1 A NOVEL APPROACH TO ESTIMATE THE DISTRIBUTION, DENSITY AND AT-SEA RISKS OF A 2 **CENTRALLY-PLACED MOBILE MARINE VERTEBRATE** 3 4 Stephen K. Pikesley ^{a,b}, Pierre Didier Agamboue ^c, Jean Pierre Bayet ^d, Jean Noel Bibang ^e, Eric 5 Augowet Bonguno^f, François Boussamba^g, Annette C. Broderick^a, Michael S. Coyne^{a,h}, 6 Philippe Du Plessisⁱ, François Edgard Faure^j, J. Michael Fay^e, Angela Formia^c, Brendan J. Godley^{a,b}, Judicael Regis Kema Kema^k, Brice Didier Koumba Mabert^j, Jean Churley 7 8 Manfoumbi^d, Georges Mba Asseko^e, Kristian Metcalfe^a, Gianna Minton^k, Sarah Nelms^a, 9 Solange Ngouessono ^f, Jacob Nzegoue ^c, Carole Ogandanga ¹, Carmen Karen Kouerey Oliwina 10 ^c, Franck Otsagha ^e, Richard J. Parnell ^c, Micheline Schummer Gnandji ¹, Guy-Philippe Sounguet ^f, Mesmin Wada ¹, Lee White ^f, 11 12 & *Matthew J. Witt ^b 13 14 Addresses: 15 ^a Centre for Ecology and Conservation, University of Exeter. Cornwall. UK 16 ^b Environment and Sustainability Institute, University of Exeter. Cornwall. UK 17 ^c Wildlife Conservation Society, Global Conservation Program, 2300 Southern Blvd., Bronx, 18 NY 10460. USA 19 ^d IBONGA-ACPE, BP 148, Gamba. Gabon 20 ^e Agence Nationale des Pêches et de l'Aquaculture, BP 20484, Libreville. Gabon 21 ^f Agence Nationale des Parcs Nationaux, BP 20379, Libreville. Gabon 22 ^g Aventures Sans Frontières, BP 7248, Libreville. Gabon 23 ^h SEATURTLE.org, Durham, NC. USA 24 ⁱ Fondation Liambissi, BP 2924, Port-Gentil. Gabon 25 ^j CNDIO-Gabon, BP 10961, Libreville. Gabon 26 ^k WWF-Gabon, BP 9144, Libreville. Gabon 27 ¹ Direction Générale des Pêches et de l'Aquaculture, BP 9498, Libreville. Gabon

- 28 *Corresponding author: Matthew J. Witt, Environment and Sustainability Institute, University
- of Exeter, Penryn Campus, Cornwall. TR10 9FE, UK. Telephone: 01326 370450, email:
- 30 M.J.Witt@exeter.ac.uk
- 31
- 32 Article type: Research
- 33

34 A NOVEL APPROACH TO ESTIMATE THE DISTRIBUTION, DENSITY AND AT-SEA RISKS OF A

35 CENTRALLY-PLACED MOBILE MARINE VERTEBRATE

36 ABSTRACT

37

38 Formulating management strategies for mobile marine species is challenging, as knowledge is 39 required of distribution, density, and overlap with putative threats. As a step towards 40 assimilating knowledge, ecological niche models may identify likely suitable habitats for 41 species, but lack the ability to enumerate species densities. Traditionally, this has been catered 42 for by sightings-based distance sampling methods that may have practical and logistical 43 limitations. Here we describe a novel method to estimate at-sea distribution and densities of a 44 marine vertebrate, using historic aerial surveys of Gabonese leatherback turtle (Dermochelys 45 *coriacea*) nesting beaches and satellite telemetry data of females at sea. We contextualise 46 modelled patterns of distribution with putative threat layers of boat traffic, including fishing 47 vessels and large ship movements, using Vessel Monitoring System (VMS) and Automatic 48 Identification System (AIS) data. We identify key at-sea areas in which protection for inter-49 nesting leatherback turtles could be considered within the coastal zone of Gabonese Exclusive 50 Economic Zone (EEZ). Our approach offers a holistic technique that merges multiple datasets 51 and methodologies to build a deeper and insightful knowledge base with which to manage 52 known activities at sea. As such, the methodologies presented in this study could be applied to 53 other species of sea turtles for cumulative assessments; and with adaptation, may have utility in 54 defining critical habitats for other central-place foragers such as pinnipeds, or sea bird species. 55 Although our analysis focuses on a single species, we suggest that putative threats identified 56 within this study (fisheries, seismic activity, general shipping) likely apply to other mobile 57 marine vertebrates of conservation concern within Gabonese and central African coastal waters, 58 such as olive ridley sea turtles (Lepidochelys olivacea), humpback dolphins (Sousa teuszii) and 59 humpback whales (Megaptera novaeangliae).

