sources (Halpern *et al.* 2008), with on-going decline in fish stocks (Vasilakopoulos, Maravelias & Tserpes 2014), and rapid warming of surface water across the basin (Philippart *et al.* 2011). The Mediterranean Sea is an area of high biodiversity (Bianchi & Morri 2000) with over 16 500 marine eukaryotic species (Costello *et al.* 2010). Fisheries likely represents the greatest threat to biodiversity by depleting targeted fish stocks, impacting species through bycatch, and directly and indirectly modifying host ecosystems (Costello *et al.* 2010). Climate change may further affect ecosystem structure, diversity and function (Doney *et al.* 2012; Gattuso *et al.* 2015; Halpern *et al.* 2015).

The revised Convention for Biological Diversity (CBD) targets called for 10% of coastal and marine biodiversity-important ecosystems to be protected by 2020 through an integrated and well-connected system of Marine Protected Areas (MPAs) (CBD 2010). Currently, the Mediterranean Sea has 677 MPAs, of which 96% are located in the north of both the east and west basins. The total sea area covered by extant MPAs is approximately 114 600 km^2 (4.6% of the Mediterranean). However, less than 0.1% of the total Mediterranean Sea area is categorised by strict protection and/or no take zones, and 66% of MPAs are no bigger than 50 km^2 (Gabrié *et al.* 2012). Typically, small protected areas offer limited conservation benefits (Gaines *et al.* 2010), particularly to mobile species.

Moreover, the current network of Mediterranean MPAs is mainly coastal; 86% of the surface area of MPAs are within 12 nautical miles of the coast (Gabrié *et al.* 2012). Globally, there are initiatives to create large-scale pelagic MPAs that could be beneficial to mobile marine species (Maxwell, Ban & Morgan 2014). Within the Mediterranean Sea, a single pelagic MPA exists, the Pelagos Sanctuary (sea area: 87 500 km^2), this accounts for approximately 76% of the region's current MPA designations (Gabrié *et al.* 2012). A formal regional process led by the United Nations Environment Programme's Mediterranean Action Plan (UNEP/MAP) identified a collection of large Ecologically and Biologically Significant Areas (EBSAs), also known as Priority Conservation Areas (PCAs), throughout the Mediterranean. These PCAs have since been endorsed by all contracting parties to the Barcelona Convention (the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean, formerly known as the Convention for the Protection Of The Mediterranean Sea Against Pollution) and have therefore been adopted as areas of priority conservation within the Mediterranean Sea (Portman *et al.* 2013); although other existing and proposed initiatives exist (Micheli *et al.* 2013).

The design of effective protected areas is especially challenging when species are far-ranging and pelagic (*e.g.* sea turtles, cetaceans, sharks, sea birds), as species are likely to migrate between foraging and breeding areas, and therefore, requires knowledge of species ecology and habitat variability (Hyrenbach, Forney & Dayton 2000). Ecological niche modelling, using telemetry and remotely sensed environmental data, can provide insight into potential distribution patterns of both terrestrial and marine species at broad and fine spatial scales (Razgour, Hanmer & Jones 2011; Gschweng *et al.* 2012; Matawa, Murwira & Schmidt 2012). This increased knowledge of likely spatio-temporal distributions can help inform management planning and practice to achieve effective conservation (Hart *et al.* 2012).

The Mediterranean Sea provides favourable habitat for three species of sea turtles: the green turtle (*Chelonia mydas* Linnaeus, 1758) the loggerhead turtle (*Caretta caretta* Linnaeus, 1758), and the leatherback turtle (*Dermochelys coriacea* Vandelli, 1761). The loggerhead turtle is the most common (Casale & Margaritoulis 2010). Nesting beaches for both green and loggerhead turtles are confined to the east of the Mediterranean. At sea, green turtles predominantly occur in the eastern basin. Loggerhead turtles occur throughout the east and west basin, with high densities recorded in the west (Casale & Margaritoulis 2010). Leatherback turtles are less abundant and can occur throughout the Mediterranean, but do not nest in the region (Casale & Margaritoulis 2010). All species face multiple threats, both within the marine and terrestrial environments of the Mediterranean (Casale & Margaritoulis 2010). But because of their high mobility, protection beyond nesting beaches is challenging, and requires more knowledge and new approaches.

In this study, we investigate the pan-Mediterranean habitat niche for post-nesting green and loggerhead turtles, satellite tracked from the eastern Mediterranean, in the context of protected areas within the Mediterranean basin. More specifically, we: (i) identify and describe observed foraging sites of satellite tracked green and loggerhead turtles, (ii) model likely areas of suitable foraging habitats using Ensemble Ecological Niche Models (EENMs) for both species, and determine key areas for both, (iii) model the potential change in the distribution of these foraging habitats under future climate change, and (iv) integrate available MPA data (current and speculative) to determine the protection afforded to these species.

METHODS

Satellite tracking data: collection and processing

To determine the location of foraging sites we used satellite tracking data. Platform Transmitter Terminals (PTTs) were attached to eighty-eight adult female sea-turtles (green turtles n = 35, loggerhead turtles n = 53) over the nesting seasons 1998 to 2012 at five nesting locations in the eastern Mediterranean (Figure 1). Method of turtle capture, transmitter type and process of attachment are detailed in (Godley *et al.* 2002, 2003; Broderick *et al.* 2007; Zbinden *et al.* 2008, 2011; Stokes *et al.* 2015; Snape *et al.* in review). Satellite telemetry data were collected using the Argos satellite system (CLS 2011) and downloaded using the Satellite Tracking and Analysis Tool (STAT) (Coyne & 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 2008; R package: argosfilter (Freitas 2010)). Filtered location data were then reduced to best daily locations, 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 imported into the Geographical Information System (GIS) ArcMap 10.1 (ESRI, Redlands, USA http://www.esri.com) and visually inspected to determine conclusive foraging sites for each turtle. A foraging site was deemed to be an area where an individual turtle remained resident for more than 30 days (Blumenthal *et al.* 2006) and was less than 150 km in diameter (defined by visual assessment of foraging patterns): see PTT metadata in Supplementary Material, Tables S1 and S2. To minimise the potential for pseudo-replication within our data we limited the maximum number of days retained for analysis at any one foraging site to 365 d. To define the centre of each foraging site we computed a 50% geometric peeled polygon (locations farthest from the arithmetic mean coordinates were sequentially excluded) and calculated the centroid. Location data for both green and loggerhead turtles were then separated to seasonal datasets: (i) winter/spring (December - May), and (ii) summer/autumn (June - November). These seasonally grouped data were used as our response variable in our EENMs (see Habitat modelling).

Habitat modelling

For our habitat modelling we used Ensemble Ecological Niche Models (EENMs) (Araújo & New 2007; Rangel & Loyola 2012; Pikesley *et al.* 2013, 2014). Our modelling area was described by latitudes N 46 º, N 30º, and longitudes W 6º, E 37º (WGS84), this extent bounded the Mediterranean Sea; approximately 2.5 million square kilometres.

We prepared spatially coincident physical and biological environmental data (2003-2012) using R (R Development Core Team 2008; R package: raster (Hijmans & Etten 2012)) from a number of datasets. These data were: (a) bathymetric depth (m) (www.gebco.net), (b) seabed slope (derived from depth data), (c) monthly averaged MODIS L3 night-time Sea Surface Temperature (SST: °C) (http://podaac.jpl.nasa.gov), (d) Net Primary Production (NPP: mg C m^{-2} day^{-1}) (http://orca.science.oregonstate.edu) and (e) euphotic depth (m) (http://oceancolor.gsfc.nasa.gov). We used Marine Geospatial Ecological Tools v0.8a49 (MGET; Roberts *et al.* 2010) to model the presence of SST frontal activity for the study area. Frontal features can represent significant areas of enhanced primary productivity that in turn may provide areas of increased prey availability for marine vertebrates (Scales et al. 2015). We sourced daily MODIS L3 night-time SST (°C) (http://podaac.jpl.nasa.gov) to create SST frontal activity rasters using the Cayula and Cornillon Single Image Edge Detection (SIED) algorithm (Cayula & Cornillon 1992) for each day between 2003-2012. A minimum frontal edge detection threshold of 0.5°C (SST) was used (Roberts *et al.* 2010). These daily SST frontal activity rasters were aggregated into monthly rasters with cumulative totals for daily frontal activity. Monthly data, for SST, NPP, euphotic depth and SST frontal activity were averaged into long-term monthly products, and then averaged into long-term biannual seasonally aggregated products: winter/spring and summer/autumn. To calculate the available biannual thermal niche for each of our species of turtle we extracted SST values for our seasonally grouped turtle location data from our long-term biannual SST surfaces. We selected the 1st percentile of these data to represent the minimum temperature for the thermal niche, no maximum value was set. These threshold values were then applied to the long-term biannual SST surfaces to create binary surfaces that described species, and seasonal specific thermal niches. To investigate the potential effect of sea surface temperature rise on our EENMs we applied an increase of 2º C (skin surface temperature) to our species-specific biannual SST thermal niche surfaces. These values represent the 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) scenario RCP 8.5 (IPCC 2013). The RCP 8.5 scenario reflects the current trajectory of business-as-usual CO_2 emissions (Gattuso *et al.* 2015). All environmental data surfaces were sampled to a 9 km x 9 km resolution using bilinear interpolation (the coarsest resolution of our environmental data). To test for correlation within these data a random sample of arbitrary size (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 ($n = 10$) of environmental variables.

Our modelling approach followed that detailed in Pikesley *et al.* (2013, 2014). We used the Generalised Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS) and MaxEnt modelling algorithms within the biomod2 package (R Development Core Team 2008; R package: biomod2 (Thuiller, Georges & Engler 2013)) to produce Ecological Niche Models (ENMs). These ENMs were run with both present day and forecast environmental surfaces, to identify favourable seasonal (winter/spring, summer/autumn) foraging habitats for both green and loggerhead turtles. Our response variables were binary, either 'presence' described by our seasonally apportioned location data, or randomly generated 'pseudo absences'. ENMs were run with the environmental surfaces of depth, slope, SST thermal niche, NPP, euphotic depth and SST frontal activity. Preliminary models were run with SST in place of the SST thermal niche layer. However, green turtle models produced implausible outputs whereby habitats predicted to be suitable in the Eastern basin under present day environmental conditions were forecast to become less suitable with increases in SST. We therefore chose to incorporate a thermal niche layer in place of SST which allowed the forecast model to retain the predicted present day surface whilst allowing expansion in suitable habitats with the increased thermal niche.

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 Table S3. 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, Table S3). There was little variability in model evaluation metrics within seasonal models indicating a good level of consensus, therefore, we combined our season-specific ENMs to form ensemble projections using an un-weighted average (mean) across each seasonal model for both green and loggerhead turtles. These seasonal 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 surface to the model was calculated using a randomisation process (Thuiller *et al.* 2009); see Supplementary Material, Table S4. To investigate spatial autocorrelation within model residuals we calculated Moran's *I* coefficients (Dormann *et al.* 2007) for each of our EENMs within ArcMap 10.1. As the preliminary green turtle summer/autumn foraging model revealed residual spatial autocorrelation, we sub-sampled the location data to reduce the spatial structure within these data. This was achieved using a stepwise, percentage reduction, random sample of these data, to iteratively arrive at a sub-sample of locations (70%) where spatial auto-correlation was no longer present in the model's residuals.

We then aggregated the resultant seasonal EENMs (winter/spring, summer/autumn; Supplementary Material, Figure S1) for both present day and forecast models to produce predictive surfaces where favourable habitat areas were weighted by the number of seasons in which the predicted area was suitable. To test the predictive performance of our present day loggerhead EENM with previously published tracking data we digitised known foraging sites from Schofield *et al.* (2013) and calculated the percentage coincidence between these and our present day loggerhead EENM.

Marine Protected Areas

To contextualise our data with current MPAs and speculative PCAs throughout the Mediterranean we sourced spatially referenced MPA data (MAPAMED 2014) from the Mediterranean Protected Areas Network (MedPAN). MedPAN aim to facilitate the exchange of best practice and development of tools between managers of Mediterranean MPAs in order to improve the efficiency of the management of these areas. Secondly, we digitised and geo-referenced available PCA map data from the United Nations Environment Programme (UNEP 2010). These were compared with our observed, modelled and forecast foraging habitats for green and loggerhead turtles.

RESULTS

Satellite tracking and habitat use

Seventy-six PTTs transmitted location data for 341 days (median), 177 to 420 days (d) (inter-quartile range (IQR)). Twelve PTTs failed to transmit location data; reasons may include premature failure of the transmitter or the attachment, or mortality (Hays *et al.* 2007). Sea turtles were resident for > 30 d within eighty-three foraging sites: green turtles *n* = 27, foraging sites *n* = 29; loggerhead turtles *n* = 49, foraging sites *n* = 54 (two green and four loggerhead turtles foraged at multiple sites, see metadata in Supplementary Material, Tables S1 and S2). All foraging sites were primarily located in continental shelf waters (< 200 m depth) (Figure 1). Green turtles were predominantly located in shallower waters closer to shore than loggerhead turtles. Foraging habitat depths for: (i) green turtles, 9 m (median), 3 to 23 m (IQR), (ii) loggerhead turtles, 43 m (median), 22 to 75 m (IQR). Distance from shore for: (i) green turtles, 1.4 km (median), 0.5 to 3.7 km (IQR), (ii) loggerhead turtles, 6.9 km (median), 1.9 to 34.8 km (IQR). All green turtle, and 74% (*n* = 40) of loggerhead foraging site centroids, were within Mediterranean States' 12 nautical mile waters (Figure 1).

Habitat modelling

Green turtles: seasonally aggregated EENMs (RS ≥ 0.5), based on present day environmental data (2003-2012), indicated that the continental shelf of the eastern Mediterranean basin, from eastern Turkey through to Tunisia provided for areas of year-round suitable foraging habitats (Figure 2a, Table 1). Depth and thermal niche were the most important contributory variables to these EENMs (Supplementary Material, Table S4) with mean Relative Importance of the Contribution to the model Coefficients (RICC) for depth: 0.55 (winter/spring), 0.43 (summer/autumn), and for thermal niche: 0.35 and 0.49 respectively. Models incorporating increases of 2º C to the thermal niche (subsequently referred to as forecast models), indicated that there would be a north and westward expansion in suitable foraging habitat for green turtles. These areas included waters of the north African coast, the Balearic, Tyrrhenian, Adriatic and Aegean Sea. There was a notable gain of 153% (present day: 36 378 km^2, forecast: 91 895 km^2) in year-round suitable foraging habitat that was coincident with Mediterranean States' 12 nautical mile waters. Countries with greatest gains included: Algeria, Greece, Italy, Libya, Spain, Tunisia and Turkey. Countries with greatest coincidence with suitable forecast foraging habitats included: Egypt (11% coincidence), Greece (11%), Italy (11%), Libya (20%), Spain (10%) and Tunisia (24%) (Figure 2b, Table 1).

Loggerhead turtles: seasonally aggregated EENMs (RS ≥ 0.5), based on present day environmental data (2003-2012), indicated that the continental shelf of the eastern Mediterranean basin, from Greece through to Tunisia, including southern Sicily, provided near continuous year-round suitable foraging habitat. Favourable habitat was also predicted for continental shelf waters to the north and west of the Mediterranean. These included areas of the Balearic Sea (eastern Spain and the Balearic Islands), the west coast of Italy, Sardinia and the Aegean Sea (Figure 3a, Table 1). Depth was the single most important contributory variable to these seasonal EENMs (Supplementary Material, Table S4) with mean RICCs of: 0.84 (winter/spring) and 0.72 (summer/autumn). The second most important contributory variables to these models were: NPP (winter/spring, RICC 0.07), and thermal niche (summer/autumn, RICC: 0.17). Ninety-one percent (91%, n = 114) of all loggerhead turtle foraging sites (92% female, n = 81; 89% male, n = 33) as found by Schofield *et al.* (2013) were coincident with our present day loggerhead EENM (Supplementary Material, Figure S2, Table S5). Forecast models, indicated that the habitat niche would likely increase to the north of the Mediterranean basin. With marginal year-round gains in suitable foraging habitat predicted in the Aegean and Adriatic Sea (Figure 3b, Table 1).

Foraging habitats (present day) with year-round suitability for both species principally occurred in 12 nautical mile waters of Egypt (22% coincidence) and Libya (51%); total combined sea area: 24 239 km^2 (Table 1). There were smaller congruencies of habitats in coastal waters of Cyprus, Israel, Lebanon, Syria, Tunisia and Turkey. Under forecast models there was a gain of 144% (present day: 32 807 km^2, forecast: 80 181 km^2) in year-round suitable foraging habitat for both species in Mediterranean States' 12 nautical mile waters. These countries included: Greece, Italy, Libya, Spain, Tunisia and Turkey (Figure 4. Table 1). Countries with greatest coincidence with suitable forecast foraging habitats included: Egypt (9%), Greece (11%), Italy (10%), Libya (23%), Spain (11%) and Tunisia (25%).

Moran's *I* coefficients indicated no spatial autocorrelation within the residuals of our final seasonal models (green turtles, winter/spring: z = 1.41, p = 0.16, summer/autumn: z = 1.67, p = 0.09; loggerhead turtles, winter/spring: z = 0.99, p = 0.32, summer/autumn: z = 0.56, p = 0.58).

Marine Protected Areas

Fourteen (17%, total *n* = 83) sea turtle foraging site centroids were coincident with IUCN classified or un-classified MPAs (classified : green turtles *n* = 0, loggerhead turtles *n* = 1; un-classified : green turtles *n* = 8, loggerhead turtles *n* = 5). IUCN protected areas are defined by management category: Ia strict nature reserve, Ib wilderness area, II national park, III natural monument or feature, IV habitat/species management area, V protected landscape or seascape and VI protected areas with sustainable use of natural resources (see full IUCN protected area definitions and management categories in Supplementary Material, Table S6). In this study 'un-classified' refers to MPAs where there was no clear assignment of IUCN category within the MAPAMED (2014) metadata (MedPAN pers. comm.). An additional thirteen foraging centroids were coincident with UNEP PCAs: green turtles *n* = 0, loggerhead turtles *n* = 13 (Table 2).

Of the total footprint of our seasonally aggregated green and loggerhead turtle EENMs (RS ≥ 0.5, based on present day environmental data), 1.3% (1830 km^2: green turtles), and 5.3% (28 846 km^2: loggerhead turtles), spatially overlapped with MPA zones. Under forecast models this coincidence increased to 4.0% (13 526 km^2) for green turtles and 5.6% (31 100 km^2) for loggerhead turtles (Table 3), primarily due to the expansion of these habitat niches into the western basin. Similarly, 23.8% (33 260 km^2) of our green turtle EENM, and 25.3% (137 206 km^2) of our loggerhead EENM spatially overlapped UNEP PCAs; under forecast models this percentage marginally decreased to 20.2% (69 050 km^2) for green turtles, and 24.9% (139 198 km^2) for loggerhead turtles.

Within MPA zones, our green turtle EENM (total footprint: present day environmental data) occupied 2.2% (240 km^2) of all current IUCN classified MPAs, and 1.5% (1590 km^2) of all un-classified MPAs. Our forecast models indicated that this would increase to 31.4% (3390 km^2) for classified MPAs and 9.4% (10 136 km^2) for un-classified. Our loggerhead turtle EENMs occupied 40.9% (4428 km^2) and 22.6% (24 418 km^2) of classified and un-classified MPA zones respectively. This increased under forecast models to 45.7% (4946 km^2) for classified MPAs, 24.2 % (26 154 km^2) for un-classified (Table 4).

DISCUSSION

The current network of Mediterranean MPAs is mainly located within the northern basin and is coastal (Figure 5a, b and c), with the vast majority of all MPAs sited within 12 nautical mile waters (Gabrié et al. 2012). However, strict protection is potentially limited; approximately only 9% (~ 11 000 km^2) of the total area of all MPAs (analysis in this study) are known to be assigned an IUCN category. Moreover, assignment of an IUCN category to a MPA need not necessarily confer protection to specific species within that classified area; see IUCN protected area definitions and management categories in Supplementary Material, Table S6. Additionally, MPAs may also fail to protect through limited size, poor design or inappropriate/lack of management (Agardy, Di Sciara & Christie 2011).

Our analysis revealed that green and loggerhead turtle foraging sites were primarily located in coastal shelf waters of the eastern Mediterranean Sea in the Levantine and Ionian Basins; with loggerhead turtles also occurring in coastal shelf waters to the north in the Adriatic Sea, and in off-shore shelf waters in the Gulf of Gabes and off the Nile delta. Green turtles occupied shallower water, closer to shore than loggerhead turtles. Foraging sites for green turtles occurred exclusively within 12 nautical mile waters from Turkey through to Tunisia; hotspots of clustered foraging sites were observed in near-shore coastal waters of Turkey, Libya and Tunisia. Loggerhead turtle foraging sites were more dispersed, extending from northern Italy southwards through the Adriatic and around the coasts of Cyprus and Syria through to Tunisia; 26% (n = 14) of loggerhead turtle foraging sites were located outside 12 nautical mile waters. Hotspots of clustered foraging sites occurred in the northern Adriatic, the eastern Levantine Basin and in the Gulf of Gabes.

Despite being located in near-shore coastal waters, none of our green turtle foraging site centroids were within IUCN classified MPAs; eight (28%) were located within un-classified areas. Similarly, only one (2%) loggerhead turtle foraging site centroids were located within a classified MPA (IUCN category VI, the lowest IUCN category); five (9%) were located within un-classified MPAs. As a consequence, none of our observed green or loggerhead turtle foraging sites are afforded any noteworthy protection within the current Mediterranean MPA network.

Our modelled present day habitat niche for green turtles was confined to the south and east of the eastern Mediterranean basin, and highlighted suitable year-round foraging sites in Iskenderun Bay, Turkey and Gulf of Sidra, Libya, that were not occupied by our tracked turtles. Under forecast models, this niche expanded to the north and west. Most notably, forecast models indicated that suitable habitat may become available for green turtles in the western basin. Areas of year-round suitable habit were predicted in near-shore coastal waters of Spain, the Balearic Islands, Algeria, Tunisia, southern Italy, Sicily and Greece. Spatial overlap between habitat niche and MPA zones increased with forecast models. The majority of this increase was within IUCN category II and IV MPAs, which potentially represents greater protection for green turtles within these habitats, depending on the management objectives of individual MPAs.