60

61 Keywords: inter-nesting, leatherback turtles, marine protected area (MPA), spatial analysis,

62 Automatic Identification System (AIS), Vessel Monitoring System (VMS)

63 1. INTRODUCTION

64

65 Multiple modelling techniques exist to build an understanding of habitat niches for 66 species in the marine environment (Aarts et al., 2008; Edrén et al., 2010; Forney et al., 2015; 67 Matthiopoulos et al., 2004; Pikesley et al., 2014; Wedding et al., 2016). These methods are 68 challenged by the issue of enumerating species densities, which has traditionally relied upon 69 sightings-based distance sampling (Buckland et al., 2001), with data being collected primarily 70 by way of boat or aerial surveys (Aerts et al., 2013; Becker et al., 2014; Hammond et al., 2002). 71 Typically, distance sampling relies on three key assumptions being met (Thomas et al., 2010); 72 species are detected with certainty, species do not move, distance measurements are exact 73 (Thomas et al., 2010). As such, application of distance sampling methodologies to aerial based 74 surveys have helped reveal density patterns across a broad spectrum of marine species 'at sea' 75 (Lauriano et al., 2011; Scheidat et al., 2012; Seminoff et al., 2014) and have also proved their 76 efficacy in enumerating densities of marine species whilst on land (Stapleton et al., 2015). 77 However, many marine species are challenging to observe at sea because of their

cryptic nature, spending limited time at the sea surface, or due to restrictions imposed by
environmental conditions (weather and sea state) (Evans & Hammond 2004). To provide for an
alternative complementary process to estimate at-sea distributions and relative densities, we
formulated a method that was independent of the need to visually sight species at sea, that
instead utilised existing available data: aerial surveys of leatherback turtle nest counts and
satellite tracking data.

Increased understanding of spatial and temporal habitat use, together with associated densities, may facilitate successful management strategies. However, design, implementation and regulation of protection for mobile marine species is challenging; particularly for far ranging, pelagic and migratory species (Briscoe et al., 2016; Hyrenbach et al., 2000). Defining appropriate spatial and temporal bounds to managed areas is more tractable when animals seasonally aggregate (Maxwell et al., 2014; Whittock et al., 2014; Witt et al., 2008). In 2002, the central African country of Gabon created a system of coastal and terrestrial National Parks

91 with the aim of protecting key areas of biodiversity-rich habitats. Thirteen National Parks were 92 designated, including a single marine park to the south of the country at Mayumba (Fig. 1). 93 Gabon's beaches support important nesting sites for sea turtles, including globally important 94 breeding aggregations for the leatherback turtle (Dermochelys coriacea); the Southeast Atlantic 95 Ocean subpopulation is currently listed as IUCN Red List Data Deficient (Tiwari et al., 2013). 96 The northern and southern extremes of the Gabon coast (Pongara and Mayumba National Park) 97 receive the highest densities of nesting activity (Witt et al., 2009). Additionally, the olive ridley 98 (Lepidochelys olivacea), green (Chelonia mydas) and hawksbill sea turtles (Eretmochelys 99 *imbricata*) also nest (Casale et al., 2017; Maxwell et al., 2011; Metcalfe et al., 2015). 100 The leatherback turtle is highly migratory with expansive post-nesting dispersal patterns 101 (Fossette et al., 2014; Roe et al., 2014), but will seasonally aggregate off Gabon's nesting 102 beaches. Protection of large scale aggregations likely represents a significant management target 103 within coastal waters (Hitipeuw et al., 2007; Nel et al., 2013; Roe et al., 2014; Witt et al., 2008). 104 However, for protection to be effective, density and distributions of turtles need to be 105 ascertained and relevant threats identified, and if possible quantified, preferably in space and 106 time. In the marine environment, sea turtles may negatively interact with a broad suite of vessel 107 activity. These interactions can lead to by catch from coastal (Alfaro-Shigueto et al., 2007; Lum, 108 2006; Witt et al., 2011) and oceanic (Huang, 2015; Lewison et al., 2004) fisheries, boat strike 109 (Denkinger et al., 2013; Nabavi et al., 2012), crude oil contamination (Follett et al., 2014), or 110 possible displacement from critical habitats or auditory damage from seismic surveying (Nelms 111 et al., 2016). Within Gabon's territorial waters by catch from fisheries (Casale et al., 2017) 112 and/or boat strike (Billes et al., 2003) may negatively impact leatherback turtles. There is also 113 extensive offshore petrochemical extraction primarily located to the south of Port Gentil 114 (http://www.seaturtle.org/mtrg/projects/gabon/MarineAtlas.pdf). 115 At-sea vessel activity may be gathered by both Vessel Monitoring System (VMS) and 116 Automatic Identification System (AIS) data. The use of VMS, primarily as a tool for providing

117 at-sea densities of fisheries (Hintzen et al., 2012; Vermard et al., 2010; Witt and Godley, 2007)

118 has revolutionised the process of mapping, analysing and interpreting fisheries activity patterns.

119The advent of AIS may prove to provide additional capabilities due to time resolution of data120(Natale et al., 2015) and inclusion of multiple vessel types (Shelmerdine, 2015). The installation121and operation of VMS is discretional among maritime nations; the requirement to fit AIS122systems is, however, mandatory aboard vessels making international voyages with gross123tonnage \geq 300 t, cargo vessels \geq 500 t and all passenger ships regardless of size (Shelmerdine,1242015).

125 In this study, we combine aerial survey nest count data for leatherback turtles together 126 with satellite telemetry data from nesting females and contextualise these with VMS and AIS 127 data. Our aims were to: (i) model leatherback turtle distribution and relative density at sea using 128 a method that was independent of the need to sight species at sea, (ii) investigate areas of spatial 129 overlap between leatherback turtles and putative threats from vessels associated with multiple 130 industry categories, and (iii) identify key areas for inter-nesting leatherbacks within the 131 Gabonese Exclusive Economic Zone (EEZ) that may benefit from application of Marine 132 Protected Areas (MPAs).

133

134 2. METHODS

135

136 2.1. Aerial survey data

137

138 Aerial surveys were flown along the Gabonese coast using a variety of high-wing light 139 aircraft (Supplementary Material, Table A.1) as described in (Pikesley et al., 2013). Surveys 140 were organised to coincide with the main period of leatherback turtle nesting activity 141 (December-February; (Witt et al., 2009)). Multiple surveys were conducted in 2002/03 (n = 2), 142 2005/06 (n = 3) and 2006/07 (n = 3), with no surveys in 2003/04 and 2004/05. Each survey 143 represented a 600 km flight path (approximate straight-line distance). Flights commenced at 144 dawn. Surveys were timed to coincide with periods when the maximum width of the nesting 145 beach was unaffected by tide during early morning daylight hours, hence ensuring the greatest 146 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 a 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 (Fig. 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 are unlikely to support leatherback turtle nesting activity.