Our modelled present day habitat niche for loggerhead turtles indicated suitable foraging habitats throughout the majority of continental shelf waters in the eastern Mediterranean basin, with further, fragmented sections in the western basin. This habitat model successfully predicted in excess of 91% (*n* = 114) of previously identified foraging locations from an independent tagging study (Schofield *et al.* 2013). Forecast models indicated that this niche would likely increase to the north of the Mediterranean basin. There was a marginal increase in coincidence between forecast habitat niche and classified and un-classified MPAs: as such, it is unlikely that there would be a tangible increase in protection for loggerhead turtles through the extant MPA network.

As a step towards establishing a regional, ecologically coherent network of MPAs outside 12 nautical mile waters, Priority Conservation Areas (PCAs) have been identified throughout the Mediterranean Sea (Portman *et al.* 2013) (Figure 5d). These areas are intended to be core regions in which MPAs may be identified and implemented. None of our green turtle foraging site centroids were located within PCAs. Notwithstanding, our models did identify the PCA within the Gulf of Gabes to host suitable foraging habitat for green turtles (Figure S3a, area F). Thirteen loggerhead turtle foraging site centroids were located within PCAs, reflecting the greater use of off-shore waters by loggerhead than green turtles. Present day and forecast models identified that the PCAs within the Adriatic, Straits of Sicily and Gulfs of Gabes and Tunis coincided with substantial areas of loggerhead turtle habitat niche (Figure S3b, areas E,F and G). These areas could represent very significant areas for future consideration for MPA status for this species. Smaller areas also existed; notably, within the Balearic Sea and the east of the Levantine basin (Figure S3b, areas B,K and L).

Under present day environmental conditions, our analysis suggests a fundamental lack of protection for both green and loggerhead turtles within observed and modelled foraging habitats inside the current Mediterranean MPA network. Far-ranging marine species are difficult to protect due to their migratory/foraging ecology; however, these distributions need not be random, but may be influenced by favourable areas of habitat (Hyrenbach, Forney & Dayton 2000). Our analysis revealed distinct hotspots for both green and loggerhead turtles. A large proportion of our green turtle foraging site centroids (76%, foraging sites: *n* = 22, green turtles: *n* = 21) were within four small, well-defined areas of near-shore coastal waters of Turkey (*n* = 1), Libya (*n* = 2) and Tunisia (*n* =1) (Figure 1a: also see Stokes *et al.* (2015)). Only one of these areas lies within a designated MPA (Ain Al-Ghazalah Gulf, Libya); however, this is without IUCN classification (MAPAMED 2014). As adult green sea turtles are primarily herbivorous (Bjorndal 1997), and forage predominantly on seagrass in the Mediterranean (Cardona *et al.* 2010), it seems likely that food availability may concentrate these turtles within these areas. Designation of MPAs that bound these foraging areas, together with assignment and enforcement of appropriate IUCN classification, could appreciably increase protection to this species within these areas. Loggerhead turtle foraging sites were more diverse, this probably reflects the more cosmopolitan nature of their diet (Bjorndal 1997); it is possible that this trophic plasticity may confere a greater ability for loggerhead turtles to adapt to climate change induced shifts in habitat suitability. It is difficult to identify site-specific near-shore locations that may benefit foraging loggerhead turtles. However, loggerhead turtles foraged coincidently with green turtles in near-shore coastal water of Tunisia, and within Lake Bardawil, Egypt, the latter being an un-classified MPA.

Under forecast models, 94% of combined green and loggerhead foraging habitat was located outside the boundaries of all current classified and un-classified MPAs. Fisheries likely represent a significant threat to sea turtle populations throughout the Mediterranean Sea by way of bycatch (Casale 2011), with associated impacts dependent on foraging grounds used and fisheries gear type encountered (Clusa *et al.* 2016). Our analysis indicates that adoption of appropriately designed IUCN categorised pelagic MPAs within the northern Adriatic and the Gulfs of Gabes and Tunis could provide notable gains in protection for loggerhead turtles; areas previously identified as both important foraging habitats for loggerhead turtles (Casale, Laurent & De Metrio 2004; Casale *et al.* 2012; Schofield *et al.* 2013; Snape *et al.* in review) and regions where turtles may be the subject of bycatch (Casale, Laurent & De Metrio 2004; Casale *et al.* 2007). Large pelagic MPAs, however, may require their own suite of management strategies (Maxwell, Ban & Morgan 2014) and may therefore be difficult to enforce. In addition, to be acceptable to all stakeholders, such large managed areas need to be cost-effective, both in terms of the level of protection afforded to species within these zones, and the socio-economic impact that they may have (Leathwick *et al.* 2008).

Under climate change scenarios, maximum ocean warming is projected for the surface in tropical and Northern Hemisphere subtropical regions. On a global scale the upper 75 m warmed, on average, by 0.11º C (0.09 to 0.13° C) per decade over the period 1971 to 2010 (IPCC 2013). Analysis of satellite derived sea surface temperature data for the Mediterranean Sea (Skliris *et al.* 2012) indicated a mean annual warming of 0.037°C year^{-1} for the whole basin (1985-2008). However, magnitude of warming and warming rate were not homogeneous across basins, with short-term (decadal) shifts in warming rates between basins. Our forecast models apply a generic projected global sea surface (top 100 m) temperature increase of 2º C, based on CMIP5 RCP scenarios RCP8.5 (IPCC 2013), uniformly across our study area. Therefore, our models may not capture any nuances in spatio-temporal variability of habitat niche associated with variable warming rates. Our approach does, however, allow for basin-wide modelling of forecast habitats under realistic sea surface temperature increases within the basin.

This study provides further insight into the habitat use of post-nesting green and loggerhead turtles across the Mediterranean Sea. Our analyses clearly discriminate key foraging areas for both species, under present day environmental conditions and under predicted sea surface temperature rises. We suggest that there are profound shortcomings within the current Mediterranean MPA network that result in a notable lack of protection within foraging habitats for both green and loggerhead sea turtles. However, appreciable gains in protection for both species could be made by designating new MPAs within key foraging areas identified in this analysis; and by designating current MPAs with appropriate IUCN classifications and ensuring effective management and enforcement. Adoption of suitably designed IUCN categorised pelagic MPAs within the northern Adriatic, the Gulf of Gabes and the Gulf of Tunis as part of the UNEP/MAP PCAs could also provide a notable increase in protection for sea turtles, in particular loggerhead turtles. Our analysis focuses on a single facet of species life-history in assessing the present and future protection afforded by the current, and speculative, Mediterranean MPA network. As such, comprehensive protection will only be afforded to these species if consideration is also given to protecting key breeding habitats (on land and at sea) and migratory routes (*e.g.* Schofield *et al.* 2013; Stokes *et al.* 2015; Snape *et al.* in review). In addition, to be holistic, this network needs to protect multiple species with variable residency and migratory spatial patterns; moreover, this network needs to be flexible enough to accommodate potential range shifts as the Mediterranean basins warm under climate change. As such, we believe that the analytical process that we have developed here has utility in defining critical areas for other species of concern within the Mediterranean Sea.

ACKNOWLEDGEMENTS

We thank the following for their support: Ecological Research Society (EKAD), Israel National Nature and Parks Authority (INNPA), Marine Turtle Conservation Project (MTCP), North Cyprus Department of Environmental Protection, seaturtle.org, Society for the Protection of Sea Turtles in North Cyprus (SPOT), Turkish Republic Ceyhan and Yumurtalýk District Governorates; and for funding: ARCHELON, Apache, Baku-Tbilisi-Ceyhan Crude Oil Pipeline Company, British Chelonia Group, BP Egypt, the British High Commission and British Residents Society of North Cyprus, Darwin Initiative, Ektam Kıbrıs, Erwin Warth Foundation, Friends of SPOT, INNPA, Karl Mayer Foundation and the Ocean Science and Research Foundation, Kuzey Kýbrýs Turkcell, NERC, MAVA Foundation for the Protection of Nature, Marine Conservation Society Sea Turtle Conservation Fund, MEDASSET UK., seaturtle.org. K.L.S. is funded by the European Social Fund. R.S. has been supported by the Peoples Trust for Endangered Species, British Chelonia Group and United States Agency for International Development.

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Table 1. Table 1. Sea area (km^2) of Mediterranean state 12 nautical mile waters coincident with seasonally aggregated green and loggerhead turtle Ensemble Ecological Niche Models (EENMs), with year-round relative suitability ≥ 0.5 (areas with category 2 (red) in Figures 2 and 3), based on present day environmental data, and forecast models. Sea area (km^2) also expressed as a % of total coincident sea area. Net gain or no change in coincidental sea area indicated by + or 0 respectively.

Country	**12 nautical mile waters: total sea area (km^2)**	**Green turtles: present day**		**Green turtles: forecast +2°C**		**gain (+) no change (0) in sea area (km^2)**	**Loggerhead turtles: present day**		**Loggerhead turtles: forecast +2°C**		**gain (+) no change (0) in sea area (km^2)**	**Green & Loggerhead turtles: present day**		**Green & Loggerhead turtles: forecast +2°C**		**gain (+) no change (0) in sea area (km^2)**
		(km^2)	**(%)**	**(km^2)**	**(%)**		**(km^2)**	**(%)**	**(km^2)**	**(%)**		**(km^2)**	**(%)**	**(km^2)**	**%**	
Albania	6024	0	0	600	1	+	1779	1	1779	1	0	0	0	470	1	+
Algeria	28034	0	0	2794	3	+	1351	1	1351	1	0	0	0	654	1	+
Croatia	31569	0	0	0	0	0	15233	8	17456	8	+	0	0	0	0	0
Cyprus	13561	1134	3	1134	1	0	2006	1	2006	1	0	1070	3	1070	1	0
Egypt	25340	10096	28	10096	11	0	10141	5	10141	5	0	7375	22	7375	9	0
France	24509	0	0	0	0	0	2484	1	3220	2	+	0	0	0	0	0
Gaza strip	218	137	0	137	0	0	59	0	59	0	0	59	0	59	0	0
Gibraltar	412	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Greece	114036	22	0	9817	11	+	27945	14	30669	15	+	0	0	8455	11	+
Israel	3897	2003	6	2003	2	0	2718	1	2718	1	0	2003	6	2003	2	0
Italy	154802	0	0	9854	11	+	43735	22	46939	23	+	0	0	8153	10	+
Lebanon	4710	632	2	632	1	0	624	0	624	0	0	576	2	576	1	0
Libya	38673	17006	47	18744	20	+	32742	17	32742	16	0	16864	51	18600	23	+
Malta	3991	0	0	276	0	+	1905	1	1905	1	0	0	0	276	0	+
Monaco	73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Morocco	9431	0	0	181	0	+	226	0	249	0	+	0	0	111	0	+
Serbia and Montenegro	2324	0	0	0	0	0	677	0	677	0	0	0	0	0	0	0
Slovenia	236	0	0	0	0	0	62	0	174	0	+	0	0	0	0	0
Spain	56583	0	0	8873	10	+	19454	10	19932	10	+	0	0	8568	11	+
Syria	3902	428	1	428	0	0	554	0	554	0	0	357	1	357	0	0
Tunisia	36904	2018	6	22452	24	+	25053	13	25053	12	0	1875	6	19968	25	+
Turkey	49271	2902	8	3874	4	+	7718	4	9944	5	+	2628	8	3486	4	+
UK sovereign base (Cyprus)	377	0	0	0	0	0	24	0	24	0	0	0	0	0	0	0
Total		36378		91895			196490		208216			32807		80181		

Table 2. Green and loggerhead turtle foraging site centroids, counts (*n*) and expressed as a percentage of conspecific foraging site centroids coincident with classified and un-classified Marine Protected Areas (MPAs), and proposed United Nations Environment Programme (UNEP) Priority Conservation Areas (PCAs). Total turtles tracked: green turtles *n* = 27, loggerhead turtles *n* = 49. Total foraging sites: green turtles *n* = 29, loggerhead turtles *n* = 54.

	Green turtle foraging sites		**Loggerhead turtle foraging sites**	
	n	**%**	**n**	**%**
Classified MPAs	0	0	1[a]	2
Un-classified MPAs	8[b]	28	5[c]	9
UNEP PCA	0	0	13[d]	24

[a] MPAs: *n* = 1. Amvrakikos Wetlands, National Park, Greece, IUCN category VI.

[b] MPAs: *n* = 3.

[c] MPAs: *n* = 3.

[d] UNEP PCAs: *n* = 4. Areas; F: Southern Strait of Sicily, G: Northern and Central Adriatic, K: North-eastern Levantine Sea and Rhodes Gyre, L: Nile Delta Region (Figure 5d).

Table 3. Area (km^2), and percentage, of the total footprint of species-specific aggregated EENMs (relative suitability ≥ 0.5), for present and forecast models, coincident with classified and un-classified Mediterranean Marine Protected Areas (MPAs).

	Present				**Forecast**			
	Greens		**Loggerheads**		**Greens**		**Loggerheads**	
	km^2	**%**	**km^2**	**%**	**km^2**	**%**	**km^2**	**%**
Classified MPAs	240	0.2	4428	0.8	3390	1.0	4946	0.9
Un-classified MPAs	1590	1.1	24418	4.5	10136	3.0	26154	4.7
Total	*1830*	*1.3*	*28846*	*5.3*	*13526*	*4.0*	*31100*	*5.6*

Table 4. Area (km^2), of classified and un-classified protected areas coincident with of the total footprint of species-specific aggregated EENMs (relative suitability ≥ 0.5), for present and forecast models. Areas (km^2) are also expressed as a % of total area of either; classified areas or un-classified areas.

			Present				**Forecast**			
			Greens		**Loggerheads**		**Greens**		**Loggerheads**	
			km^2	**%**	**km^2**	**%**	**km^2**	**%**	**km^2**	**%**
Classified MPAs	**IUCN category**	**II**	15	0.1	1758	16.3	1939	17.9	1890	17.5
		III	< 1	< 0.1	25	0.2	21	0.2	25	0.2
		IV	225	2.1	2523	23.3	1362	12.6	2898	26.8
		V	0	0	80	0.7	40	0.4	80	0.7
		VI	0	0	42	0.4	28	0.3	53	0.5
		Total	*240*	*2.2*	*4428*	*40.9*	*3390*	*31.4*	*4946*	*45.7*
Un-classified MPAs			1590	1.5	24418	22.6	10136	9.4	26154	24.2

IUCN protected areas are defined by management category: Ia strict nature reserve, Ib wilderness area, II national park, III natural monument or feature, IV habitat/species management area, V protected landscape or seascape and VI protected areas with sustainable use of natural resources (see full IUCN protected area definitions and management categories in Supplementary Material, Table S6).

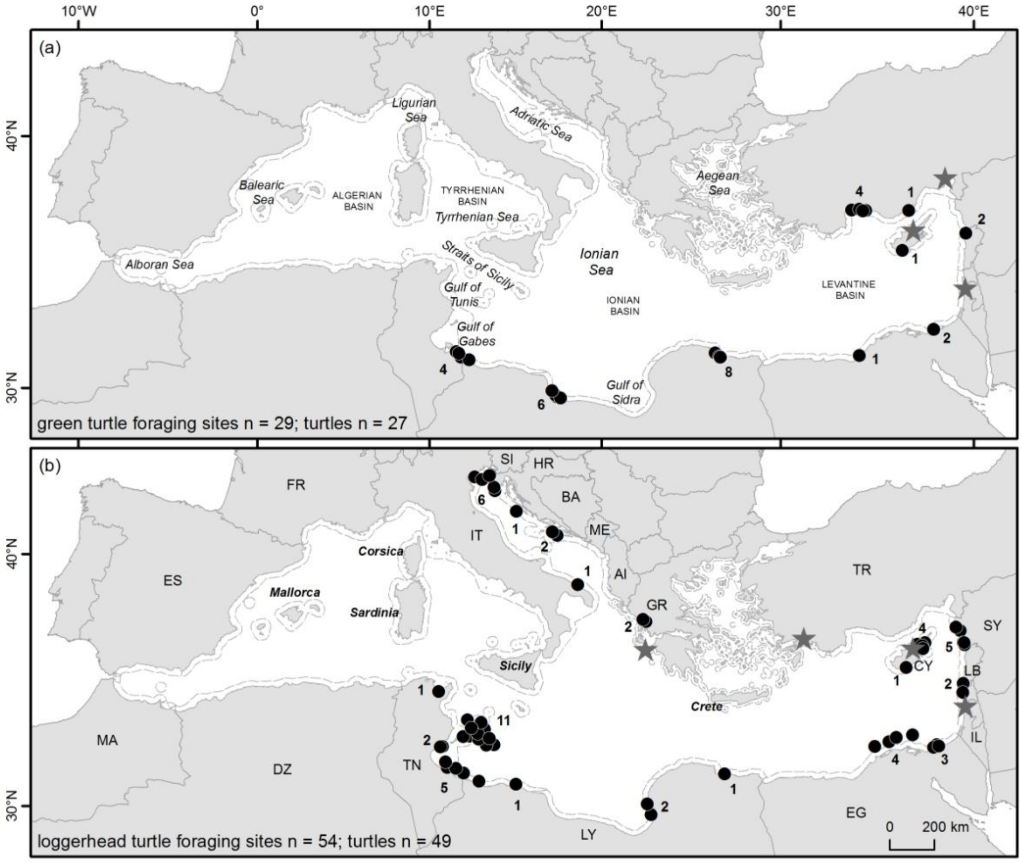

Figure 1. Post-nesting foraging site centroids (1998 to 2013) (black circles), based on satellite tracked, best daily locations for, (a) green turtles (foraging sites *n* = 29; turtles *n* = 27), (b) loggerhead turtles (foraging sites *n* = 54; turtles *n* = 49). The total number of foraging sites at grouped locations are numbered in bold. Twelve nautical mile limit (broken line). Release locations (grey stars). In part (a) maritime areas are labelled as follows: Mediterranean basins (roman capitals), seas, gulfs and straits (italics). In part (b) countries are identified using their 2 digit sovereign state ISO code (roman capitals) as follows: Spain (ES), France (FR), Italy (IT), Slovenia (SI), Croatia (HR), Bosnia (BA), Montenegro (ME), Albania (Al), Greece (GR), Turkey (TR), Syria (SY), Lebanon (LB), Israel (IL), Egypt (EG), Libya (LY), Tunisia (TN), Algeria (DZ) and Morocco (MA). Islands (bold italics) labelled in full. All parts are drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

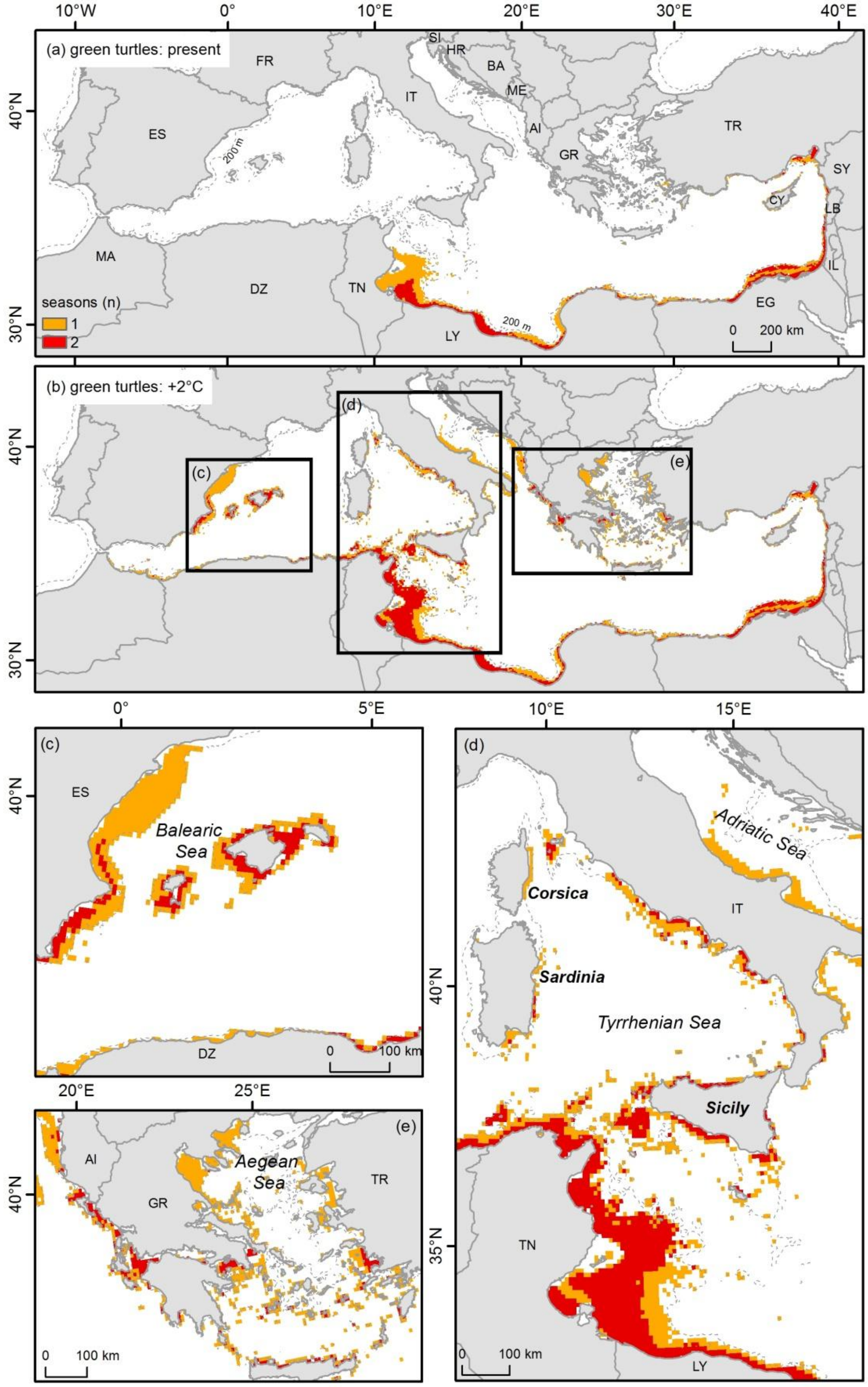

Figure 2. Aggregated seasonal Ensemble Ecological Niche Models (EENMs) for post-nesting green turtles run with: (a) present day and (b) forecast, environmental data. Parts (c), (d) and (e) are located according to the insets of

part (b). Present day models were run with best daily location data, and with the environmental surfaces of depth, slope, euphotic depth, Sea Surface Temperature (SST) thermal niche, net primary productivity (NPP), and SST frontal activity using long-term biannual seasonally aggregated products. Forecast models were run with an increase of 2º C to species-specific biannual SST thermal niche surfaces in accordance with Coupled Model 5 (Intercomparison Project Phase CMIP5) Representative Concentration Pathway (RCP) scenario RCP 8.5 (IPCC 2013). Seasonal EENMs: (i) winter/spring (December - May), and (ii) summer/autumn (June - November) with a relative suitability ≥ 0.5 were aggregated to form a predictive surface where habitat niches were weighted by the number of seasons in which the predicted area was suitable. These surfaces are drawn in accordance with the figure legend in part (a). Countries, islands and seas are labelled in accordance with Figure 1, 200 m isobath drawn and labelled. Parts (a) and (b) are drawn to the same spatial scale, all other parts are drawn to differing spatial scales. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