157 A video camera was used to record footage of the nesting beach during each aerial 158 survey. Leatherback turtle nesting activities were then counted from this video data in 159 accordance with the methodology described by (Witt et al., 2009). These counts were 160 aggregated into approximate 500 m linear sectors of beach (data bins) that were defined by 161 waypoint data collected continuously by hand-held Global Positioning System (GPS) receivers 162 aboard the aircraft at the time of the aerial surveys. A longitude/latitude (World Geodetic 163 System (WGS) 1984 format) midpoint was determined for each of these data bins to which the 164 counts were then associated.

165

- 166 **2.2. Satellite tracking data**
- 167

168 Platform Transmitter Terminals (PTTs) were attached to thirty-seven adult female

169 leatherback turtles at nesting locations in Gabon throughout the nesting season (October to

170 February: 2005/06 (n = 8), 2006/07 (n = 2), 2007/08 (n = 5), 2008/09 (n = 10), 2009/10 (n = 2)

171 and 2012/13 (n = 10)). Turtles were tagged within the National Parks of Pongara (n = 18) and

172 Mayumba (n = 19); inter-nesting movements of 7 of these turtles were previously published in

173 (Witt et al., 2008) (Fig. 1, and see metadata in Supplementary Material, Table A.2.). Methods of

turtle capture, transmitter type and process of attachment are detailed in Witt et al. (2011).

175	Satellite telemetry data were collected using the Argos satellite system (CLS, 2011) and
176	downloaded with the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley, 2005).
177	All locations with accuracy class Z and 0 were removed (Witt et al., 2010). Data were imported
178	into the Geographical Information System (GIS) ArcMap 10.1 (ESRI, Redlands, USA
179	http://www.esri.com) and visually assessed to determine nesting events for each female. Nesting
180	events typically occurred every 9 to 11 days, the night-time location with the highest accuracy
181	location class and located on, or nearest to land within this time-frame was chosen as indicative
182	nesting event. Satellite tracking location data were then apportioned by these inter-nesting
183	periods. Five turtles departed the Gabon coast immediately after attachment of the PTT; these
184	data were not used in further analysis.
185	
186	2.3. Modelling leatherback turtle distribution and relative density at sea
187	
188	2.3.1. Estimating leatherback turtle inter-nesting footprint at sea
189	
190	For each set of inter-nesting data (turtles $n = 32$, inter-nesting datasets $n = 121$: 2005/06
191	(n = 4), 2006/07 $(n = 3)$, 2007/08 $(n = 6)$, 2008/09 $(n = 35)$, 2009/10 $(n = 12)$ and 2012/13 $(n = 12)$
192	61)) we applied a speed and azimuth filter (Freitas et al., 2008; Witt et al., 2010); filtering was
193	undertaken in R (R Development Core Team 2008; R package: argosfilter (Freitas, 2010)).
194	Working in a projected coordinate system (Africa Albers Equal Area Conic (AAEAC)) the
195	geometric centroid of these data was determined together with the distance of each location
196	
	from the centroid; to remove spatial outliers we peeled data to the 95th quantile. The ellipsoid
197	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
197 198	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
197 198 199	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. An ellipsoid hull was chosen as this represents a regular
197 198 199 200	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. An ellipsoid hull was chosen as this represents a regular geometric form which can be constructed from component metrics (i.e. semi major/minor axis,
197 198 199 200 201	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. An ellipsoid hull was chosen as this represents a regular geometric form which can be constructed from component metrics (i.e. semi major/minor axis, centroid and azimuth). In the presented analysis, the number of inter-nesting locations used to

203	range: min $n = 10$, max $n = 218$). The length (km) of the semi-major and semi-minor axes, the
204	area (km ²) of the bounding ellipse, together with the shortest distance (km) (great-circle-
205	distance: Haversine formula) of the centroid to the coast were determined. All metrics were
206	expressed as a single value per turtle, averaging (mean) where necessary for multiple inter-
207	nesting periods. There was no significant difference in the median semi-major, semi-minor, or
208	offshore distance for leatherback turtles between the nesting locations of Pongara and Mayumba
209	National Parks (Supplementary Material, Table A.3.). We therefore calculated single
210	countrywide median values for each ellipse metric irrespective of release location.
211	
212	2.3.2. Linking inter-nesting footprint to aerial survey data
213	
214	The average (mean) number of leatherback turtles km ⁻² (at sea) per nesting season was
215	calculated using the following approach. We produced a smoothed coastline vector using a 40
216	km smoothing window. For each aerial survey dataset we used a spatial join in ArcMap to
217	assign ellipse metrics and coastal orientation to the midpoint coordinates of the data bins (data
218	were joined to the nearest existing location). These coordinates (projected coordinate system:
219	AAEAC) were then transposed offshore, perpendicular to the coast, using distance of centroid

220 to the coast (offshore distance) and coastal bearing.

221 For each offshore coordinate pair, with its associated aerial survey data bin, we 222 projected an ellipsoid polygon (major axis parallel to the coast), using grand averaged semi-223 major/minor axes and azimuth (coastal bearing). Each individual polygon surface was coerced 224 to a raster of 1 x 1 km resolution and each raster cell assigned a turtle density at sea (km^{-2}) 225 which was calculated from the aerial survey data as follows. To provide for an annual estimate 226 of the total number of nesting activities attributable to the data bin we divided the number of 227 tracks recorded on the day of the aerial survey by the proportion of nesting activities expected 228 for the day of the aerial survey. This proportion was determined from a normally distributed 229 seasonal nesting curve with approximations for the beginning and end of the nesting season of 230 1st October to 30th April respectively (see Witt et al., (2009) for detailed analysis of leatherback

turtle nesting effort in Gabon). This newly calculated annual nesting effort was then divided by a clutch frequency of 6.17 (\pm 0.47 SD (Miller 1997)), to provide the total number of turtles nesting within the data bin for the season. 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) which was then assigned to each raster cell. Resulting rasterised polygons were then stacked and summed to provide a composite raster surface (for each aerial survey) that described an estimate of the at-sea density (km⁻²) of inter-nesting leatherback turtles for the nesting season.

These raster surfaces 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.

244

245 2.4. VMS data: density mapping

246

247 We sourced Vessel Monitoring System (VMS) data from the Government of Gabon, for 248 Gabon flagged trawl vessel fishing activity within the Exclusive Economic Zone (EEZ) of 249 Gabon for 2010, 2011 and 2012. Fisheries primarily target prawns and shrimp, sardines, tuna 250 and a range of demersal fish species (Casale et al., 2017). The VMS data represented the best 251 possible continuous dataset available and contained 1 053 923 recorded locations (2010 (n =252 209 033), 2011 (n = 452 531), 2012 (n = 392 359)). All vessel identifications numbers were 253 anonymised, as such, each VMS record consisted of a pseudo-vessel reference number, 254 date/time stamp (UTC), geographic coordinates in decimal degrees (WGS 1984) and vessel type 255 (by fishing gear). Data were apportioned annually; 1st October to 30th September to reflect the 256 seasonality of leatherback turtle nesting: 2010/11 (*n* = 429 554), 2011/12 (*n* = 420 807). 257 For each annual VMS dataset, data were ordered by vessel reference number and 258 date/time stamp. Distance and time elapsed were calculated between each location, and vessel