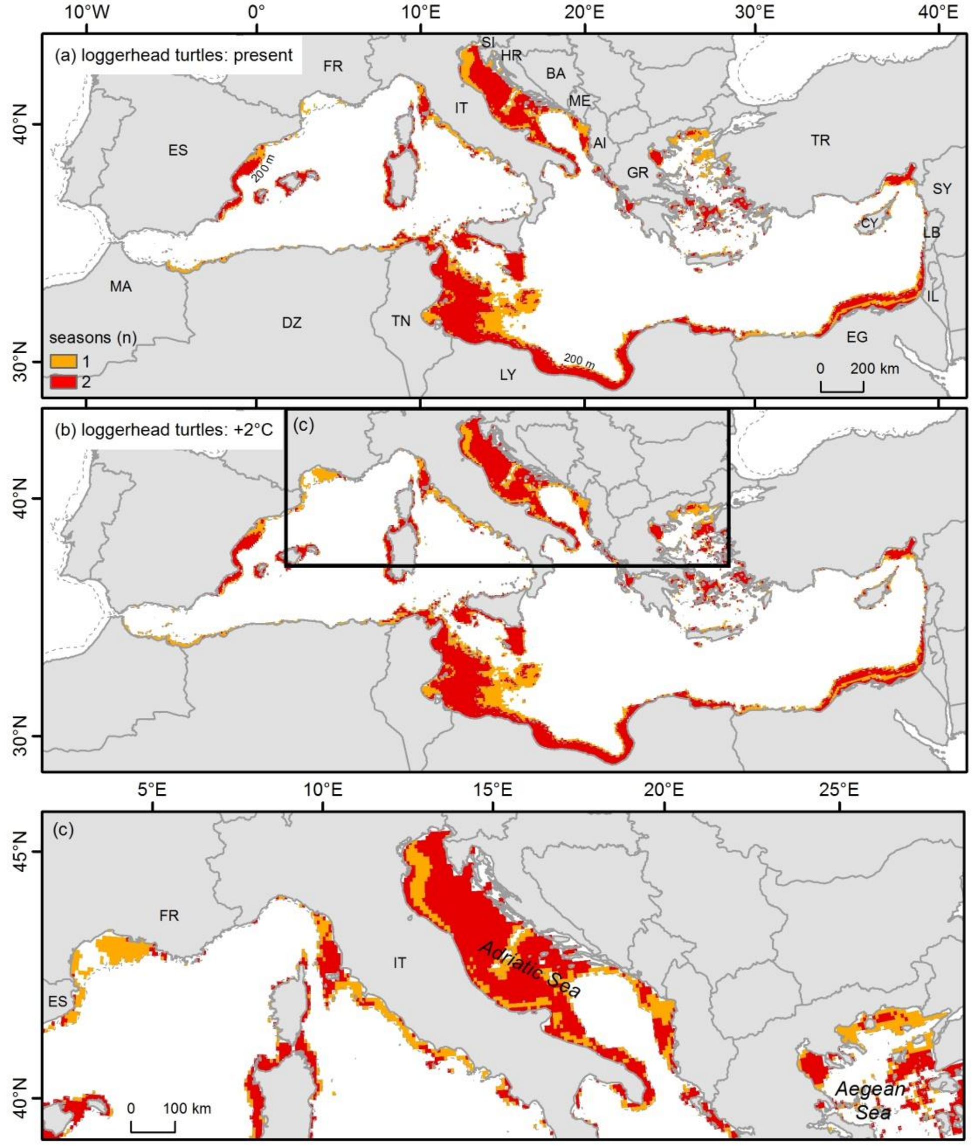

Figure 3. Aggregated seasonal Ensemble Ecological Niche Models (EENMs) for post-nesting loggerhead turtles run with: (a) present day and (b) forecast, environmental data. Part (c) is located according to the inset of part (b). See Figure 2 for modelling details. Countries, and seas are labelled in accordance with Figure 1, 200 m isobath drawn and labelled. Parts (a) and (b) are drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

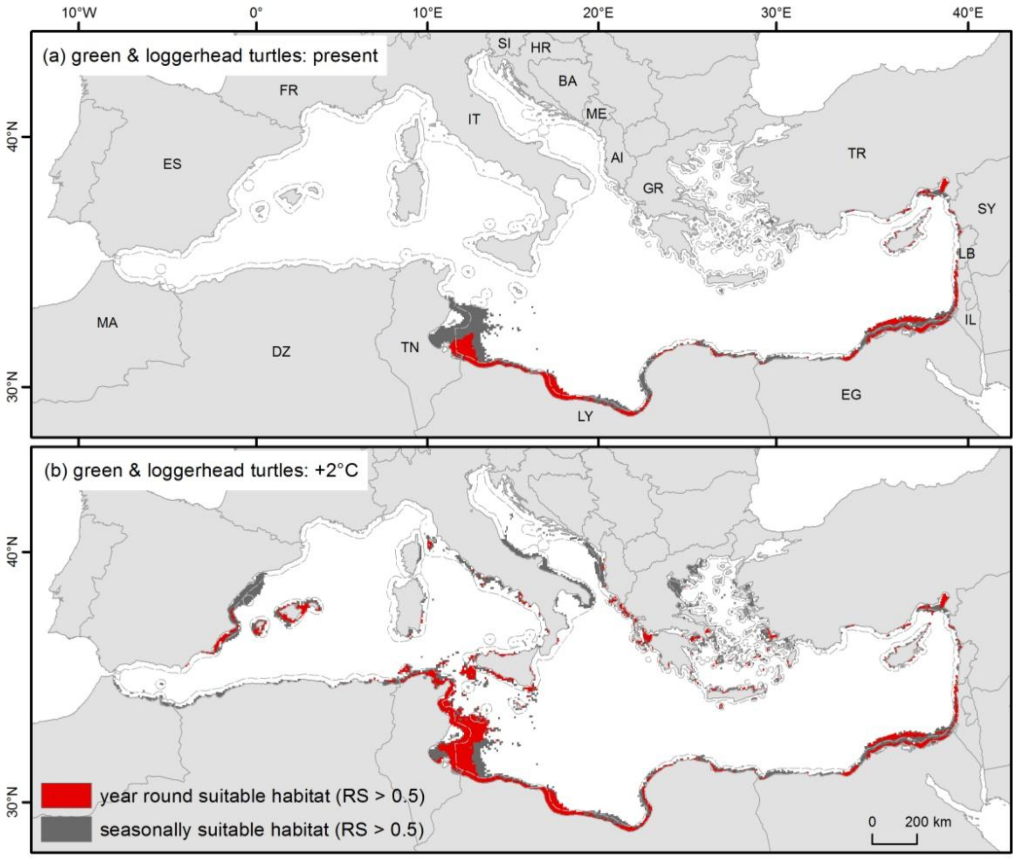

Figure 4. Combined foraging habitats (relative suitability ≥ 0.5) suitable for both species under: (a) present day and (b) forecast, environmental data. Year-round habitat (red polygons), seasonally dependent habitat (mid grey polygons). Countries are labelled in accordance with Figure 1, 12 nautical mile waters (broken line). Both parts drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

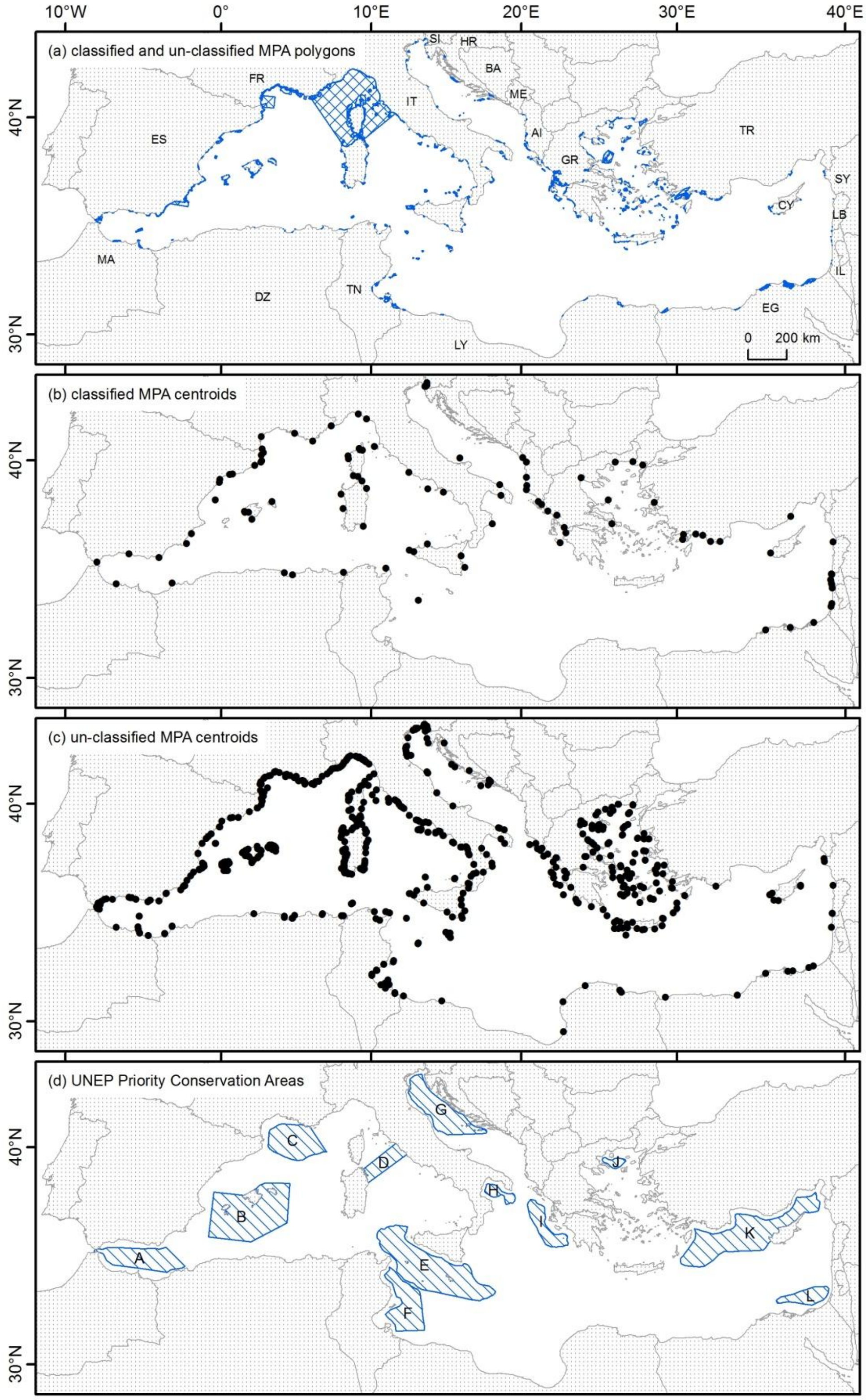

Figure 5. Marine Protected Areas (MPAs) within the Mediterranean. (a) Current IUCN classified and un-classified MPAs (blue cross-hatched polygons) (MAPAMED 2014). MPA centroids (black circles) for, (b) IUCN classified and (c)

un-classified MPAs. (d) United Nations Environment Programme (UNEP) Priority Conservation Areas (PCAs) (blue hatched polygons). A: Alborán Seamounts, B: Southern Balearic, C: Gulf of Lions shelf and slope, D: Central Tyrrhenian, E: Northern Strait of Sicily, F: Southern Strait of Sicily, G: Northern and Central Adriatic, H: Santa Maria di Leuca, I: North-eastern Ionian, J: Thracian Sea, K: North-eastern Levantine Sea and Rhodes Gyre, L: Nile Delta Region (UNEP 2010). In part (a) countries are labelled in accordance with Figure 1. All parts are drawn to the same spatial scale. Maps drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Table S1. Summary of PTT data for foraging post-nesting female green turtles, detailing: PTT ID, nesting season, release location and date, days tracked, days at foraging site and PTT manufacturer and model. A foraging site was deemed to be an area where an individual turtle remained resident for more than 30 days (Blumenthal *et al.* 2006) and was less than 150 km in diameter. To minimise the potential for pseudo-replication within our data we limited the maximum number of days retained for analysis at any one foraging site to 365 d.

Id	PTT	Season	Release location	Release date	Days tracked	Days foraging	PTT make	Model
1	4148	1998	Cyprus	1998-08-01	288	282	Wildlife Computers	SDR-SSC3
2	4149		Cyprus	1998-07-29	222	199	Wildlife Computers	SDR-SSC3
3	4150		Cyprus	1998-07-27	295	269	Wildlife Computers	SDR-SSC3
4	6598	1999	Cyprus	1999-07-17	244	178	Telonics	ST-18
5	4405	2002	Cyprus	2002-07-27	404	121	Telonics	ST-6
6	36638	2003	Cyprus	2003-07-12	348	247	Sirtrack	KiwiSat 101
7	36639	2004	Cyprus	2004-06-24	385	284	Sirtrack	KiwiSat 101
8	49813		Cyprus	2004-07-23	312	236	Sirtrack	KiwiSat 101
9	49815		Cyprus	2004-07-09	60	55	Sirtrack	KiwiSat 101
10	49816		Cyprus	2004-07-22	359	328	Sirtrack	KiwiSat 101
11	49822		Yumurtalik, Turkey	2004-07-15	99	84	Sirtrack	KiwiSat 101
12	49823		Yumurtalik, Turkey	2004-07-18	113	101	Sirtrack	KiwiSat 101
13	49824		Yumurtalik, Turkey	2004-07-19	131	119	Sirtrack	KiwiSat 101
14	49825		Yumurtalik, Turkey	2004-07-21	53	38	Sirtrack	KiwiSat 101
15	93699	2009	Israel	2009-06-27	55	50	Sirtrack	KiwiSat 101
16	93702		Israel	2009-06-20	355	308	Sirtrack	KiwiSat 101
17	95097		Cyprus	2009-07-04	487	421	Sirtrack	KiwiSat 101
18	95098		Cyprus	2009-07-15	117	54	Sirtrack	KiwiSat 101
19	95101		Cyprus	2009-07-05	716	673	Sirtrack	KiwiSat 101
20	95102		Cyprus	2009-07-24	111	93	Sirtrack	KiwiSat 101
21	52820	2010	Cyprus	2010-06-16	752	693	Sirtrack	KiwiSat 101
22	52949		Cyprus	2010-07-07	479	445	Sirtrack	KiwiSat 101
23	86898		Cyprus	2010-06-26	476	280	Sirtrack	KiwiSat 101
24	86900		Cyprus	2010-07-13	413	410	Sirtrack	KiwiSat 101
25	52827		Cyprus	2010-07-01	408	225 | 101 *	Sirtrack	KiwiSat 101
26	52846		Cyprus	2010-06-28	349	53 | 99 *	Sirtrack	KiwiSat 101
27	52888		Cyprus	2010-07-21	123	42	Sirtrack	KiwiSat 101

* multiple foraging locations

Table S2. Summary of PTT data for foraging post-nesting female loggerhead turtles, detailing: PTT ID, nesting season, release location and date, days tracked, days at foraging site and PTT manufacturer and model. A foraging site was deemed to be an area where an individual turtle remained resident for more than 30 days (Blumenthal *et al.* 2006) and was less than 150 km in diameter. To minimise the potential for pseudo-replication within our data we limited the maximum number of days retained for analysis at any one foraging site to 365 d.

Id	PTT	Season	Release location	Release date	Days tracked	Days foraging	PTT make	Model
1	29359	2001	Cyprus	2001-06-13	59	38	Telonics	ST-14
2	4206	2002	Cyprus	2002-07-04	138	68	SMRU	SRDL
3	4242		Cyprus	2002-07-08	422	57 | 137 | 42 *	SMRU	SRDL
4	4406		Cyprus	2002-08-03	86	71	Telonics	ST-14
5	4407		Cyprus	2002-07-17	391	89	Telonics	ST-14
6	15340		Cyprus	2002-06-05	226	190	Telonics	ST-6
7	15414	2003	Cyprus	2002-07-04	375	348	Telonics	ST-6
8	29034		Cyprus	2003-07-21	627	611	Telonics	ST-18
9	29050		Cyprus	2003-06-14	1404	1402	Telonics	ST-18
10	49193a	2004	Zakynthos	2004-06-26	130	50	Sirtrack	KiwiSat 101
11	49194a		Zakynthos	2004-06-27	398	81	Sirtrack	KiwiSat 101
12	49195a		Zakynthos	2004-06-28	761	83	Sirtrack	KiwiSat 101
13	57389	2005	Cyprus	2005-07-01	137	83	Sirtrack	KiwiSat 101
14	49194b		Zakynthos	2005-08-10	118	79	Sirtrack	KiwiSat 101
15	49196a		Zakynthos	2005-06-16	189	30	Sirtrack	KiwiSat 101
16	49197		Zakynthos	2005-06-19	419	345 | 157 *	Sirtrack	KiwiSat 101
17	49198		Zakynthos	2005-06-21	392	43 | 49 *	Sirtrack	KiwiSat 101
18	53182	2006	Cyprus	2006-06-21	351	262	SMRU	SRDL
19	53184		Cyprus	2006-06-05	389	272	SMRU	SRDL
20	68561	2007	Cyprus	2007-06-20	166	102	SMRU	SRDL
21	72128		Dalyan, Turkey	2007-07-19	333	277	Sirtrack	KiwiSat 101
22	75969		Zakynthos	2007-07-22	143	51	Sirtrack	KiwiSat 101
23	75970		Zakynthos	2007-07-26	450	408	Sirtrack	KiwiSat 101
24	75971		Zakynthos	2007-07-27	671	571	Sirtrack	KiwiSat 101
25	75998		Zakynthos	2007-07-10	112	57	Telonics	A-2010
26	75999		Zakynthos	2007-07-13	428	390	Telonics	A-2010
27	76022		Zakynthos	2007-07-14	410	377	Telonics	A-2010
28	76024		Zakynthos	2007-07-12	384	328	Telonics	A-2010
29	76025		Zakynthos	2007-07-21	202	201	Telonics	A-2010
30	76026		Zakynthos	2007-07-11	323	279	Telonics	A-2010
31	76027		Zakynthos	2007-07-12	218	198	Telonics	A-2010
32	68557		Cyprus	2007-06-08	260	189	SMRU	SRDL
33	76023		Zakynthos	2007-07-18	416	375 | 46 *	Telonics	A-2010
34	77171	2008	Cyprus	2008-07-16	707	699	SMRU	SRDL
35	86392		Israel	2008-07-19	474	391	Sirtrack	KiwiSat 101
36	77172	2009	Cyprus	2009-07-02	267	244	SMRU	SRDL
37	86390		Israel	2009-05-28	628	527	Sirtrack	KiwiSat 101
38	86393		Israel	2009-02-22	180	159	Sirtrack	KiwiSat 101
39	93698		Israel	2009-07-08	328	316	Sirtrack	KiwiSat 101
40	93700		Israel	2009-07-05	179	95	Sirtrack	KiwiSat 101
41	86391	2010	Israel	2010-06-23	427	393	Sirtrack	KiwiSat 101
42	52813	2011	Cyprus	2011-06-17	836	806	Sirtrack	K2G
43	52816		Cyprus	2011-06-23	403	382	NA	NA
44	52819		Cyprus	2011-06-05	440	370	Sirtrack	K2G
45	43755	2012	Cyprus	2012-06-05	174	99	Sirtrack	F4
46	52815		Cyprus	2012-06-01	334	245	Sirtrack	K2G
47	52817		Cyprus	2012-06-01	219	180	Sirtrack	K2G
48	118184		Cyprus	2012-06-01	212	72	Wildlife Computers	SPOT
49	118185		Cyprus	2012-05-31	499	406	Wildlife Computers	SPOT

* multiple foraging locations

NA: data not available

Table S3. Ecological Niche Modelling evaluation metrics for 10-fold cross validation (mean and 1SD). Algorithm abbreviations: Generalised Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MaxEnt). Key algorithm modelling parameters and evaluation metric descriptions are detailed at the foot of the table.