259	speed calculated in knots. A speed rule was used to distinguish fishing from steaming or near-
260	stationery movement (Witt and Godley, 2007); only data with speeds ≥ 1 or ≤ 5 knots were
261	retained. Data were then apportioned into three seasonal groups: (i) October and November
262	(pre-peak leatherback nesting season), (ii) December to February (peak) and (iii) March and
263	April (post-peak). Seasonally grouped data were then processed as follow. For each vessel,
264	location data were then summarised (counts) to a 10 x 10 km resolution raster with only the first
265	location per day per cell being counted. This raster resolution was iteratively determined to
266	provide an optimum cell size that facilitated meaningful map interpretation. This process was
267	repeated for both annual datasets and the resulting rasters averaged (mean). These seasonal
268	vessel-density rasters were then divided by the respective numbers of days of the season (<i>i.e.</i>
269	October - November: $n = 61 d$) to provide a surface that described the average (mean) number
270	of unique vessels day ⁻¹ within each 10 x 10 km raster pixel.
271	
272	2.5. AIS data: density mapping
273	
274	We sourced ground and space merged Automatic Identification System (AIS) data from
275	ExactEarth (http://www.exactearth.com) for 2012, 2013 and 2014 for the EEZ of Gabon (space-
276	borne AIS data are not available prior to 2012). This dataset contained 22 791 353 recorded
277	locations (2012 (<i>n</i> = 3 719 235), 2013 (<i>n</i> = 7 043 142), 2014 (<i>n</i> = 12 028 976)). Each record
278	consisted of Maritime Mobile Service Identity (MMSI) number, date/time stamp (UTC),
279	geographic coordinates in decimal degrees (WGS 1984) and speed (knots). Records with speed
280	= 0 knots were removed. Vessels were assigned into one of five categories: cargo $n = 2240$
281	(39%), oil (support vessels: including tankers carrying crude/refined oil and other petrochemical
282	related products) $n = 1535$ (27%), oil (seismic research) $n = 45(1\%)$, fishing $n = 106$ (2%) and
283	miscellaneous (<i>e.g.</i> tug, passenger, recreational: $n = 1150 (20\%)$); 685 (12%) vessels could not
284	be assigned to a category due to insufficient metadata. Data were apportioned annually, 1st
285	October to 30th September to reflect the seasonality of leatherback turtle nesting: $2012/13$ (<i>n</i> =

4 637 128), 2013/14 (n = 6 327 527) and then divided into three seasonal groups (i) October and
November (ii) December to February and (iii) March and April.

288 For each seasonal dataset location data for the categories, cargo, oil (support vessels), 289 oil (seismic research) and fishing were treated as follows. A speed rule was used to remove 290 locations where vessels were not 'under-way' or exhibited near-stationery movement; only data 291 with speeds ≥ 1 knot were retained. For each category, location data for each vessel were 292 summarised (counts) to a 10 x 10 km resolution raster with only the first location per day per 293 cell being counted. This process was repeated for both annual datasets. Resultant rasters were 294 averaged and seasonal vessel-density rasters calculated that described the average (mean) 295 number of unique vessels day⁻¹ within each 10 x 10 km raster pixel.

296

297 **2.6.** Calculating spatial overlap between leatherback turtles and vessel distribution

298

299 Spatial overlap between vessel distribution and inter-nesting leatherback turtles was 300 calculated as follows. Seasonal vessel density rasters (trawl and longline/purse seine fisheries, 301 oil support, research and cargo vessels) were re-scaled to 0-1, summed and clipped to the extent 302 of the leatherback turtle density raster. These were then multiplied with our seasonally 303 apportioned leatherback density rasters to provide seasonal unitless relative threat indices for: (i) 304 the complete nesting season, (ii) the peak months (December, January, February) and (iii) the 305 pre- and post-peak months (October, November, and March, April). To provide for data at the 306 same spatial resolution we re-sampled our leatherback turtle at-sea density raster to the same 307 resolution (10 x 10 km) as our VMS and AIS layers using bilinear interpolation. 308 309 **3. RESULTS** 310 311 3.1. Leatherback turtle satellite tracking and spatial density patterns