Model	**Evaluation metric**	**Modelling algorithm**				
		GLM	**MARS**	**MaxEnt**	**mean**	**sd**
Greens: winter - spring	AUC	0.994	0.996	0.998	0.996	0.001
	KAPPA	0.980	0.983	0.982	0.982	0.002
	TSS	0.980	0.983	0.982	0.982	0.002
	SR	0.988	0.995	0.999	0.994	0.002
	ACCURACY	0.990	0.991	0.991	0.991	0.001
Greens: summer - autumn	AUC	0.993	0.995	0.998	0.995	0.003
	KAPPA	0.978	0.971	0.970	0.973	0.003
	TSS	0.978	0.971	0.970	0.973	0.003
	SR	0.990	0.994	0.999	0.995	0.004
	ACCURACY	0.989	0.986	0.985	0.986	0.002
Loggerheads: winter - spring	AUC	0.956	0.969	0.969	0.965	0.008
	KAPPA	0.842	0.873	0.863	0.859	0.015
	TSS	0.835	0.866	0.862	0.854	0.017
	SR	0.969	0.985	0.995	0.983	0.013
	ACCURACY	0.925	0.939	0.935	0.933	0.007
Loggerheads: summer - autumn	AUC	0.962	0.968	0.970	0.967	0.004
	KAPPA	0.854	0.878	0.865	0.865	0.012
	TSS	0.848	0.859	0.849	0.852	0.006
	SR	0.985	0.996	0.998	0.993	0.007
	ACCURACY	0.945	0.953	0.949	0.949	0.004

Biomod2 modelling parameters

Randomly generated 'pseudo absence' locations (background data), with no minimum or maximum distance to presence locations were generated for each habitat model. All locations that had missing coincident environmental data were removed from the analysis (background data locations that were spatially referenced on land).

The key algorithm modelling parameters in biomod2 were as follows:

GLM: package = 'stats', family= 'binomial'.

MARS: package = 'mda', maximum interaction degree = 2, penalty (cost per degree of freedom) = 2, thresh (forward stepwise stopping threshold) = 0.001, prune = (TRUE).
MaxEnt: Run within biomod2, maximum iterations (for training) = 200, linear/quadratic/product/threshold/ hinge features (the transformation coefficients applied to each environmental variable), default prevalence = 0.5.

Evaluation metrics
AUC (Area under the curve): a measure of the ratio of true positives out of the positives vs. the ratio of false positives out of the negatives.
KAPPA (Cohen's Kappa, Heidke skill score) and TSS (True Skill Statistic): measures of accuracy relative to that of random chance.
SR (Success Ratio): the fraction of the true positives that were correct.
Accuracy (fraction correct): the fraction of the predictions (true and false) that were correct.

To compute the threshold value used to transform the probability of presence model output data to binary data for model evaluation metrics based on the comparison of binary data (*e.g.* True Skill Statistic (TSS)), the algorithm calculates the evaluation metric in question (*e.g.* TSS) for a sequence of thresholds from 0 to 1 (100 values). The value that maximises this evaluation metric is then selected as the threshold value used. (Thuiller *et al.* 2009).

Table S4. Ecological Niche Modelling variable importance for 10-fold cross validation.

Model	**Modelling algorithm**	**Environmental variable**					
		Depth	**Euphotic depth**	**NPP**	**SST thermal niche**	**Slope**	**SST frontal activity**
Greens: winter - spring	**GLM**	0.48	0.06	0.05	0.32	0.04	0.04
	MARS	0.58	0.03	0.03	0.34	0.01	0.00
	MAXENT	0.60	0.00	0.00	0.37	0.00	0.01
	mean	0.55	0.03	0.03	0.35	0.02	0.02
	sd	0.06	0.03	0.02	0.03	0.02	0.02
Greens: summer - autumn	**GLM**	0.34	0.07	0.02	0.51	0.03	0.05
	MARS	0.52	0.00	0.00	0.43	0.02	0.02
	MAXENT	0.44	0.00	0.01	0.54	0.01	0.00
	mean	0.43	0.02	0.01	0.49	0.02	0.02
	sd	0.09	0.04	0.01	0.05	0.01	0.02
Loggerheads: winter - spring	**GLM**	0.84	0.02	0.06	0.00	0.07	0.01
	MARS	0.78	0.06	0.10	0.00	0.06	0.00
	MAXENT	0.90	0.03	0.05	0.00	0.02	0.00
	mean	0.84	0.04	0.07	0.00	0.05	0.00
	sd	0.06	0.02	0.03	0.00	0.03	0.00
Loggerheads: summer - autumn	**GLM**	0.67	0.07	0.06	0.16	0.04	0.00
	MARS	0.69	0.04	0.06	0.17	0.04	0.01
	MAXENT	0.80	0.00	0.01	0.17	0.02	0.00
	mean	0.72	0.04	0.04	0.17	0.03	0.00
	sd	0.07	0.03	0.03	0.01	0.01	0.00

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. This was repeated for each environmental variable. The calculation of the relative importance was made by subtracting these mean correlation coefficients from 1 (Thuiller *et al.* 2009).

Table S5. Loggerhead turtle foraging sites and foraging records apportioned by sex (Schofield *et al.* 2013) coincident with Loggerhead EENM based on present day environmental variables.

	Foraging sites	**Foraging records**		
		M	**F**	**Combined**
Total (*n*)	32	37	88	125
Within EENM (*n*)	26	33	81	114
Within EENM (%)	81	89	92	91

Table S6. Summary of IUCN protected area definition and management categories.IUCN defines a protected area as: A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values. The definition is expanded by six management categories (one with a sub-division), summarised below.

IUCN category	**Definition**
Ia Strict nature reserve	Strictly protected for biodiversity and also possibly geological/ geomorphological features, where human visitation, use and impacts are controlled and limited to ensure protection of the conservation values.
Ib Wilderness area	Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, protected and managed to preserve their natural condition.
II National park	Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities.
III Natural monument or feature	Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove.
IV Habitat/species management area	Areas to protect particular species or habitats, where management reflects this priority. Many will need regular, active interventions to meet the needs of particular species or habitats, but this is not a requirement of the category
V Protected landscape or seascape	Where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values
VI Protected areas with sustainable use of natural resources	Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management and where low-level non-industrial natural resource use compatible with nature conservation is seen as one of the main aims.
The category should be based around the primary management objective(s), which should apply to at least three-quarters of the protected area – the 75 per cent rule.	

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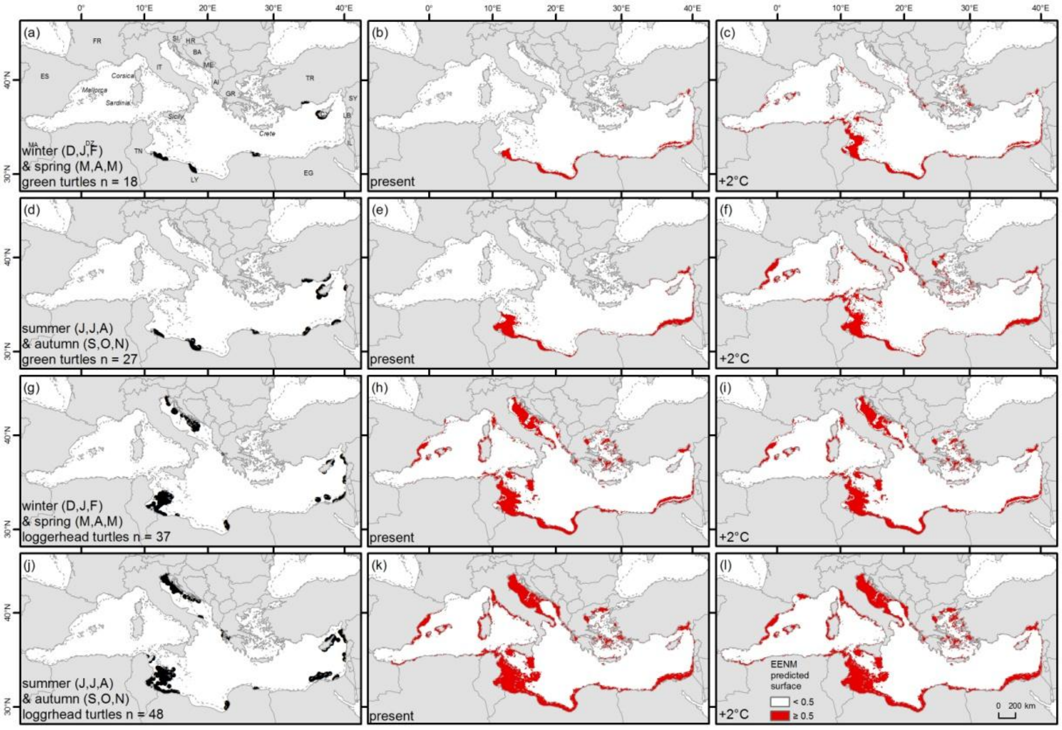

Figure S1. Seasonal Ensemble Ecological Niche Models (EENMs) for post-nesting green and loggerhead turtles run with best daily location data, and with the environmental surfaces of depth, slope, euphotic depth, Sea Surface Temperature (SST) thermal niche, net primary productivity (NPP), and SST frontal activity using long-term biannual seasonally aggregated products. Seasonal figure parts: (a,b,c,g,h,i) winter/spring, (d,e,f,j,k,l) summer/autumn. (a,d,g,j) Location data. EENMs run with, (b,e,h,k) present day environmental data, and (c,f,i,l) forecast models with an increase of 2º C to species-specific biannual SST thermal niche surfaces in accordance with Coupled Model 5 (Intercomparison Project Phase CMIP5) Representative Concentration Pathway (RCP) scenario RCP 8.5 (IPCC 2013). The relative suitability of habitats are scaled between 0 and 1 (where 0 represents lowest suitability and 1 highest suitability). Habitats with relative suitability ≥ 0.5 are drawn as red polygons. In part (a) countries and islands are labelled in accordance with Figure 1, 200 m isobath drawn (broken line). All parts are drawn to the same spatial scale. Map drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

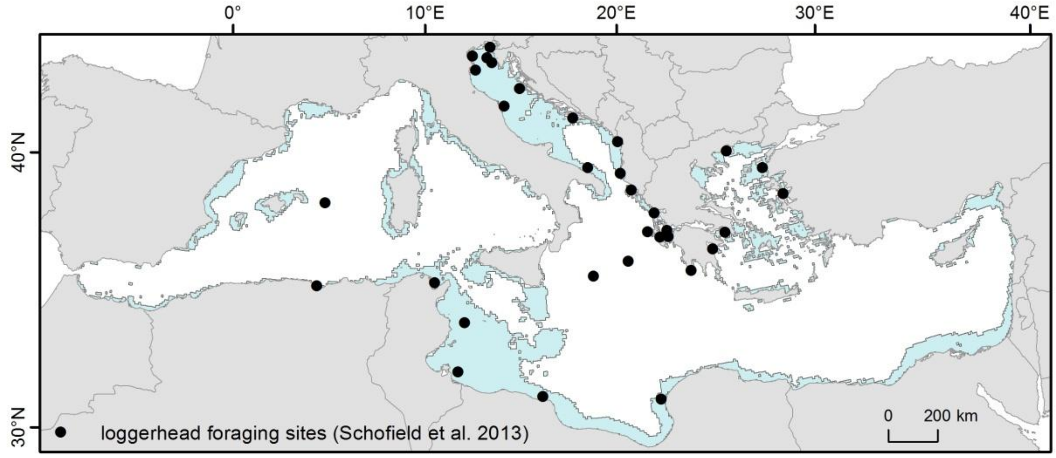

Figure S2. Discrete loggerhead foraging sites digitised from Schofield *et al.* (2013) (black circles) with present day loggerhead EENM (light blue polygons). Map drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

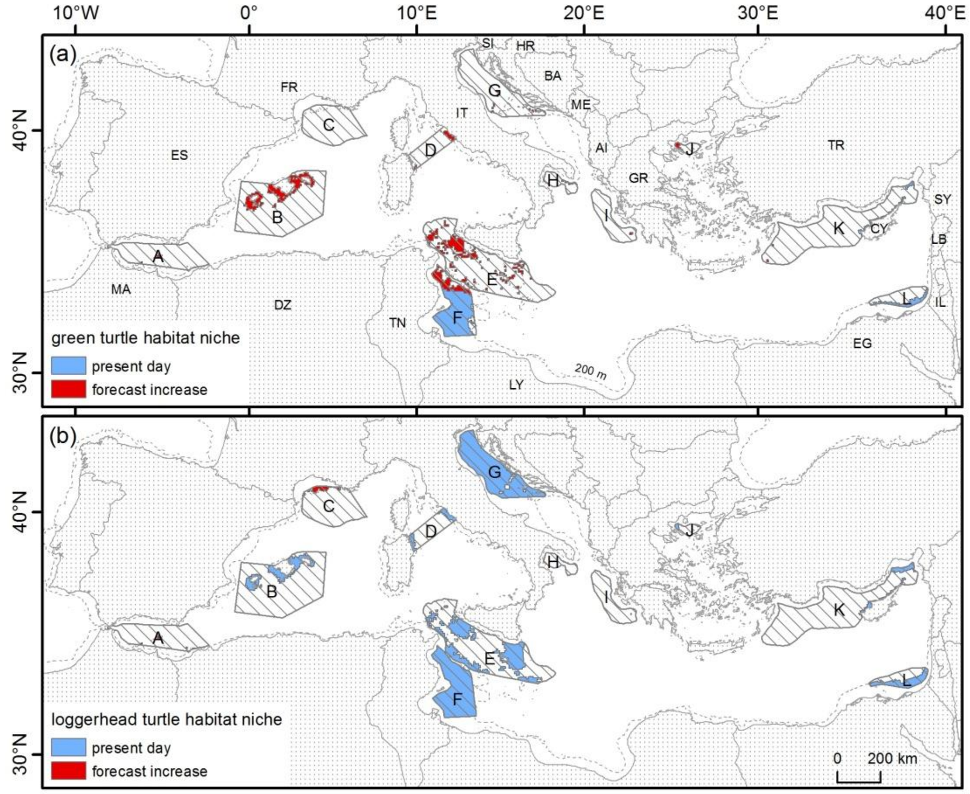

Figure S3. Spatial coincidence of modelled green and loggerhead turtle habitat niche (based on present day and forecast environmental data) with United Nations Environment Programme (UNEP) Priority Conservation Areas (PCAs). Present day (blue), forecast model (red). Countries are labelled in accordance with Figure 1, UNEP PCAs are drawn and labelled in accordance with Figure 5d. 200 m isobath drawn and labelled. Map drawn to Projected Coordinate System: Europe Albers Equal Area Conic.

Chapter IV: Here today, here tomorrow: beached timber in Gabon, a persistent threat to nesting sea turtles

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Published in Biological Conservation (2013) Volume 162: 127-132

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ABSTRACT

The African country of Gabon has seen decadal increases in commercial logging. An unforeseen consequence of this has been that many coastal areas, including several National Parks and Reserves, have suffered severe pollution from beached timber. This has the potential to adversely affect nesting sea turtles, particularly the leatherback turtle (*Dermochelys coriacea*) for which Gabon constitutes the world's largest rookery. In this study, we analyse aerial survey data (2003, 2007 and 2011) to determine the temporal persistence and spatial extent of beached timber, and by integrating spatial data on nesting, ascertain regions where beached timber poses the greatest threat to nesting leatherback turtles. There was no marked difference in the number of beached logs recorded across the study area during the period, with 15 160, 13 528 and 17 262 logs recorded in the three years, respectively. There was, however, a significant difference in abundance of beached logs among geographical areas. Analysis highlighted two coastal areas where nesting leatherback turtles were likely to be at greatest risk from beached timber. At one such site, Kingere, within Pongara National Park, where both logs and turtle densities are high, monitoring in 2006/07 and 2007/08 suggested that between 1.6% and 4.4% of leatherback turtles could be entrapped at this site. Given the dynamic nature of Gabon's coastal environment, and the potential limitations of aerial surveys, densities of beached timber could be greater than this analysis reveals. We also propose, that despite recent export restrictions of whole logs, their environmental persistence potentially represents a long term problem.

Keywords: aerial survey, beach, logs, leatherback turtle, threat, timber

INTRODUCTION

Industrial logging in Central Africa has shown decadal increases and now contributes to a large proportion of land use in the region (Laporte *et al.* 2007). Historically, Gabon was able to resist such commercial pressure due to its natural oil and mineral reserves, but recently, pressure to expand commercial logging activities has increased (Laurance *et al.* 2006). Export revenue from timber and associated products contributed an average of 6.5% to Gabon's Gross Domestic Product (GDP) from 1995 to 2010 (World Bank 2011). The commercial value of all exported timber products more than tripled in the decade up to 2008, although the exported cubic volume remained consistent since the peak export years of 1997 and 2000 (ITTO 2010a). The fast-growing hardwood, okoumé (*Aucoumea klaineana*) is a key forest species in Gabon (Medzegue *et al.* 2007), and is the principal species associated with the export market (Collomb *et al.* 2000).

Traditionally, as part of the commercial export process, roundwood (whole logs) were transported by barge, or as rafts of timber, downriver towards the coast; Gabon's river systems have been associated with the transportation of cut timber since the onset of commercial logging at the beginning of the 20th century (Gray and Ngolet 1999). However, logs that broke free during transport, were carried to coastal waters and some became beached, forming large aggregations in several areas (Laurance *et al.* 2008). In a move towards sustainable forest management policies and steps to diversify the economy of Gabon, the export of roundwood was formally banned in May 2010 (ITTO 2010b) thereby promoting the processing of timber beyond sawn lumber and veneers towards finished products.

In 2002, a system of National Parks was created with the aim of protecting key areas of Gabon's biodiversity-rich coastal and terrestrial habitats (Figure 1). In total, 13 National Parks encompassing more than 25 000 km^2 or 10% of its territory were designated. These protected coastal zones, together with many other beaches of Gabon, represent some of the world's most important nesting sites for sea turtles. These include the globally important breeding aggregation for the leatherback turtle (*Dermochelys coriacea*), with the northern and southern extremes of the Gabonese coast (Pongara and Mayumba National Park) receiving the highest densities of nesting activity (Witt *et al.* 2009): 23 and 33 percent respectively of all nesting activity (this study: 2003 aerial survey data), as well as olive ridley (*Lepidochelys olivacea*) and green sea turtles (*Chelonia mydas*) (Fossette *et al.* 2008; Maxwell *et al.* 2011).

Beached logs represent a threat to nesting sea turtles through obstruction, entrapment and disorientation (Laurance *et al.* 2008; Bourgeois *et al.* 2009). An initial assessment of the threats posed to Gabon's nesting sea turtles by beached timber was made by Laurance et al (2008) using a single year's aerial survey data (January 2003), together with ground surveys of a 4.2 km section of Pongara National Park (March 2005). This analysis suggested that beached log densities were highest in the vicinity of Pongara and Mayumba National Parks and that 8 - 14% of all nesting attempts (97.6% involving leatherback turtles) at Pongara Natonal Park were negatively affected.

Our study builds upon this initial assessment with rigorous and comprehensive statistical analyses of multiple year aerial survey data over a nine year period (February 2003, 2007 and 2011). We couple this analysis with ground surveys (38 km) of leatherback/log interaction impact assessments from three disparate coastal regions over two nesting seasons. In addition, we formulate a threat index for interaction between nesting leatherbacks and beached timber for the majority of the Gabonese coast.

We demonstrate that the temporal and spatial extent of beached timber, and therefore the threat from beached timber to leatherback turtles, alluded to by Laurance et al. (2008), is persistent and has the potential to remain so, until remedial action to remove beached timber is taken. We concur with the initial findings of Laurance et al. (2008) regarding impacts to leatherback turtles at Pongara National Park, but also demonstrate that this threat is a national issue within both protected and unprotected areas.

METHODS

Aerial surveys and data management

Aerial surveys were flown along the Gabonese coast using a variety of high wing light aircraft on 12th February 2003, 23rd / 24th February 2007 and 23rd / 24th February 2011; these surveys were timed to coincide with leatherback turtle nesting activities (Witt *et al.* 2009). To quantify the potential for discrepancies between counts derived from aerial survey analysis and ground counts, a further limited aerial survey was flown on 30th January 2012 that was spatially concordant with a ground-based validation survey. The aircraft were flown at an approximate groundspeed of 180 to 190 km hr^{-1} at an altitude of 50 to 60 m, with the aircraft positioned 100 to 200 m offshore. Surveys were flown in a southeast direction from northern to southern Gabon, parallel to the coastline. The start location for all surveys was Pointe Pongara, south of the capital, Libreville (Figure 1). The survey end location in 2003 was 42 km northwest of the southern limit of Mayumba National Park's border with the Republic of Congo. Aerial survey end locations for 2007 and 2011 were further to the southeast near the Gabon-Congo border. A 50 km section of coast to the east of Cap Lopez, Port Gentil was excluded from all surveys as this area consisted of mangroves and mudflats that would not support nesting leatherback turtles (Figure 1).

Continuous video footage was captured using an analogue video camera recording to tape in 2003 and 2007 (subsequently digitised to .avi format) and in High Definition (HD) using a digital video camera in 2011 and 2012 (.m2ts format). A hand held Global Positioning System (GPS) receiver (Garmin GPS60) was used to record waypoints of the aerial survey comprising longitude, latitude, altitude, date/time, distance from start and speed. Differences occurred in total distances flown between survey years; these small differences arose due to discrepancies in aircraft flight path or where the video recording was stopped to change tape (2003 and 2007) or memory card (2011) or if surveys occurred across two days (2007 and 2011). Date and time stamps were burnt to the recorded video footage, this was then viewed at half frame speed, or where log densities required, with the frame paused. All logs that lay on the shore between the surf-zone/foreshore interface and back-shore/coastal vegetative terrain were counted. Logs that lay further inland were deemed to be outside of the area of extreme storm activity and therefore, as they had little potential to be re-mobilised into the marine/beach environment, were not included in the count. The method for counting leatherback turtle nests from aerial surveys is fully described in Witt *et al.* (2009).

Log counts and leatherback turtle nesting counts were imported into the Geographical Information System (GIS) ArcView 9.2 (ESRI, Redlands, USA http://www.esri.com). This was used to generate distribution maps and to identify protected and unclassified land areas, as well as to perform spatial analysis. GPS waypoint data were used to partition the flown survey route into sections, or data bins, for analytical purposes. Mean data bin length varied slightly among survey years; 2003: 617 m (standard deviation (SD) 46 m), 2007: 516 m (SD 15 m) and 2011: 525 m (SD 16 m). Therefore, direct comparisons between years using log counts per data bin were not conducted.

To facilitate statistical analysis, the 2007 and 2011 surveys were clipped to the same spatial extent of the 2003 survey. To standardise data to a common spatial resolution we created a raster of discrete 25 km^2 coastal polygons that encompassed the spatial extent of the 2003 aerial survey path. The aerial survey raw data bins for 2003, 2007 and 2011 surveys were then aggregated into the raster squares to which they were spatially coincident. Log densities km^{-1}, and leatherback turtle nest densities km^{-1}, for each 25 km^2 were then calculated.

A threat index ((logs km^{-1} * nests km $^{-1}$) / Σ (logs km^{-1} * nests km $^{-1}$)) was formulated from the 2003 raw bin count data to represent the potential for interaction between nesting leatherback turtles and beached logs. To identify coastal areas with the highest threat indices we calculated relative estimates of density using a kernel smoothing approach (Worton 1989; Laver & Kelly 2008). This provides an estimate of the probability density function for a spatially referenced variable using a defined smoothing parameter and optional weighting to the variable. So as not to over-smooth the resulting kernel a smoothing parameter of 5 km was chosen.

All statistical analysis was undertaken with R (R Development Core Team 2008). A Linear Mixed Effect (LME) model (R package: nlme (Pinheiro *et al.* 2012)) was used to investigate the relationships of year and classified/unclassified area on log densities. Results were validated using residuals vs. fitted values diagnostic plots.

Ground-based surveys

Ground-based log surveys were conducted for a 9 km section of Pongara National Park on 18th / 19th September 2010 (N 0.306, E 9.301 to N 0.226, E 9.314; all coordinates given as decimal degrees according to WGS 1984), on 13th / 14th July 2011 (N 0.306, E 9.302 to N 0.223, E 9.313) and on 9th February 2012 (N 0.294, E 9.304 to N 0.228, E 9.313); the latter being carried out within ten days of an aerial survey. For 2012, all logs that lay on the shore between the surf-zone/foreshore interface and back-shore/coastal vegetative terrain within this 9 km section were counted. For 2010 and 2011, the lengths and diameters of all beached logs within the first 2 km of this section were recorded. Where measurement of length was not possible due to the log, or portion of the log, being embedded in the sand, the log was recorded as ‘buried’.

Daily counts of leatherback turtle tracks were made during the early morning by beach patrols at three coastal regions during the nesting seasons 2006/07 to 2010/11. Counts were made at Pongara National Park (N 0.352, E 9.355 to N 0.221, E 9.313) (19 km), Sette Cama Reserve, (S 2.798, E 10.027 to S 2.825, E 10.065) (5 km), and Mayumba National Park (S 3.729, E 10.975 to S 3.782, E 11.017) (7 km) and (S 3.908, E 11.080 to S 3.863, E 11.028) (7 km). All encountered tracks were assessed for whether they had been impacted by logs, each track being categorised: 0) no impact, 1) nesting was definitely abandoned due to logs, 2) nesting was probably abandoned due to logs, 3) the turtle was blocked by logs but was able to nest above the High Tide Line (HTL), 4) the turtle was blocked by logs but was able to nest below the HTL, 5) the turtle was blocked by logs after nesting, whilst returning to sea. Additional monitoring of turtle entrapment was undertaken in the 2006/07 and 2007/08 season at Kingere, (S 0.298 E 9.303 to S 0.221 E 9.313) (a 7 km section of Pongara National Park).

RESULTS

Spatial density patterns and threat index

In total, 15 160, 13 528 and 17 262 logs were recorded in 2003, 2007 and 2011, respectively, along the ca. 550 km coastline (Supplementary Material, Table S1). Log densities were greatest in the north and towards the south of the Gabonese coastline; areas both associated with river estuaries (Figure 1). Within protected areas, Pongara National Park had the highest recorded number of logs km^{-1} for all years; whereas, Mayumba National Park had the lowest (Supplementary Material, Table S1).

Spatial mapping of standardised log densities (logs km^{-1} / 25 km^2) showed that across all survey years, there was a consistently high density of beached logs within Pongara National Park and unclassified area 1 (Figures 2, 3). Log densities for Wonga Wongue Reserve and for unclassified area 2 were greater to the north of these areas (Figure 2). Log densities for the Gamba Complex of reserves (including Loango National Park, Sette Cama Reserve and Ouanga Reserve) were greater in the centre and to the south of this complex (Figure 2). Mayumba National Park demonstrated a consistently low density of beached logs (Figure 2). Standardised log densities were not influenced by the main effect of year ($Chi^2_1 = 0.40$, $p = 0.53$) or by any relationship with survey year and area ($Chi^2_8 = 5.38$, $p = 0.72$). There was, however, a significant difference in the density of beached logs recorded among areas ($Chi^2_8 = 77.56$, $p < 0.001$) (Figure 3).

Mapping of leatherback turtle nest densities indicated that Mayumba National Park, the northern end of unclassified area 1 and Pongara National Park had the highest densities of leatherback turtle nests (Figure 2) with 33, 24 and 23 percent of all leatherback nesting activity occurring in these areas respectively.

Risk mapping, however, identified the 75% volume contour of the kernelled density distribution of the threat index as including: 22 km of Pongara National Park, 16 km of unclassified area 1, and 21 km (non-contiguous) of Sette Cama Reserve (Figure 4).

Ground-based surveys

Within the ground surveyed section of Pongara National Park, a total of 1561 (212 logs km^{-1}) were recorded for 2012. This compared with 1254 logs (170 logs km^{-1}) for the 2012 aerial survey analysis, with the aerial survey being specifically undertaken temporally close to the ground survey; this represents an aerial survey undercount of 20%.

Within a 2 km sub-section, for 2010, mean log length was 9.31 m (SD 2.32) with a mean diameter of 0.73 m (SD 0.25); 219 logs (68.7%) out of a total of 319 could not be measured and were classified as buried. In 2011, for the same 2 km sub-section, mean log length was 8.52 m (SD 3.02) with a mean diameter of 0.66 m (SD 0.20); 210 logs (57.2%) out of a total of 367 could not be measured and were classified as buried.

Daily counts of leatherback turtle activities and impacts to nesting associated with beached logs indicated that, on average, across 2006/07 to 2010/11 nesting seasons, 17% (Pongara National Park), 6% (Sette Cama Reserve) and < 1% (Mayumba National Park) of all recorded leatherback turtle beach movements were likely to have been impacted in some way by beached logs (Supplementary Material, Table S2). At Kingere, however, (a 7 km section of Pongara National Park), where there was a high density of logs and nests, the impact was greatest. In 2006/07, 22 females were discovered entrapped in logs (8 dead, 14 rescued). This number was lower in 2007/08 (2 dead, 2 rescued) but nesting was at a lower level in the latter season. A total of 3043 and 1506 leatherback turtle tracks were counted at Kingere in 2006/07 and 2007/08 respectively, likely resulting in 3013 and 1491 clutches, respectively (Witt et al 2009). If we assume all females lay approx. 6 clutches (Miller 1997) then we can estimate that mortality, without intervention, at this site would have been 4.4% of all nesting females in 2006/07 and 1.6% in 2007/08.

DISCUSSION

River transportation and storage of timber represents an inexpensive logistic solution for the industry (Sedell *et al.* 1991), however, this practise may bring changes to channel structure and other allied habitat degradation. The impacts to marine and coastal habitats from beached timber related with this practise are understudied. Gabon's river systems have been associated with the transportation of harvested timber for over a century, and therefore the coastline of Gabon, its species and habitats, have had the potential to have been be impacted by beached timber for a considerable time.

Analysis of aerial survey data obtained from the Gabonese coast indicated that there has been no significant change in the relative density of beached logs amongst 2003, 2007 and 2011. With a ban on the export of roundwood in May 2010 (ITTO 2010b) it would be reasonable to expect the fresh input of whole logs to the marine environment to have largely ceased. Timber experts have indicated that 35% of the logs examined in the 2 km ground survey area in Pongara National Park were still of exploitable quality in 2010, with an 11% reduction by 2011 (Cardiec unpublished data). Given the durability of this timber, this relatively consistent density of logs potentially represents a long term problem.

Spatial variation in the relative density of logs does exist among coastal areas. Log densities were highest in areas adjoining river estuaries. To the north of the country, the rivers of the Komo (the Gabon Estuary) and the Ogooué discharge to the coastal regions of Pongara National Park, Wonga Wongue Reserve, unclassified area 1 and the northern part of unclassified area 2. Likewise, to the south of the country, the Nyanga River discharges to the coastal regions of Sette Cama Reserve, Ouanga Reserve and the northern end of unclassified area 3. The Ogooué River is the principal river of Gabon and drains the vast majority of the country (McShane 1990) and for decades, has served as a significant internal transport link to the main Gabonese port of Port Gentil (Gray & Ngolet 1999). The increased spatial density of beached logs, associated with river mouths, is likely an artefact of the historic transportation practice related to the movement of felled timber, allied with the coastal morphology of these regions. Predominant wind direction is southerly (Peterson and Stramma, 1991) and both the Southern and Northern Equatorial Counter currents flow in an easterly direction. Mean tidal ranges are small (1.0 – 1.2 m) and the swell has a long period, generally from a south-westerly direction (Giresse 2010). These factors may singularly, or collectively, increase the likelihood for logs to remain *in situ* after becoming beached and limit their propensity for remobilisation.

The beaches of Gabon are subject to alteration by storm wave erosion and fine weather accretion; where remobilisation and transport of sand occurs, this is generally in a northerly direction (Giresse 2010). Ground-based surveys gave clear evidence of the effect of this accretion process on beached timber, with more than half of all logs surveyed unable to be measured. Aerial video footage also highlighted this accretion and erosion process; in some coastal sections, only small radial segments of log circumference would be visible, or if burial and erosion had occurred, part buried logs would protrude from the sand. This process of concealment and exposure could account, in part, for the fluctuation in the relative densities of logs within areas, between aerial surveys; although, the potential for some remobilisation and shift in log distribution should not be dismissed.

Leatherback turtle nesting densities were highest in Mayumba National Park, the northern end of unclassified area 1 and Pongara National Park. Areas identified as posing the highest threat to nesting leatherback turtles through beached logs were Pongara National Park, the 16 km northern end of unclassified area 1, and sections of Sette Cama Reserve. Of the three sites subject to long term monitoring, impacts of beached logs on leatherback turtle nesting were highest within Pongara National Park and Sette Cama Reserve. It is clear that there is the potential for increased mortality in high impact areas such as Kingere and possibly other areas not yet subject to ground survey. Logs have the potential for multiple impacts on marine turtles. Harder to quantify is the reduced nesting success as a result of a higher numbers of clutches being laid lower down the beach. Logs are also a problem for hatchlings when making their way to the sea, not only physically but also through blocking visibility of the sea and increasing predation and dehydration risk due to extended dispersal time on the beach. Buried logs have been seen to hinder females digging nest chambers, and the decomposition of logs may influence the chemical and biochemical composition of beaches thereby affecting incubation conditions. Finally, the presence of logs has the potential to affect erosion/accretion dynamics with unknown impacts.

As the method of data capture from the video footage requires the images to be interpreted by eye there is the potential for a degree of observer error. This interpretation can be hindered by variation in video quality, with loss of image definition and contrast. Image interpretation is also compromised by variation in aircraft height, look angle and camera zoom. The physical character of the logs, *i.e.* size, part buried or in stacks, and the beach environment *i.e.* shadows, flotsam or overhanging trees, can also contribute to the potential for undercounts of logs; particularly in areas of higher log densities. Underestimates of log density from aerial surveys, as compared to ground-based surveys, were highlighted by the 20% undercount between the two methods in 2012. Given this potential for aerial survey underestimation it must be considered that the assessment of threat from logs to nesting leatherback turtles may be conservative, particularly in areas of higher log densities. Similarly, there is no way to quantify the number of fully buried logs that may exist within the beach environment, or the threat that these may pose to nesting turtles. Notwithstanding these caveats, this analysis clearly demonstrates the advantage of using aerial surveys where large areas need to be surveyed over a limited time-frame.

Laurance *et al.* (2008) suggest that initiatives to remove timber from critical nesting beaches may be the most effective way to reduce impacts to sea turtles. However, this would require support from the Gabon government due to legal restrictions (Laurance *et al.* 2008). To have the greatest effect initiatives should be focussed on the areas of Pongara National Park, Sette Cama Reserve and unclassified area 1 where threat to nesting leatherback turtles is greatest. Due to the general inaccessibility of the coastline and scale of the problem, > 5900 logs lay along 43 km of the coastline within Pongara National Park and unclassified area 1 (this study: 2011 aerial survey data), removal may be difficult to achieve. However, this may be a solution in areas where immediate local access is available and log densities are modest *e.g.* Sette Cama Reserve and unclassified area 3. If commercially viable extraction using access from the sea were plausible, and limited in respect of its negative impacts to nesting beaches and turtles, this may prove a worthwhile consideration in higher impacted areas. Although costly, an alternative solution in high impact areas may be to dismember logs and remove sections to behind the beach to decay.

International awareness has increased over the direct and indirect, regional and global impacts of unsustainable harvesting of timber from tropical rainforests. Deforestation and its associated impacts to ecosystems are well documented; downstream effects on marine and coastal species and habitats are less so, but are clearly an unforeseen consequence of these terrestrial activities. The aggregation of many thousands of logs along the biodiversity-rich coastal habitats of the central African Atlantic coast attributable to rainforest logging has led to insidious implications for nesting sea turtles, particularly the leatherback turtle, for which the beaches of Gabon support globally important breeding aggregations.

ACKNOWLEDGEMENTS

This study was supported by the Darwin Initiative Marine Biodiversity Action Plan for Gabon, the Wildlife Conservation Society and by the Gabon Sea Turtle Partnership with funding from the Marine Turtle Conservation Fund (United States Fish and Wildlife Service, U.S. Department of the Interior). Additional support was provided by the Waitt Foundation through the Wildlife Conservation Society's Congo Basin Coast Program. We are sincerely grateful to the field teams and logistics staff who assisted in the aerial and ground surveys. The authors would like to acknowledge the constructive input of two anonymous referees and the editor.

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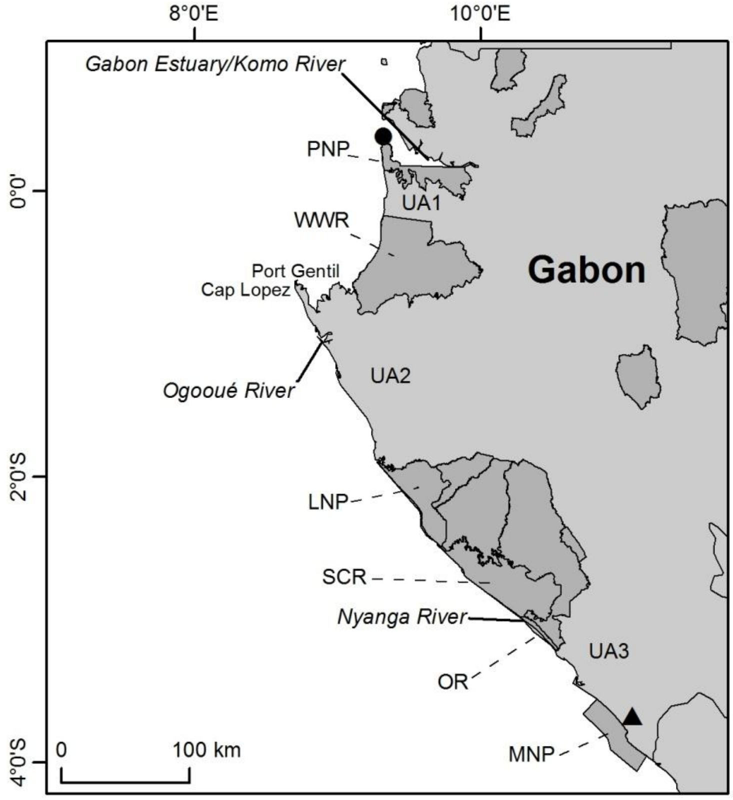

Figure 1. Gabon National Parks, Reserves and Rivers. National Parks and Reserves are shown in mid grey, unclassified areas in light grey; PNP: Pongara National Park, UA1: unclassified area 1, WWR: Wonga Wongue Reserve, UA2: unclassified area 2, LNP: Loango National Park, SCR: Sette Cama Reserve, OR: Ouanga Reserve, UA3: unclassified area 3, MNP: Mayumba National Park. The river mouths of the Komo, Ogooué and Nyanga are indicated by solid black lines and labelled in italics. The start and end locations for all surveys are shown as a filled circle and filled triangle respectively. Maps drawn to Geographic Coordinate System: WGS 1984.

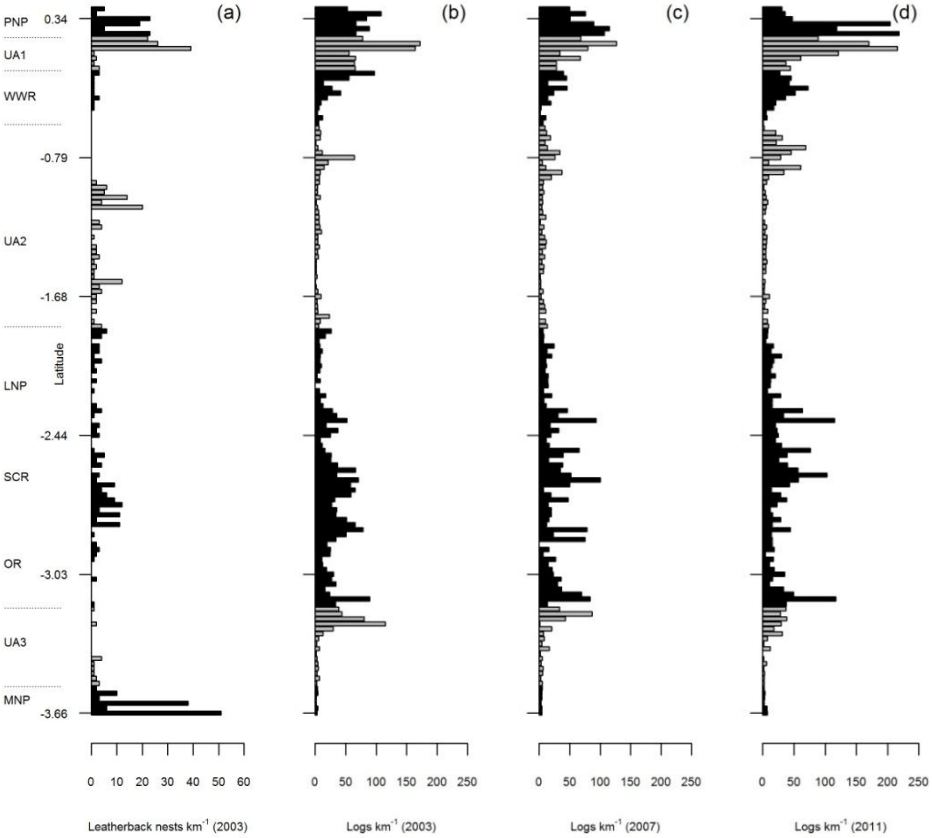

Figure 2. Spatial density patterns by latitude. (a) Leatherback turtle nests for 2003 (Witt *et al.* 2009). Beached logs km^{-1} for (b) 2003, (c) 2007 and (d) 2011. Data were standardised to a common spatial resolution of discrete 25 km^2 squares derived from the 2003 survey. National Parks and Reserves are shown as black bars and unclassified areas as mid grey bars. For abbreviations see Figure 1.

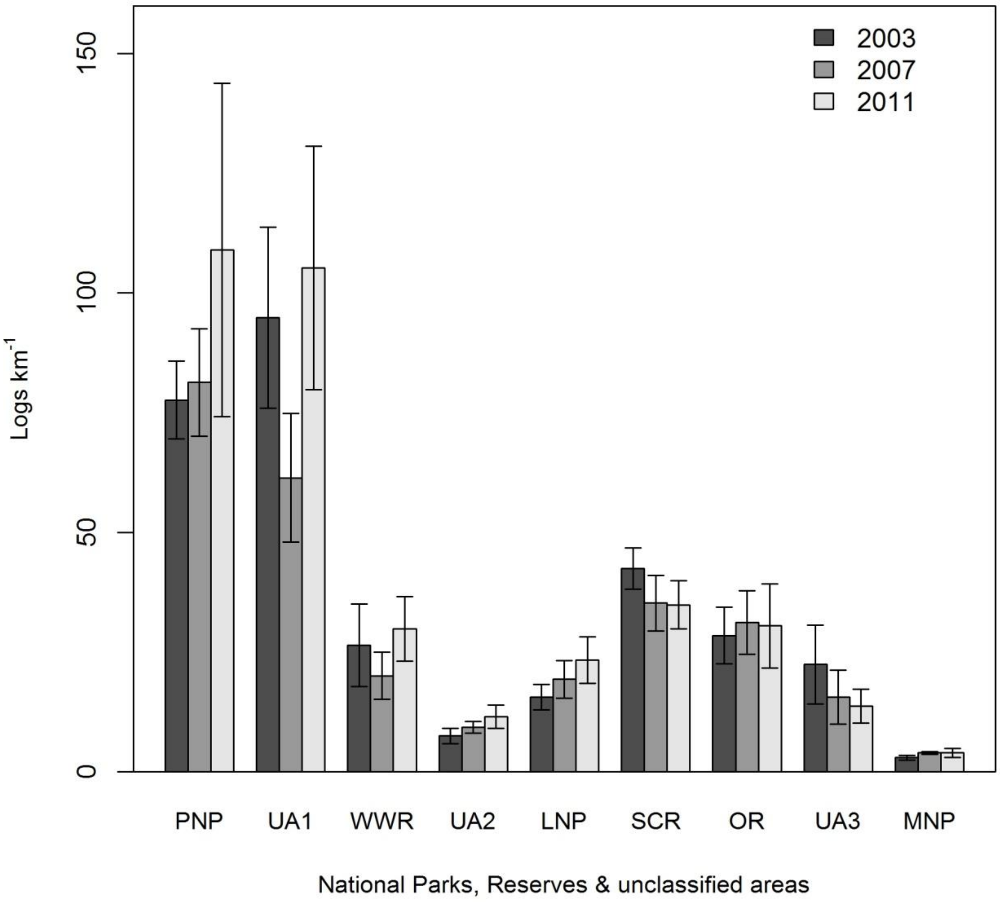

Figure 3. Mean logs km^{-1} (Mean ± SE) for 2003 (dark grey bars), 2007 (mid grey bars) and 2011 (light grey bars). A LME indicated that log densities were not influenced by the main effect of year (Chi$^2_1$ = 0.40, p = 0.53) or by any relationship with survey year and area (Chi$^2_8$ = 5.38, p = 0.72). There was a significant difference in the density of beached logs recorded among areas (Chi$^2_8$ = 77.56, p < 0.001). For abbreviations see Figure 1.