313	Thirty-two leatherback turtles (Pongara $n = 18$, Mayumba $n = 14$) were tracked for 121
314	inter-nesting periods (Pongara $n = 101$, Mayumba $n = 20$) with an average time between nest
315	events of 10 ± 1 days (mean ± 1 SD; range 7 - 13 days). Turtles primarily remained within
316	continental shelf waters (depths ≤ 200 m), with 93.8% (Pongara; $n = 9530$) and 93.1%
317	(Mayumba; $n = 1504$) of all recorded locations in these waters. Off the coast of Gabon, the
318	continental shelf break lies approximately 45 km from the coast to the north of the country
319	(north of Port Gentil), 50 to 60 km to the south of the country and within 6 km of the coast at
320	Port Gentil. Nintey-one percent ($n = 10749$) of all locations were located within the Exclusive
321	Economic Zone (EEZ) of Gabon (Fig. 1).
322	The modelled spatial pattern of inter-nesting leatherback turtles at sea indicated that the
323	coastal waters of Pongara and Mayumba National Parks had high densities of inter-nesting
324	leatherbacks, with a smaller hotspot offshore from Sette Cama Reserve and to the south of Port
325	Gentil; greatest density was within and neighbouring the Mayumba Marine Park (Fig. 1).
326	
327	3.2. VMS and AIS density mapping
328	
329	3.2.1 Fisheries
330	
331	Mapping of VMS data for Gabon trawl vessels (October to April) indicated presence of
332	vessels across the majority of coastal waters, with peaks in density to the south of Pongara
333	National Park, and in near-shore waters of Loango National Park. There was negligible activity
334	off the continental shelf (Fig. 2a). Analysis of AIS fishing vessel data for longline and purse
335	seine fisheries, in general, indicated higher density of vessels in offshore waters, approximately
336	100 - 200 km southwest of Loango National Park (Fig. 2e). There was relatively little activity
337	on the continental shelf, with the exception of a small high-density area to the south of
338	Mayumba National Park. These distinctions in spatial patterns largely reflect the difference in
339	gear type used by these fisheries. There was no duplication of vessels among AIS and VMS
340	datasets.

341	Apportioning AIS and VMS fisheries data by leatherback nesting season revealed
342	seasonal patterns for both these datasets. Mapping of VMS data indicated a north/south shift in
343	fishing activity. Maximum densities occurred in October/November near Pongara and Loango
344	National Park. Densities remained high at Loango within the months of December to April, but
345	decreased at Pongara (Fig. 2b,c,d). Mapping of AIS data indicated that October/November were
346	peak months for longline and purse seine fisheries with maximum densities occurring southwest
347	of Loango National Park. There was an indication of increased fisheries activity immediately to
348	the south of Mayumba Marine Park during October to February (Fig. 2f,g,h).
349	
350	3.2.2. Oil industry and cargo vessels
351	
352	Mapping of AIS data (October to April) revealed marked differences between vessel
353	categories. For example, oil support vessels formed defined routes between the ports of
354	Libreville and Port Gentil, as well as westward from Port Gentil (Fig. 3a). Mapping the
355	distribution of cargo vessels (<i>i.e.</i> bulk carriers, container vessels) identified two routes. The first
356	lay parallel to the coast from Port Gentil in the north to the Gabon/Congo EEZ border in the
357	south and broadly mirrored the 200 m isobath, the second ran westward from the port of
358	Libreville (Fig. 3i). There was no marked differences among seasonal density mapping for oil
359	support vessels, or for cargo vessels (Fig. 3b,c,d,j,k,l). Hotspots of seismic vessel movement
360	occurred in continental shelf waters, and were primarily concentrated to the south of Port Gentil
361	and in coastal waters of Loango National Park and Sette Cama Reserve (Fig. 3e). There were
362	clear differences among seasonal density mapping for seismic vessels. There was relatively high
363	seismic vessel presence to the southwest of Mayumba Marine Park at the beginning of the
364	nesting season (October/November), to the south of Port Gentil during peak season (December
365	to February) and in coastal waters of Loango National Park in March/April (Fig. 3f,g,h). These
366	seasonal differences may reflect seasonal legislative restrictions or indicate interest in
367	exploitation. However, it should be noted that presence of seismic vessels does not necessarily
368	indicate vessels were engaged in seismic survey activity.