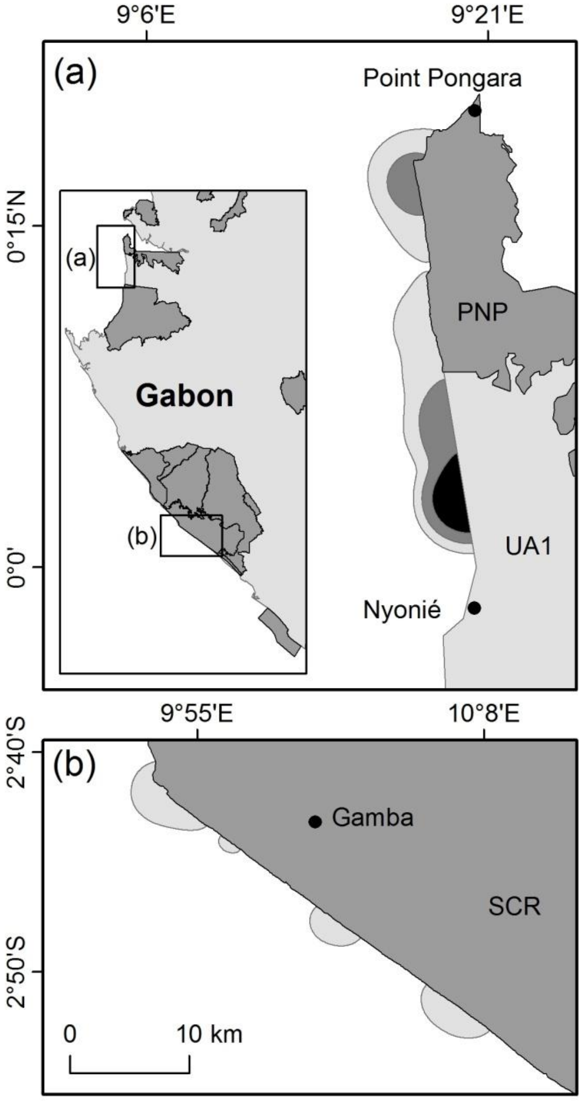

Figure 4. Threat maps for nesting leatherback turtles. Weighted kernelled distribution of threat indices with a 5 km smoothing factor for (a) Pongara National Park and unclassified area 1 and (b) Sette Cama Reserve. 25%, 50% and 75% polygons of the density distribution are shown with black, mid and light grey fill respectively. National Parks and Reserves are shown in mid grey and unclassified areas in light grey. Maps (a) and (b) are drawn to the same spatial scale and are located according to the inset of part (a). Maps drawn to Geographic Coordinate System: WGS 1984.

Table S1. Total log counts, distance flown and number of logs km^{-1} for the survey years 2003, 2007 and 2011 assigned to their respective classified or unclassified status.

	Survey Year: 2003			**Survey Year: 2007**			**Survey Year: 2011**		
	log count	**distance (km)**	**mean logs km^{-1}**	**log count**	**distance (km)**	**mean logs km^{-1}**	**log count**	**distance (km)**	**mean logs km^{-1}**
Pongara National Park	2061	26	79	2245	26	85	3062	25	121
Unclassified area 1	3492	36	97	2191	36	61	3858	37	104
Wonga Wongue Reserve	1274	48	26	1031	50	21	1524	42	36
Unclassified area 2	1257	163	8	1683	162	10	2136	152	14
Loango National Park	1247	83	15	1391	84	17	1679	83	20
Sette Cama Reserve	3252	80	40	2567	77	33	2720	79	34
Ouanga Reserve	1258	42	30	1433	42	34	1434	42	34
Unclassified area 3	1257	55	23	905	56	16	776	55	14
Mayumba National Park	62	20	3	82	23	4	73	23	3
Entire coast	15 160	554	27	13 528	555	24	17 262	539	32

Table S2. Mean proportion (percentage, standardised for survey effort) of leatherback turtle beach movements impeded by logs, at sites for the nesting seasons 2006/07 to 2010/11 within Pongara National Park, Sette Cama Reserve and Mayumba National Park. Impacts to leatherback turtles were assessed using the following criteria: (0) no impact, (1) nesting was definitely abandoned due to logs, (2) nesting was probably abandoned due to logs, (3) the turtle was blocked by logs but was able to nest above the High Tide Line (HTL), (4) the turtle was blocked by logs but was able to nest below the HTL, (5) the turtle was blocked by logs after nesting, whilst returning to sea.

Park / Reserve	**Category**	**Mean proportion as % of all categories**	**Range**
Pongara National Park	1	1.6	0.4-2.5
	2	0.5	0.1-1.2
	3	9.5	4.1-17.0
	4	2.9	1.7-3.5
	5	2.7	1.6-4.0
	total 1-5	17.2	
Sette Cama Reserve	1	0.5	0.0-0.9
	2	0.6	0.0-1.2
	3	3.6	0.0-7.2
	4	0.2	0.0-0.3
	5	1.3	0.0-2.6
	total 1-5	6.2	
Mayumba National Park	1	< 0.1	0.0-0.1
	2	< 0.1	0.0-0.1
	3	0.2	0.0-0.4
	4	< 0.1	0.0-0.1
	5	0.1	0.0-0.2
	total 1-5	0.3	

Chapter V: A novel approach to estimate the distribution, density and at-sea risks of a centrally-placed mobile marine vertebrate

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ABSTRACT

Formulating management strategies for mobile marine species is challenging, as knowledge is required of distribution, density, and threats. As a step towards assimilating knowledge, ecological niche models may identify likely suitable habitats for species, but lack the ability to enumerate species densities. Traditionally, this has been catered for by sightings based distance sampling methods which may have practical and logistical limitations. Here we describe a novel method to estimate at-sea distribution and densities of a centrally-placed marine vertebrate (leatherback turtles: Gabon), using historic aerial surveys of nesting beaches and satellite telemetry data of females at-sea. We contextualise resultant modelled patterns of distribution with putative threat layers of boat traffic, including fishing vessels and large ship movements, using Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data. We identify key at-sea areas in which protection for inter-nesting leatherback turtles should be considered within the Gabonese Exclusive Economic Zone (EEZ). Our approach offers an holistic technique that merges multiple datasets to build a deeper and more useful knowledge base with which to manage known activities at-sea in an effective manner. Although our analysis focuses on a single species, we suggest that threats identified within this study (fisheries, seismic activity, general shipping) likely apply to other mobile marine vertebrates of conservation concern within Gabonese waters such as olive ridley sea turtles (*Lepidochelys olivacea*), humpback dolphins (*Sousa teuszii*) and humpback whales (*Megaptera novaeangliae*).

Keywords: AIS, inter-nesting, leatherback turtles, MPA, spatial analysis, VMS

INTRODUCTION

Multiple modelling techniques exist to build an understanding of habitat niches for species in the marine environment (Matthiopoulos *et al.* 2004; Aarts *et al.* 2008; Edrén *et al.* 2010; Pikesley *et al.* 2014). These methods are challenged by the issue of enumerating species densities, which has traditionally relied upon sightings based distance sampling (Buckland *et al.* 2001), with data being collected primarily by way of boat or aerial surveys (Hammond *et al.* 2002; Aerts *et al.* 2013). As such, aerial based surveys have helped elucidate density patterns across a broad spectrum of marine species 'at-sea' (Lauriano *et al.* 2011; Scheidat, Verdaat & Aarts 2012) and have also proved their efficacy in enumerating densities of marine species whilst on land (Witt *et al.* 2009; Stapleton, Peacock & Garshelis 2015). Increased understanding of spatial and temporal habitat use, together with associated densities, may facilitate successful management strategies. However, effective design, implementation and regulation of protection for mobile marine species is challenging; particularly for far ranging, pelagic and migratory species (Hyrenbach, Forney & Dayton 2000). Defining appropriate spatial and temporal bounds to managed areas is more tractable when animals may seasonally aggregate (Witt *et al.* 2008; Maxwell *et al.* 2011).

The use of Vessel Monitoring System (VMS) data, primarily as a tool for providing at-sea densities of fisheries (Witt & Godley 2007; Vermard *et al.* 2010; Hintzen *et al.* 2012) has revolutionised the process of mapping, analysing and interpreting fisheries activity patterns. The advent of Automatic Identification System (AIS) data may prove to provide additional capabilities due to time resolution of data (Natale *et al.* 2015) and inclusion of multiple vessel types (Shelmerdine 2015). The installation and operation of VMS is discretional among maritime nations; the requirement to fit AIS systems is however mandatory aboard vessels making international voyages with gross tonnage ≥ 300 t, cargo vessels ≥ 500 t, and all passenger ships regardless of size (Shelmerdine 2015).

In 2002, the central African country of Gabon created a system of coastal and terrestrial National Parks with the aim of protecting key areas of biodiversity-rich habitats. Thirteen National Parks were designated, including a single marine park to the south of the country at Mayumba (Figure 1). Gabon's beaches support important nesting sites for sea turtles, including globally important breeding aggregations for the leatherback turtle (*Dermochelys coriacea*), with the northern and southern extremes of the Gabonese coast (Pongara and Mayumba National Park) receiving the highest densities of nesting activity (Witt *et al.* 2009). Additionally, the olive ridley (*Lepidochelys olivacea*) and green sea turtles (*Chelonia mydas*) also nest (Fossette *et al.* 2008; Maxwell *et al.* 2011; Metcalfe *et al.* 2015).

The leatherback turtle is highly migratory with expansive post-nesting dispersal patterns (Hays, Houghton & Myers 2004; Fossette *et al.* 2014; Roe *et al.* 2014), but may seasonally aggregate off nesting beaches (Witt *et al.* 2008). Protection of large scale aggregations likely represents a significant management target within coastal waters (Hitipeuw *et al.* 2007; Witt *et al.* 2008; Nel, Punt & Hughes 2013; Roe *et al.* 2014); however, to be effective, relevant threats need to be identified, and if possible quantified, preferably in space and time.

In this study we combine aerial survey nest count data for leatherback turtles together with satellite telemetry data from nesting females and contextualise these with VMS and AIS data. Our aims were to: (i) model leatherback turtle distribution and relative density at-sea using a method that was independent of the need to sight species at-sea, (ii) identify potential at-sea threat from vessels associated with multiple industry categories, and (iii) identify key areas for inter-nesting leatherbacks within the Gabonese Exclusive Economic Zone (EEZ) that may benefit from application of appropriately designated Marine Protected Areas (MPAs).

METHODS

Aerial survey data

Aerial surveys were flown along the Gabonese coast using a variety of high-wing light aircraft (Supplementary Material, Table S1). Surveys were organised to coincide with the main period of leatherback turtle nesting activity (December-February; Witt *et al.* (2009)). Multiple surveys were conducted in 2002/03, 2005/06 and 2006/07, with no surveys in 2003/04 and 2004/05. Each survey represented a 600 km flight path (approximate straight-line distance). Flights commenced at dawn. Surveys were timed to coincide with periods when the maximum width of the nesting beach was unaffected by tide during early morning daylight hours, hence ensuring the greatest number of nesting activities could be recorded after sunrise and before the next high tide removed traces of activity. Surveys were typically split over two days to take advantage of morning low sun angle, which aids detection of marine turtle nesting tracks during video analysis.

Survey aircraft were flown at an approximate groundspeed of 180 to 190 km hr^{-1} at an altitude of 50 to 60 m, with the aircraft positioned 100 to 200 m offshore. Surveys were flown in a southeast direction from north to south, parallel to the coastline. The survey start location was northern most limit of Pongara National Park (Figure 1). The survey end location was the southern limit of Mayumba National Park's border with the Republic of Congo. A 50 km section of coast to the north and east of Port Gentil was excluded from all surveys as this area consisted of mangroves and mudflats, which is unlikely to support appreciable levels of leatherback turtle nesting activity.

A video camera was used to record footage of the nesting beach during each aerial survey. Counts of leatherback turtle nesting activity were then enumerated from this video footage in accordance with the methodology described by (Witt *et al.* 2009). These counts were aggregated into approximate 500 m linear sectors of beach (data bins) that were defined by waypoint data collected continuously by hand-held Global Positioning System (GPS) receivers aboard the aircraft at the time of the aerial surveys. A longitude/latitude (World Geodetic System (WGS)1984 format) midpoint was determined for each of these data bins to which the counts were then associated.

Satellite tracking data

Platform Transmitter Terminals (PTTs) were attached to thirty-seven adult female leatherback turtles at nesting locations in Gabon throughout the nesting season (October to February). Turtles were instrumented within the National Parks of Pongara (*n* = 18) and Mayumba (*n* = 19; inter-nesting movements of 7 of these turtles were previously published in Witt *et al.* (2008)) over 2005/06 (Mayumba *n* = 8), 2006/07 (Mayumba *n* = 2), 2007/08 (Mayumba *n* = 5), 2008/09 (Mayumba *n* = 4, Pongara *n* = 6), 2009/10 (Pongara *n* = 2), and 2012/13 (Pongara *n* = 10) (Figure 1, and see metadata in Supplementary Material, Table S2). Methods of turtle capture, transmitter type and process of attachment are detailed in Witt *et al.* (2011). Satellite telemetry data were collected using the Argos satellite system (CLS 2011) and downloaded with the Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005). All locations with accuracy class Z and 0 were removed (Witt *et al.* 2010). Data were imported into the Geographical Information System (GIS) ArcMap 10.1 (ESRI, Redlands, USA http://www.esri.com) and visually assessed to determine individual-specific nesting events. Nesting events typically occurred every 9 to 11 days, the night-time location with the highest accuracy location class and located on, or nearest to land within this time-frame was chosen as the definitive nesting event. Location data were then apportioned by these inter-nesting periods. Five turtles departed the Gabon coast immediately after attachment of the PTT.

Modelling leatherback turtle distribution and relative density at-sea

Estimating leatherback turtle inter-nesting footprint at-sea

For each set of inter-nesting data (inter-nesting datasets *n* = 121: turtles *n* = 32) we applied a speed and azimuth filter (Freitas *et al.* 2008; Witt *et al.* 2010); filtering was undertaken in R (R Development Core Team 2008; R package: argosfilter (Freitas 2010)). Working in a projected coordinate system (Africa Albers Equal Area Conic (AAEAC)) the geometric centroid of these data was determined together with the distance of each location from the centroid; to remove spatial outliers we peeled data to the 95th quantile. The ellipsoid hull of these data was then calculated (R Development Core Team 2008; R package: cluster (Maechler *et al.* 2015)), this being the minimum area such that all given points lay inside, or on the boundary of the ellipsoid. The length (km) of the semi-major and semi-minor axes, the area (km^2) of the bounding ellipse, together with the shortest distance (km) (great-circle-distance: Haversine formula) of the centroid to the nearest coastal vertex were determined. All metrics were expressed as a single value per turtle, averaging (mean) where necessary for multiple inter-nesting periods. There was no significant difference in the median semi-major, semi-minor, or offshore distance for leatherback turtles between the nesting locations of Pongara and Mayumba National Parks (Supplementary Material, Table S3). As a result, we calculated grand means irrespective of release location, to give a single country-wide value for each ellipse metric.

Linking inter-nesting footprint to aerial survey data

We set out to calculate the annual mean average number of leatherback turtles km^{-2} using the following approach. We produced a smoothed coastline vector using a 40 km smoothing window. For each aerial survey dataset we used a spatial join in ArcMap to assign ellipse metrics and smoothed coastal bearings to the midpoint coordinates of the data bins (data were joined to the nearest existing location). These coordinates (projected coordinate system: AAEAC) were then transposed offshore, perpendicular to the coast, using distance of centroid to the coast (offshore distance) and coastal bearing.

For each offshore coordinate pair we projected an ellipsoid polygon (major axis parallel to the coast), using grand averaged semi-major/minor axes and azimuth (coastal bearing). Each individual polygon surface was rasterized to a 1 x 1 km resolution and each raster cell assigned a turtle density at-sea (km^{-2}) which was calculated as follows. (i) We divided the number of tracks recorded on the day of the aerial survey by the proportion of nesting activities expected for the day of the aerial survey. This proportion was determined from a seasonal nesting curve (Witt *et al.* 2009). This calculation provided for an annual estimate of the total number of nesting activities attributable to the data bin. (ii) Annual nesting effort was then divided by a clutch frequency of 6.17 (Miller 1997), to provide the total number of turtles nesting within the data bin for the season. (iii) Finally, we divided this total by the sea area of the propagated ellipse to provide an at-sea density of leatherbacks turtles (turtles km^{-2}). Resulting rasters were then summed to provide a raster surface (for each aerial survey) that described an annual estimate of the at-sea density (km^{-2}) of inter-nesting leatherback turtles.

These raster surface were then apportioned into two that reflected: (i) the peak months of the Gabonese leatherback nesting season (December, January, February) and, (ii) the pre and post-peak months (October, November, and March, April) using a ratio derived from the seasonal nesting curve. Where multiple aerial surveys had been flown within a nesting season these surfaces were then averaged (mean); a grand average (mean) raster was then calculated across all nesting seasons.

VMS data: density mapping

We sourced Vessel Monitoring System (VMS) data from the Government of Gabon, for Gabon flagged trawl vessel fishing activity within the Exclusive Economic Zone (EEZ) of Gabon for 2010, 2011 and 2012. These data represented the best possible continuous dataset available and contained 1 053 923 records (2010: *n* = 209 033, 2011: *n* = 452 531, 2012: *n* = 392 359). All vessel identifications were anonymised, as such each VMS record consisted of a pseudo-vessel identity, date/time stamp (UTC), geographic coordinates in decimal degrees (WGS 1984) and vessel type (by fishing gear). Data were apportioned annually; 1st October to 30th September to reflect the seasonality of leatherback turtle nesting: 2010/11: *n* = 429 554, 2011/12: *n* = 420 807.

For each annual dataset, data were ordered by vessel Id. and date/time stamp. Distance and time elapsed were calculated between each location, and vessel speed calculated in knots. A speed rule was used to distinguish fishing from steaming or near-stationery movement (Witt & Godley 2007); only data with speeds ≥ 1 or ≤ 5 knots were retained. Locations within 10 km of the ports of Libreville and Port Gentil were removed to reduce the influence of port traffic on our analysis. One random location a day for each vessel was extracted and these data were summarised (counts) to a 10 x 10 km resolution raster. This raster resolution was iteratively determined to provide an optimum cell size that facilitated meaningful map interpretation. This process was repeated for both annual datasets and the resultant rasters averaged. Data were then apportioned into three seasonal groups: (i) October and November (pre-peak leatherback nesting season), (ii) December to February (peak) and (iii) March and April (post-peak).

AIS data: density mapping

We sourced ground and space merged Automatic Identification System (AIS) data from ExactEarth (http://www.exactearth.com) for 2012, 2013 and 2014 for the EEZ of Gabon (space-borne AIS data are not available prior to 2012). This dataset contained 22 791 353 records (2012: *n* = 3 719 235, 2013: *n* = 7 043 142, 2014: *n* = 12 028 976). Each record consisted of Maritime Mobile Service Identity (MMSI) number, date/time stamp (UTC), geographic coordinates in decimal degrees (WGS 1984) and speed (knots). Records with speed = 0 knots, as well as data within 10 km of the ports of Libreville and Port Gentil were removed. Vessels were assigned into one of five categories: cargo *n* = 2240 (39%), oil (support vessels: including tankers carrying crude/refined oil and other petrochemical related products) *n* = 1535 (27%), oil (seismic research) *n* = 45(1%), fishing *n* = 106 (2%) and miscellaneous (*e.g.* tug, passenger, recreational: *n* = 1150 (20%)); 685 (12%) vessels could not be assigned to a category due to insufficient metadata. Data were apportioned annually, 1st October to 30th September to reflect the seasonality of leatherback turtle nesting: 2012/13: *n* = 4 637 128, 2013/14: *n* = 6 327 527.

For each annual dataset location data for the categories, cargo, oil (support vessels), oil (seismic research) and fishing were treated as follows. A speed rule was used to remove locations where vessels were not 'under-way' or exhibited near-stationery movement; only data with speeds ≥ 1 knot were retained. For each vessel category we extracted one random location a day for each vessel. These data were summarised (counts) to a 10 x 10 km resolution raster. This process was repeated for both annual datasets and the resultant rasters averaged. Data were then apportioned into seasonal groups.

Calculating leatherback turtle vs. shipping threat indices

We calculated surfaces that described relative threat to inter-nesting leatherback turtles as follows. Vessel density rasters were re-scaled to 0-1 and summed. These were then multiplied with our leatherback density rasters. To provide data at the same spatial resolution we re-sampled our leatherback turtle at-sea density raster to the same resolution (10 x 10 km) as our VMS and AIS layers using bilinear interpolation.

RESULTS

Leatherback turtle satellite tracking and spatial density patterns

Thirty-two leatherback turtles (Pongara n = 18, Mayumba n = 14) were tracked for 121 inter-nesting periods (Pongara n = 101, Mayumba n = 20) with an average time between nest events of 10 ± 1days (mean ± 1 SD; range 7 - 13 days). Turtles primarily remained within continental shelf waters (depths ≤ 200 m), with 93.8% (Pongara; n = 9530) and 93.1% (Mayumba; n = 1504) of all recorded locations in these waters. Turtles principally occupied the Exclusive Economic Zone (EEZ) of Gabon, with 91.3% (n = 10749) of all locations within the EEZ (Figure 1).

The modelled spatial pattern of inter-nesting leatherback turtles at-sea indicated that the coastal waters of Pongara and Mayumba National Parks had high densities of inter-nesting leatherbacks, with a smaller hotspot offshore from Sette Cama Reserve and to the south of Port Gentil; greatest density was within and neighbouring the Mayumba Marine Park (Figure 1).

VMS and AIS density mapping

Fisheries

Mapping of VMS data for Gabon trawl vessels (October to April) indicated presence of vessels across the majority of coastal waters, with peaks in density to the south of Pongara National Park, and in near-shore waters of Loango National Park. There was negligible activity off the continental shelf (Figure 2a). Analysis of AIS fishing vessel data for longline and purse seine fisheries, in general, indicated higher density of vessels in offshore waters, approximately 100 - 200 km southwest of Loango National Park (Figure 2e). There was relatively little activity on the continental shelf, with the exception of a small high density area to the south of Mayumba National Park. These distinctions in spatial patterns largely reflect the difference in gear type used by these fisheries. There was no duplication of vessels among AIS and VMS datasets.

Apportioning fisheries data by leatherback nesting season revealed patterns of seasonality for both these datasets. Mapping of VMS data indicated a north/south shift in fishing activity. Maximum densities occurred in October/November in the vicinity of Pongara and Loango National Park. Densities remained high at Loango within the months of December/January/February, but decreased at Pongara. There was an indication of an increase in fisheries activity immediately to the north of Mayumba Marine Park in March/April (Figure 2b,c,d). Mapping of AIS data indicated that October/November were peak months for longline and purse seine fisheries (Figure 2f,g,h).

Oil industry and cargo vessels

Density mapping of AIS data (October to April) for oil industry vessels revealed marked differences between aspects of the industry. Oil support vessels revealed obvious traffic routes between the ports of Libreville and Port Gentil, as well as westward from Port Gentil (Figure 3a). Hotspots of seismic vessel activity occurred in continental shelf waters, and were primarily concentrated to the south of Port Gentil and also in coastal waters of Loango National Park and Sette Cama Reserve (Figure 3e). There was high seismic vessel activity to the southwest of Mayumba Marine Park at the beginning of the nesting season and evidence of seismic vessels within the park during peak season (Figure 3f,g). Mapping the distribution of cargo vessels (*i.e.* bulk carriers, container vessels) identified two routes. The first lay north to the south of the county and broadly mirrored the 200 m isobath, the second ran westward from the port of Libreville (Figure 3i). There was no marked differences among seasonal density mapping for oil support vessels, or for cargo vessels (Figure 3b,c,d,j,k,l). There were clear differences among seasonal density mapping for seismic vessel activity, which may reflect seasonal legislative limitations or indicate interest in exploitation (Figure 3f,g,h).

Leatherback turtle relative threat mapping

Relative threat mapping indicated that coastal waters of Pongara and Mayumba National Park were subject to high levels of putative threat throughout the leatherback nesting season (Figure 4b). There were also isolated areas of moderate/high threat within coastal waters from Port Gentil to Sette Cama Reserve, primarily due to inshore fisheries and seismic vessels operating within the area. There was variation in severity and timing of threat among locations. Spatially, threat was greatest at Pongara at the beginning of the season (October/November) (Figure 4d), principally due to the heightened level of inshore fisheries activity, and at Mayumba during peak season (December/January/February) and post-peak (March/April). Threat mapping identified areas within the Mayumba Marine Park to be at risk throughout this period, as a result of both inshore fisheries and oil industry vessels (support and seismic) being present within the park boundaries (Figure 4f,h).

DISCUSSION

Sightings based distance sampling (Buckland *et al.* 2001) is likely the most widely used method to determine densities of animals at-sea, relying on data being collected either by way of boat or aerial transect (*e.g.* Hammond *et al.* 2002; Aerts *et al.* 2013). However, many marine species are challenging to sight as a result of their cryptic nature, or due to restrictions imposed by environmental conditions (Evans & Hammond 2004). To provide for an alternative process to estimate at-sea distributions and relative densities, we formulated a method that was independent of the need to sight species at-sea, that instead utilised existing available data: aerial surveys of leatherback turtle nest counts and satellite tracking data.

Ecosystem based impact assessments are able to identify areas where cumulative threat may be at its greatest within the marine environment (Halpern *et al.* 2008), but may not take into account distribution and densities of species within these areas. As a result, it is possible that areas subject to relatively moderate threat, but with high species densities, may fail to attract conservation effort. Indeed, identifying key areas where species aggregate may facilitate the decision process of where and when to best place conservation resources to achieve maximum benefit (Hart *et al.* 2012). With this analysis we sought to further the process of impact assessment by formulating a cumulative threat index that assessed multiple threats, whilst at the same time integrating modelled distribution and densities of a target species. Our analysis makes no attempt to differentiate threat by magnitude, or relative importance. It remains likely that many 'threats' require further knowledge or assessment to quantify probable impacts. To do so effectively, species sensitivity to threats needs to be assessed, which in turn, would additionally allow assignment of weights for calculating cumulative impact.

In the marine environment sea turtles may negatively interact with a broad suite of vessel activity. These interactions may lead to a range of potential impacts to turtles including bycatch from oceanic (Lewison, Freeman & Crowder 2004; Huang 2015) and coastal fisheries (Lum 2006; Alfaro-Shigueto *et al.* 2007; Witt *et al.* 2011), boat strike (Nabavi, Zare & Vaghefi 2012; Denkinger *et al.* 2013), crude oil contamination (Follett, Genschel & Hofmann 2014), or seismic surveying (Nelms *et al.* in press). Our analysis revealed that within the peak leatherback nesting season (December to February), when approximately 80% of the season's nesting takes place, greatest densities of leatherback turtles likely occur in coastal waters adjacent to Pongara and Mayumba National Parks, with a smaller 'hotspot' to the west of Sette Cama Reserve. Contextualising these at-sea density and distribution patterns, with vessel movements derived from VMS and AIS location data, suggests that shipping associated with various industries has the potential to interact with inter-nesting leatherback turtles within Gabonese coastal waters, throughout the nesting season.

Density mapping of the Gabon inshore trawl fisheries fleet (for which VMS data were available) indicated that this fleet could interact with at-sea leatherbacks at all high density leatherback areas. In coastal waters adjacent to Pongara National Park, the potential for this was greatest at the start of the nesting season. There was a subsequent southerly shift in vessel densities for inshore fisheries with nesting leatherback season. Analysis of AIS fisheries data, which predominantly comprised of large Distant Water Fleet (DWF) vessels suggested that there was no activity for this category of vessel within coastal waters of Pongara National Park. There was however, a hotspot of DWF vessel activity just within, and adjoining the southwest/south-easterly border of Mayumba Marine Park at the start of the nesting season. The coastal waters of Pongara National Park had the highest density of vessels associated with shipping routes; for both oil industry and cargo vessels. There were notable hotspots of shipping movements both between the ports of Libreville and Port Gentil in coastal waters, and offshore from these ports to the open ocean, throughout the nesting season. Seismic vessel activity was confined to the coastal waters south of Port Gentil and to the southwest of Mayumba Marine Park. The coastal waters of Pongara National Park had high levels of cumulative threat throughout the nesting season. Cumulative threat mapping indicated the coastal waters from south of Port Gentil to Mayumba National Park had greatest levels of cumulative threat through the peak and post-peak nesting season.

Several caveats must be considered when interpreting the findings from this study. Our method does not account for any temporal variability in nesting season that may be present between the north and south of the country (Witt *et al.* 2009). However, this would be unlikely to affect the modelled at-sea densities of leatherbacks, but should be considered when interpreting threat mapping. Similarly, our method uses a normally distributed nesting curve to calculate annual estimates of the total number of nesting activities for each data bin, with approximations for the beginning and end of the nesting season of 1st October to 30th April respectively. These estimates would be slightly modified under alternative curve scenarios.

It is also probable that our vessel densities represent underestimations. Our analysis only considers vessels that are legally required to transmit their locations by way of VMS or AIS. Similarly, these systems need to be enabled and transmitting, and satellites need to be in line of sight to receive data. Applying a slow speed filter to all AIS data to remove vessel traffic that was not 'under-way' may have the effect of removing some locations for vessels deploying purse seine gear; although, it is highly unlikely that a vessel will remain motionless 'at-sea' given the influence of wind and or tide and currents. For inshore fisheries we only evaluate data for the Gabon fleet. Vessel movements for DWFs and artisanal fisheries are not considered, therefore much of the associated threat from inshore fisheries likely remains un-assessed. In addition, our VMS data are sourced prior to September 2012, subsequent changes to management regimes within Gabon may have impacted associated vessel movement patterns. Finally, whilst some of our component data layers do not necessarily overlap temporally they represent the best available data from which to formulate this analysis.

Notwithstanding these caveats, this analysis clearly identifies at-sea areas in which protection for inter-nesting leatherback turtles should be considered. Although this analysis focuses on a single species, much of the associated threats will apply to other air-breathing mobile marine vertebrates in Gabonese coastal waters including olive ridley sea turtles (*Lepidochelys olivacea*) (Maxwell *et al.* 2011; Metcalfe *et al.* 2015), humpback dolphins (*Sousa teuszii*) (Collins 2012) and humpback whales (*Megaptera novaeangliae*) (Rosenbaum *et al.* 2014). As such, (if data were available) the methodology presented in this study could be applied to other species of sea turtles for cumulative assessments; and with adaptation, may have utility in defining critical habitats for other central-place foragers such as pinnipeds, or sea bird species (Grecian *et al.* 2010; Sharples *et al.* 2012; Cronin, Pomeroy & Jessopp 2013). Presently, Mayumba Marine Park is the only designated MPA within the

Gabon EEZ and is confined to a 15 x 60 km strip of coastal waters to the far south of the Gabonese EEZ. Protection for species within MPAs may be compromised for a number of reasons. Typically, small protected areas offer limited conservation benefits (Gaines *et al.* 2010) particularly to mobile species. Marine Protected Areas may also fail to protect through poor design, inappropriate/lack of management or through degradation of unprotected surrounding ecosystems (Agardy, Di Sciara & Christie 2011). Recently announced proposals to designate approximately 23% of Gabon's territorial waters and EEZ as MPAs, in which commercial fishing will be excluded, may go some way to securing protection for species within these zones (http://www.wcs.org/press/press-releases/world-parks-congress-2014.aspx). Indeed, associated management strategies protecting marine habitats and improving fisheries management, may already influence some vessel movements in key areas identified in this study. Ultimately, with increased spatio-temporal understanding of other categories of threat and species interaction (*e.g.* seismic surveying, boat strike) MPA design and management strategies may be tailored and fine-tuned to provide an holistic network of protected areas that provide protection for a suit of Gabon's biodiversity rich marine species.

ACKNOWLEDGEMENTS

We thank the following for support and funding: CARPE (Central African Regional Program for the Environment, Darwin Initiative, EAZA ShellShock Campaign, Gabon Sea Turtle Partnership with funding from the Marine Turtle Conservation Fund (United States Fish and Wildlife Service, U.S. Department of the Interior), Harvest Energy, Large Pelagics Research Centre at the University of New Hampshire, NERC, Vaalco, Waitt Foundation and the Wildlife Conservation Society. We are sincerely grateful to the field teams and logistics staff who assisted in the aerial and ground surveys and with field-site assistance. BJG and MJW receive funding from the Natural Environment Research Council, the European Union and the Darwin Initiative.

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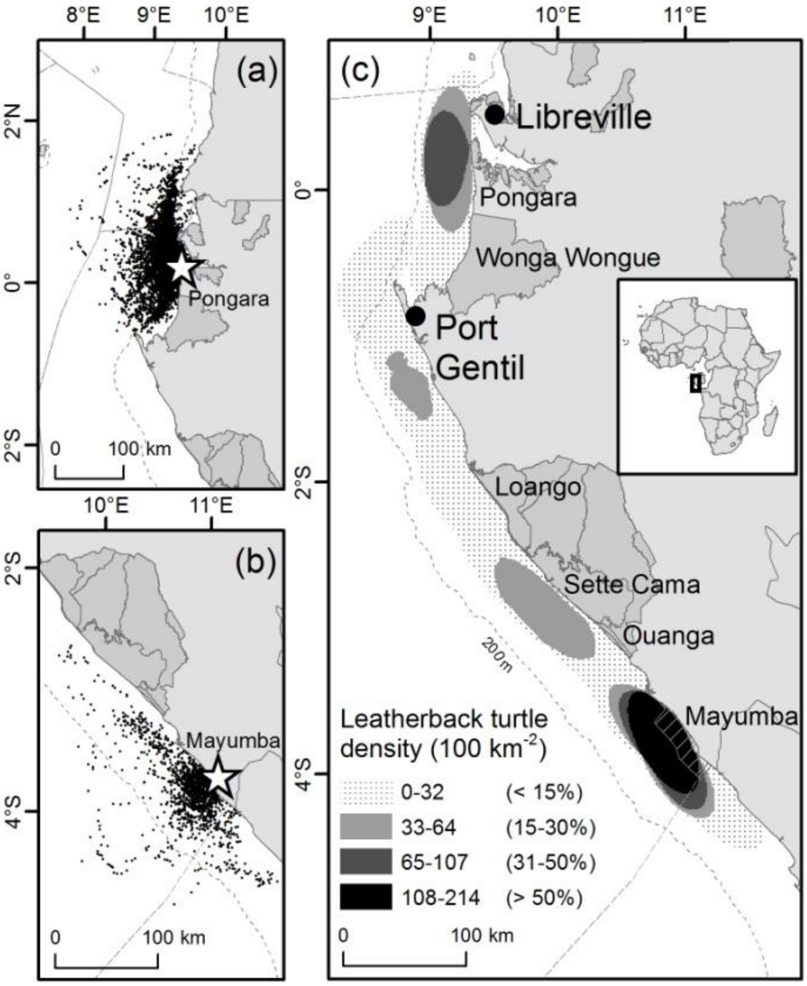

Figure 1. Location data (black circles) for satellite tracked inter-nesting leatherback turtles tracked from, (a) Pongara National Park (*n* = 18) and (b) Mayumba National Park (*n* = 14). Tagging locations (white stars). (c) Modelled leatherback turtle density at-sea October-April. Densities (turtles 100 km^{-2} apportioned by percentiles) are drawn in accordance with the figure legend. 200 m continental shelf isobath (broken line) and EEZ maritime boundaries (broken line polygon). In part (c) coastal National Parks and reserves (mid grey polygons) and the ports of Libreville and Port Gentil are labelled. Mayumba National Park (Marine Protected Area (MPA)), hatched grey polygon. Part (c) is located according to the inset. All parts are drawn to differing spatial scales. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

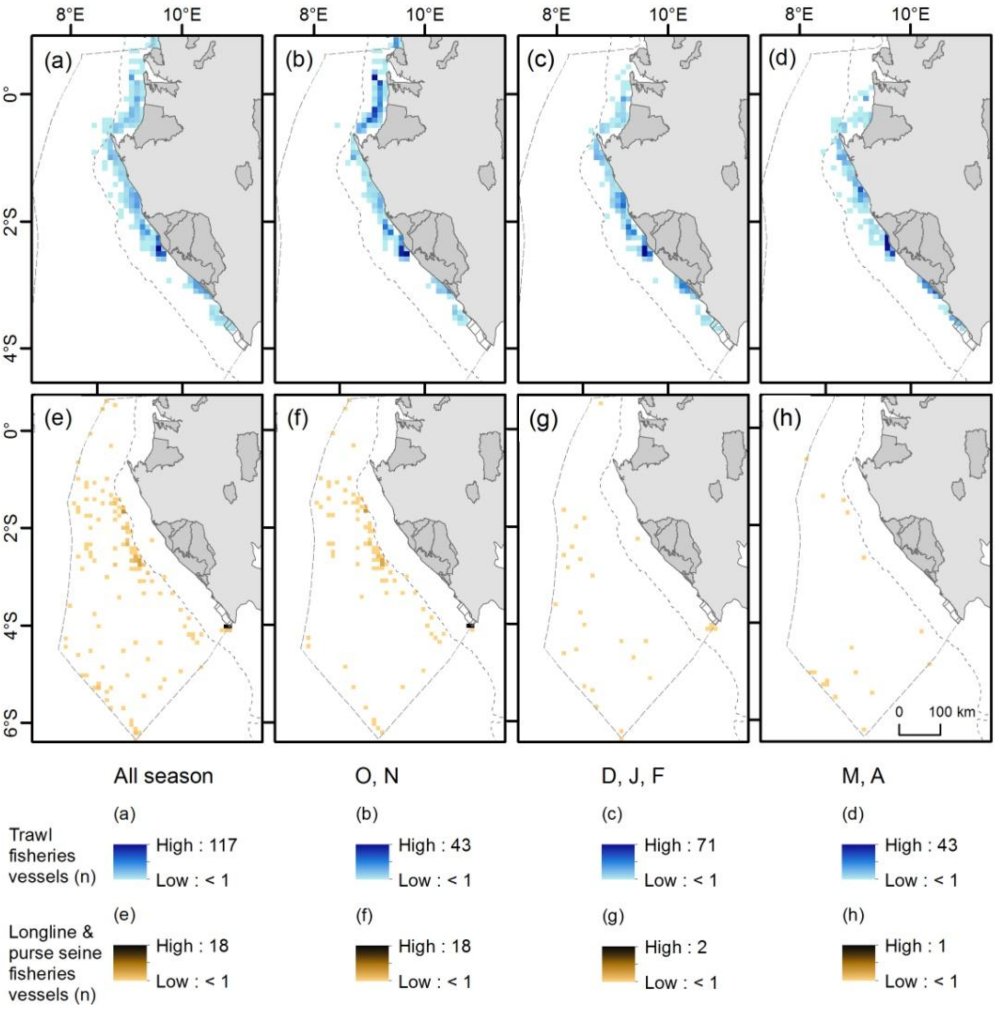

Figure 2. Mean seasonal density of fisheries activity derived from Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data. (a-d) VMS data for leatherback nesting seasons 2010/11 and 2011/12. A speed rule was applied to distinguish fishing from steaming or near-stationery movement (Witt & Godley 2007); only data with speeds ≥ 1 or ≤ 5 knots were retained. (e-h) AIS data for leatherback nesting seasons 2012/13 and 2013/14. A speed rule was applied to remove near-stationery movement; only data with speeds ≥ 1 knot were retained. For each dataset one random location a day for each vessel was extracted. Data were summarised (counts) to a 10 x 10 km resolution raster. Data for the complete nesting season (a,e) were then apportioned into three seasonal groups: (b,f) October and November, (c,g) December to February and (d,h) March and April. Parts (a,b,c,d) and (e,f,g,h) are drawn to differing spatial scales. All other map features are drawn and labelled in accordance with Figure 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

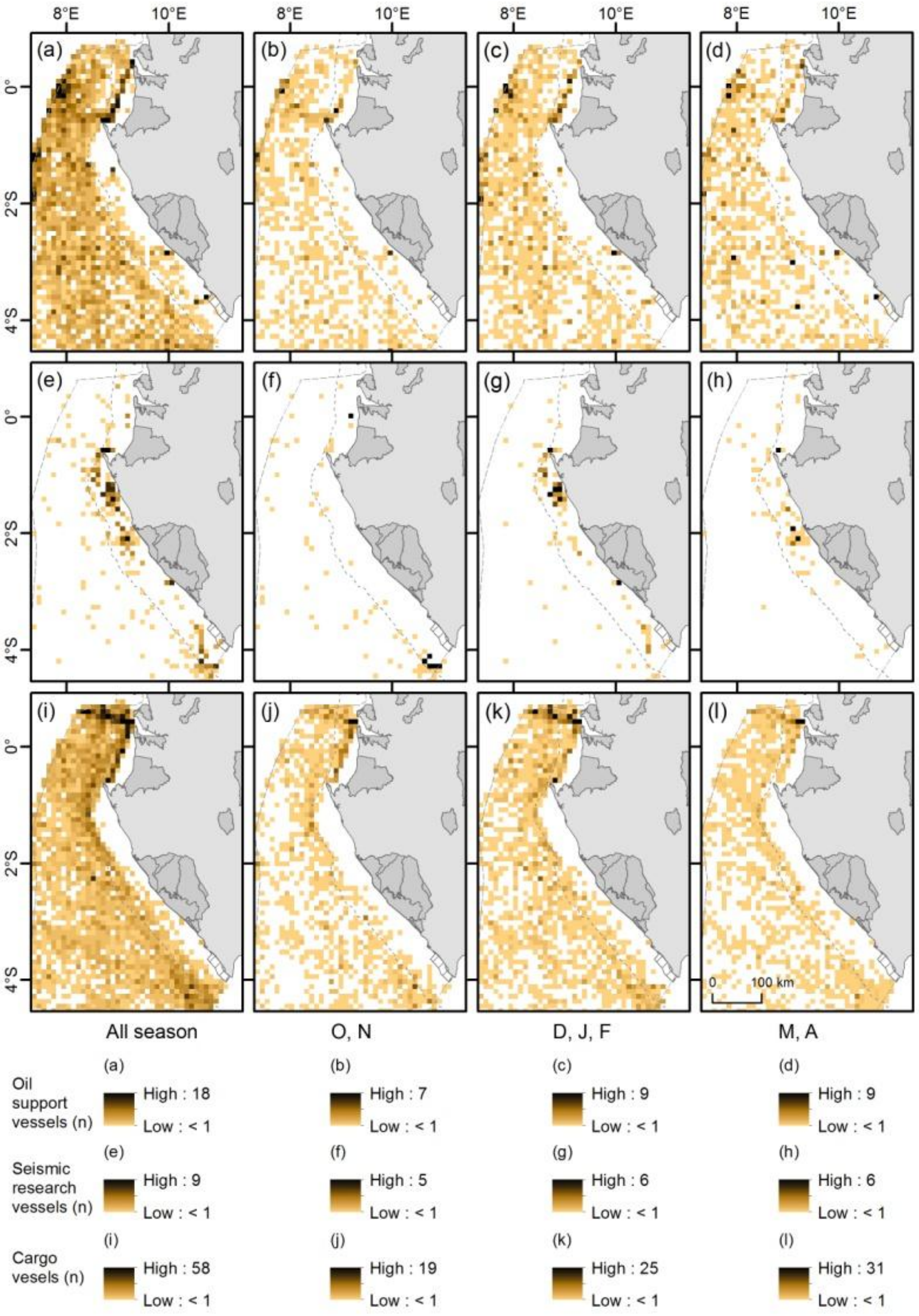

Figure 3. Mean seasonal density of vessel activity categorised as, (a-d) oil support vessels, including tankers carrying crude/refined oil and other petrochemical related products, (e-h) seismic research vessels and (i-l) cargo vessels, derived from Automatic Identification System (AIS) data for leatherback nesting seasons 2012/13 and 2013/14. A speed rule was applied to remove

near-stationery movement; only data with speeds ≥ 1 knot were retained. One random location a day for each vessel was extracted. Data were summarised (counts) to a 10 x 10 km resolution raster. Data for the complete nesting season (a,e,i) were then apportioned into three seasonal groups: (b,f,j) October and November, (c,g,k) December to February and (d,h,i) March and April. All parts drawn to the same spatial scale. All other map features are drawn and labelled in accordance with Figure 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

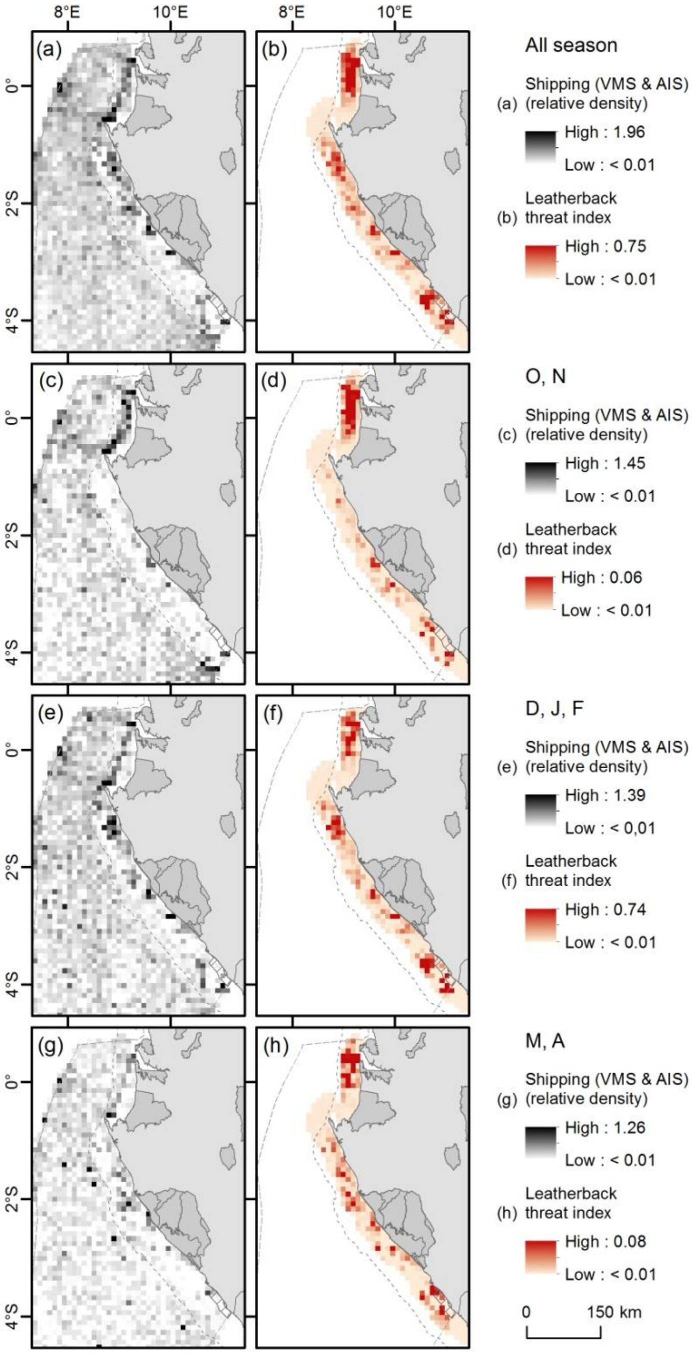

Figure 4. Cumulative seasonal shipping densities (a,c,e,g). Vessel density rasters were re-scaled 0-1and summed. Threat index for inter-nesting leatherback turtles (b,d,f,h). Cumulative shipping density rasters were multiplied by leatherback density rasters. To provide for data at the same spatial resolution leatherback turtle at-sea density raster were re-sampled to the same resolution (10 x 10 km) as the VMS and AIS layers using bilinear interpolation. Data for the complete nesting season (a,b) were then apportioned into three seasonal groups: (c,d) October and November, (e,f) December to February and (g,h) March and April. All parts drawn to the same spatial scale. All other map features are drawn and labelled in accordance with Figure 1. Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

Table S1. Aerial survey schedule for the Gabonese coast 2002/03, 2005/06 and 2006/07.

Nesting season	**Survey**	**Aerial survey dates**	
		Start	**End**
2002/03	1	2003-01-11	2003-01-12
	2	2003-01-25	2003-01-26
2005/06	1	2005-12-08	2005-12-09
	2	2006-01-23	2006-01-25
	3	2006-02-21	2006-02-22
2006/07	1	2006-12-12	2006-12-14
	2	2007-01-25	2007-01-26
	3	2007-02-23	2007-02-24

Table S2. Summary of PTT data for inter-nesting leatherback turtles, detailing: PTT Id., nesting season, release location, deployment date, inter-nesting periods (*n*), PTT manufacturer and model.

Id	PTT	Nesting season	Release location	Deployment date	Inter-nesting periods (*n*)	Inter-nesting duration (mean) (days)	PTT make	Model
1	57666	2005-2006	M	2005-12-10	1	11	Sirtrack	KiwiSat 101
2	57383		M	2005-12-11	0	no data	Sirtrack	KiwiSat 101
3	57381		M	2006-02-23	0	no data	Sirtrack	KiwiSat 101
4	57378		M	2006-02-24	1	10	Sirtrack	KiwiSat 101
5	57390		M	2006-02-24	1	13	Sirtrack	KiwiSat 101
6	65693		M	2006-03-09	0	no data	SMRU	SRDL
7	57663		M	2006-03-19	0	no data	Sirtrack	KiwiSat 101
8	65694		M	2006-03-22	1	11	SMRU	SRDL
9	68562	2006-2007	M	2007-02-03	2	10	SMRU	SRDL
10	68563		M	2007-02-09	1	11	SMRU	SRDL
11	80621	2007-2008	M	2008-02-12	0	no data	Sirtrack	KiwiSat 202
12	80622		M	2008-02-12	1	7	Sirtrack	KiwiSat 202
13	80623		M	2008-02-12	2	10	Sirtrack	KiwiSat 202
14	80620		M	2008-02-12	2	12	Sirtrack	KiwiSat 202
15	80624		M	2008-02-12	1	11	Sirtrack	KiwiSat 202
16	89072	2008-2009	P	2008-12-08	3	12	Wildlife Computers	MK10-AF
17	89071		P	2008-12-09	6	12	Wildlife Computers	MK10-AF
18	89075		P	2008-12-11	5	11	Wildlife Computers	MK10-A
19	89073		P	2008-12-15	4	11	Wildlife Computers	MK10-AF
20	89074		P	2008-12-16	3	10	Wildlife Computers	MK10-AF
21	89076		P	2008-12-16	7	10	Wildlife Computers	MK10-A
22	92577		M	2009-02-18	3	10	Wildlife Computers	MK10-A
23	92578		M	2009-02-18	2	10	Wildlife Computers	MK10-A
24	92579		M	2009-02-21	1	10	Wildlife Computers	MK10-A
25	92580		M	2009-02-21	1	12	Wildlife Computers	MK10-A
26	92581	2009-2010	P	2009-12-07	5	11	Wildlife Computers	MK10-A
27	92582		P	2009-12-07	7	10	Wildlife Computers	MK10-A
28	122425	2012-2013	P	2012-10-25	7	10	Wildlife Computers	SPLASH10-AF
29	122426		P	2012-10-26	6	11	Wildlife Computers	SPLASH10-AF
30	122427		P	2012-10-26	7	11	Wildlife Computers	SPLASH10-AF
31	122428		P	2012-10-27	7	10	Wildlife Computers	SPLASH10-AF
32	122429		P	2012-10-27	6	9	Wildlife Computers	SPLASH10-AF
33	122430		P	2012-10-28	1	9	Wildlife Computers	SPLASH10-AF
34	122431		P	2012-10-28	5	10	Wildlife Computers	SPLASH10-AF
35	122432		P	2012-10-28	7	11	Wildlife Computers	SPLASH10-AF
36	122433		P	2012-10-28	8	10	Wildlife Computers	SPLASH10-AF
37	122434		P	2012-10-28	7	11	Wildlife Computers	SPLASH10-AF
				mean	3	10		
				total	121			

Table S3. Summary of output from Wilcoxon test of semi-major, semi-minor and distance of centroid to the coast for leatherback turtles between the nesting locations of Pongara and Mayumba National Parks.

Ellipse metric	Wilcoxon z score	p value	Median value (km)	
			Pongara	Mayumba
Semi-major axis length	1.29	0.20	36.25	45.19
Semi-minor axis length	0.23	0.82	16.74	17.80
Distance of ellipse centroid to coast	0.91	0.36	16.37	19.03

Discussion

Sea turtles face multiple threats, both within marine and terrestrial environments (*e.g.* Salmon 2003; Taylor & Cozens 2010; Kamrowski *et al.* 2012; Marco *et al.* 2012; Lewison *et al.* 2013; Tanner 2013; Katselidis *et al.* 2014). Threats to sea turtles will vary in space and time, and may be species and region specific (Casale & Marco 2015). Categories of threat include fisheries bycatch (incidental capture in fisheries), direct take (*e.g.* targeted fisheries, egg harvesting), impact to nesting beaches (*e.g.* coastal development, disturbance), pollution, pathogens, and climate change (Wallace *et al.* 2011). In an assessment of the relative impacts of threats, fisheries bycatch was classified as the highest threat to sea turtles globally, followed by climate change (Wallace *et al.* 2011).

The analyses presented in this thesis clearly demonstrate the potential for negative associations between multiple species of sea turtle, across a diverse range of geographic regions and habitat niches, with a number of human activities. The potential for interaction with fisheries, and by inference the prospect of bycatch, is highlighted for many Exclusive Economic Zone (EEZ) regions of the west coast of Africa. These studies emphasise it is imperative for countries to develop marine conservation policies that not only recognise the spatial extent of highly migratory species, but that also consider the effect of climate change on the future distribution of species. The analysis of threat to nesting sea turtles, associated with the downstream consequence of industrial deforestation, emphasises that it is not only the more obvious 'threats' that should be considered when defining conservation management strategies and goals. This analysis also highlights the potential logistical difficulties in dealing with long-term persistent habitat degradation.

Analysis of coincidence between observed habitat use and modelled sea turtle habitat niche with the extant Mediterranean Marine Protected Area (MPA) network indicated profound shortcomings in the adequacy of spatial protection for sea turtle species in this region. Appreciable gains in protection for species could be made with the adoption of new suitably designed IUCN categorised MPAs within site-specific areas identified by the analysis, and by designating existing MPAs with appropriate IUCN categories. This analysis again highlights the need to accommodate potential range shifts in species associated with climate change when considering conservation strategies, and further illustrates the need for multi-country development of conservation policies. Similarly, the analysis presented of inter-nesting sea turtles in coastal waters of Gabon clearly identifies spatially explicit areas that would benefit from the adoption of appropriately designed MPAs.

The Convention for Biological Diversity calls for 10% of coastal and marine ecosystems to be protected by 2020 through an integrated network of MPAs. The modelling framework presented within this thesis likely represents a valuable tool for identifying key areas to protect, and could be a significant asset to help inform marine spatial planning. Ultimately, with increased spatio-temporal understanding of the distribution of species, favourable habitat and threat, it is likely that MPA design and management strategies may be tailored and fine-tuned to provide a holistic network of protected areas that may provide protection for many marine species.

Throughout the first three chapters of this thesis habitat models were developed and the modelling process refined; with each successive model building on the previous. An ensemble, or consensus, modelling approach was adopted for all modelling scenarios (Araújo & New 2007; Rangel & Loyola 2012). This approach allowed for the integration of multiple single-algorithm model predictions and evaluation metrics, that in turn allowed for reduction in potential bias and increased confidence in predictions (Scales *et al.* 2015). The response variable in these models were satellite tracking data collected using the Argos satellite system (CLS 2011). These data have inherent spatial accuracy errors (Witt *et al.* 2010), however with removal of locations with low spatial accuracy, and judicial filtering of maximum speed and azimuth between successive locations, representative reconstruction of animal tracked movements may be achieved (Witt *et al.* 2010). As such, within the first three chapters of this thesis, analyses of these data have allowed identification of distinct regions of habitat use, as well as enabling identification of areas where habitats may be most suitable. Future tracking studies that incorporate Global Positioning System (GPS) enabled transmitters, and therefore with the ability to collect data with a greater degree of spatial accuracy, would likely enable development of habitat models at a far finer spatial scale, and allow greater confidence in identification of threat, and where possible, protection.

Where practicable (when sufficient data were available), tracking data were apportioned seasonally (spring/summer, autumn/winter) or by behaviour (oceanic/neritic foraging turtles). With the inclusion of additional tracking data, gathered from future satellite tracking studies, habitat models could be further refined to enable construction of fine-scale temporal and spatial models (*e.g.* Razgour *et al.* 2011, Gschweng *et al.* 2012), that may allow greater insight into likely sea turtle habitat use. Similarly, the application of State Space Modelling (SSM) techniques (*e.g.* Breed *et al.* 2009; Maxwell *et al.* 2011) to infer animal behavioural state from the satellite tracking data, would enable construction of behaviour-specific habitat models to be developed, both for migratory and residency tracking data.

An important consideration to be made when analysing spatio-temporal data is to consider bias that may be introduced through spatial and temporal auto-correlation or pseudo-replication (Franklin 2010). Failure to account for such bias may result in the importance of some environmental variables being over-inflated (variable selection may be pre-disposed towards more strongly auto-correlated predictors). As a result either a variable may be retained when it should not have been, or more variables may be selected (Franklin 2010). To reduce the potential for spatial and temporal autocorrelation, all data used to construct habitat models were reduced to best daily locations. Similarly, to minimise pseudo-replication within data (where long-term sea turtle residency patterns were analysed) the maximum number of days retained for analysis at any one foraging site per turtle was limited to 365 d.

Spatial auto-correlation (or spatial auto-correlation in the residuals of the model) does not necessarily make the model unsound, but rather inflates the degrees of freedom and makes parameter estimates and associated tests uncertain and flawed (Thuiller pers. com.). Therefore, checking for, and where necessary correcting, residual spatial auto-correlation makes for robust model predictions (with confidence in the level of importance of key model predictors) that in turn allows for forecast models (through time) to be made with confidence. Where forecast models were run, spatial autocorrelation within model residuals was investigated using Moran's *I* coefficients (Dormann *et al.* 2007). If spatial autocorrelation was present, location data were sub-sampled to reduce the spatial structure within these data. This was achieved using a stepwise, percentage reduction, random sample of these data, to iteratively arrive at a sub-sample of locations where spatial auto-correlation was no longer present in the model's residuals. As a result, the forecast models presented within this thesis likely represent robust future predictions of habitat suitability, based on key environmental variables most likely to be of importance in defining sea turtle habitat niche.

Selection of environmental variable surfaces to be included within a habitat modelling framework may depend on the geographic location of the habitat being modelled, and the spatial and temporal resolution of available environmental data. Within the habitat models presented in this thesis these data included environmental surfaces such as sea surface temperature and bathymetric depth, as well as proxies for prey availability such as net primary productivity and oceanic sea surface temperature frontal activity. It is important to minimise the use of strongly correlated environmental variables within habitat models, as this will make ecological interpretation of the model difficult, but not necessarily affect accuracy (Franklin 2010). As such, inclusion of strongly correlated covariates was avoided within the modelling framework. The use of remotely sensed environmental data products within a Geographical Information System (GIS) can also be subject to inherent errors (Lunetta 1991). These may be introduced at various stages of collecting and collating data and can include: acquisition error (*e.g.* no data pixels (attributable to cloud cover) or progressive inaccuracies with measurements (sensor degradation)), processing error (*e.g.* conversion from swath images to continuous data surface), or interpolation to raster or vector products (Lunetta 1991). In addition, some remote sensing data products will have product specific biases. Within the modelling framework presented in this thesis steps were taken to overcome, or minimise many of these potential sources of error. For example, nightime SST 4 µm products were selected in analyses (against daytime products) to reduce bias introduced by diurnal warming of the skin surface attributable to solar insolation. Similarly, seasonal or annual average composites were used to provide for consistent, near cloud-free, images for the spatial extent of the modelled area.

Many of the analyses presented within this thesis identify fisheries to be a potential source of threat to both post and inter-nesting sea turtles. However, detailed analysis of sea turtle/fisheries interaction is hampered by a paucity of data for fisheries effort and reported data for sea turtle bycatch (Wallace et al. 2010). Chapters I and 2 highlight this need to increase knowledge of fishing effort and associated levels of sea turtle bycatch, attributable to gear types for both industrial and artisanal fisheries. This knowledge would help assist the formulation of sustainable and effective bycatch management strategies for both fisheries. In Chapter V analysis is made of Vessel Monitoring System (VMS) and Automatic Identification System (AIS) data with the specific aim of quantifying potential interactions between at-sea inter-nesting sea turtles and vessel movement patterns. Further analysis of fisheries distributions derived from VMS and AIS data could be augmented with knowledge of gear deployments, as well as records of gear specific bycatch data obtained from observer-based programmes (Lewison *et al.* 2004; Finkbeiner *et al.* 2011). It is also likely that habitat models developed within this thesis for identifying suitable foraging habitat for sea turtles, could be adapted to provide for fisheries distribution models. These models could be based on point data derived from either VMS or AIS datasets, together with appropriate physical and biological environmental variables (*e.g.* NPP or distance from port (for smaller vessels)). It may also be feasible to develop similar fisheries models for artisanal fisheries if vessel movement data were captured, perhaps by way of location data being recorded by GPS units attached to artisanal fishing vessel. Again, these data could be augmented with data detailing gear specificity and bycatch rates.

The analysis of interaction between vessel movements derived from AIS data and at-sea inter-nesting sea turtles is made difficult without quantification of threat. Therefore, the analysis presented within this thesis makes no attempt to differentiate threat by magnitude, or relative importance. Further knowledge of 'threats' to sea turtles, such as seismic surveying, underwater noise and boat strike, together with quantification of probable impacts is required. This would require the sensitivity of species to threats to be assessed, which in turn, would allow assignment of weights for formulating cumulative impact assessments. This field of research should likely be a priority for sea turtle ecologists, as well as researchers of other species.

Many of the chapters presented within this thesis highlight the need for stakeholder engagement at local, national and international levels. This is particularly so with regulation of fisheries. Gear modifications and adjustment to fisheries practice and/or effort restrictions may be appropriate to some fisheries and may help mitigate impacts (Gilman et al. 2009). However, enforcement of independent states' fisheries management policies is immense. This may be exacerbated where countries sell fisheries access agreements to Distant Water Fleets (DWFs) as these can be associated with non-transparent fishing agreements and Illegal, Unreported and Unregulated (IUU) fishing infringements (Gagern and van den Bergh 2013). Promotion of bycatch release programmes could be an option in some fisheries (Ferraro & Gjertsen 2009), and may be particularly appropriate in smaller scale fisheries. Coupling bycatch release programmes with 'no-blame' reporting schemes would also help inform bycatch rates. Advancement of ecosystem based fisheries management schemes that promote responsible and sustainable practice may also be a way forward for artisanal fisheries (Casale 2011).

For smaller-scale artisanal fisheries engagement with local communities could also bring conservation benefits. Sea turtle conservation projects can create local jobs and attract tourism into the area (Tanner 2013). Indeed, increasing the perceived value of sea turtle species above and beyond their immediate value as food, or end products, may bring significant conservation gains. Similarly, raising local awareness of conservation issues, particularly through the education of local children, may also bring benefits (Tanner 2013).

Much of the presented analyses integrate previously unpublished and published data, or data from multiple sources. This assimilation of data provides large datasets that incorporate observations of numerous animals over many years, allowing analyses to be made that would be otherwise unfeasible. However, sea turtle tracking data has the potential to be inherently biased, as data is frequently gathered disproportionally between sexes, with males very often being under-represented. Similarly, many satellite tracking studies focus on adult sea turtles, leaving much of the life history model of juvenile sea turtles to be inferred (Varo-Cruz *et al.* 2016). Given these limitations, it is feasible that not all movement patterns have been captured by our study animals, and different patterns of distribution and habitat use may be seen with the inclusion of male and juvenile sea turtles. As such, it would be beneficial if future tracking studies focused on instrumenting males and juvenile sea turtles to help fill these knowledge gaps. Many of the satellite tagging studies presented in this thesis would also benefit from collection of further data, over additional years, as this would help facilitate validation of the findings presented in this thesis. This may be particularly so where there is currently a sparseness of data (*e.g.* neritic foraging Cape Verde loggerhead sea turtles).

Notwithstanding these caveats, the analyses presented in this thesis emphasise the need to proactively develop marine conservation policies that will actively protect highly migratory species, whilst at the same time factoring in flexibility, as our knowledge of the distribution of species and kowledge of habitat use grows. Much of the presented analyses 'add value' to previous studies and increase knowledge of the species. A good deal of archived satellite telemetry data remains un-analysed (Luschi & Casale 2014), much of which may benefit from application of methodologies presented here, that in turn, would ultimately bring further understanding of sea turtle ecology, helping to further fill knowledge gaps. Finally, this thesis demonstrates the utility of developing and applying novel analytical methodologies to large datasets to investigate the spatial ecology of a marine vertebrate of conservation concern. As such, it is likely that many of these analytical techniques presented within this thesis could be adapted and applied to other widely dispersed marine vertebrate species, therby helping to inform global conservation management planning and practice.

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