370 **3.3. Spatial overlap between leatherback turtles and vessel distribution**

371

372 Mapping spatial overlap of leatherback turtles and vessel distribution indicated that the 373 coastal waters of Pongara and Mayumba National Park were subject to high levels of putative 374 threat throughout the leatherback nesting season (Fig. 4b). There were also isolated areas of 375 moderate/high putative threat within coastal waters from Port Gentil to Sette Cama Reserve, 376 primarily due to coastal fisheries and seismic vessels present within the area. There was 377 variation in magnitude and timing of threat among locations. Spatially, co-occurrence was 378 greatest at Pongara at the beginning of the season (October/November) (Fig. 4d), principally 379 due to the heightened level of coastal fisheries activity, and from Port Gentil to Sette Cama and 380 within and adjacent to Mayumba Marine Park during peak season (December/January/February) 381 and post-peak (March/April) (Fig. 4f,h).

382

383 4. DISCUSSION

384

385 Sightings-based distance sampling (Buckland et al., 2001) is likely the most widely 386 used method to determine densities of animals at sea, relying on data being collected either by 387 way of boat or aerial transect (Aerts et al., 2013; Hammond et al., 2002). Whilst distance-388 sampling is well established and relatively accessible it has some limitations (Evans and 389 Hammond, 2004). The presented analysis sought to develop a complementary methodology to 390 estimate at-sea distributions and relative densities that was independent of the need to sight 391 species at sea, and that in turn could be applied to other species of sea turtles for cumulative 392 assessments. With adaptation, this methodology may also have utility in defining critical 393 habitats for other central-place foragers such as pinnipeds, or sea bird species (Cronin et al., 394 2013; Grecian et al., 2010; Sharples et al., 2012).

Ecosystem based impact assessments can identify areas where cumulative threat may be at its greatest within the marine environment (Halpern et al., 2008), but may not take into

397 account distribution and densities of species within these areas. Furthermore, it is possible that 398 areas subject to relatively high cumulative threat, and with high species densities, will fail to 399 attract adequate conservation effort (Lewison et al., 2014). Identifying key areas where species 400 aggregate may facilitate the decision process of where and when to best place conservation 401 resources to achieve maximum benefit (Hart et al., 2012). With this analysis, we sought to 402 further the process of impact assessment by formulating a cumulative threat index that assessed 403 multiple threats from vessels, whilst at the same time integrating modelled distribution and 404 densities of a species of conservation concern. Our analysis does not attempt to differentiate 405 threats from vessels by magnitude, or relative importance. Whilst the presented analysis is 406 primarily spatial in nature, we also sought to present these spatial patterns in relation to the peak 407 and pre- and post-peak months of the leatherback nesting season. However, threat to turtles and 408 subsequent impacts will also be related to other compounding factors such as turtle behaviour 409 (diving or at surface) and temporal influences such as seasonal fisheries activity (deployment of 410 season-specific gear types) or oil industry activity/spills. It remains likely that many 'threats' 411 require further knowledge or assessment to quantify probable impacts. To do so effectively, 412 species sensitivity to threats needs to be assessed, this in turn, would additionally allow 413 assignment of weights for calculating cumulative impact. 414 Our analysis revealed that within the peak leatherback nesting season (December to 415 February), when approximately 80% of the season's nesting takes place (Witt et al., 2009), 416 greatest densities of leatherback turtles likely occur in coastal waters adjacent to Pongara and 417 Mayumba National Parks, with a smaller 'hotspot' to the west of Sette Cama Reserve. 418 Contextualising these at-sea density and distribution patterns, with vessel movements derived 419 from VMS and AIS location data, suggests that vessels associated with various industries have 420 the potential to interact with inter-nesting leatherback turtles within Gabonese coastal waters, 421 throughout the nesting season.

422 Density mapping of the Gabon trawl fisheries fleet (for which VMS data were
423 available) indicated that this fleet could interact with at-sea leatherbacks at all high-density
424 leatherback areas. In coastal waters adjacent to Pongara National Park, the potential for this was

425 greatest at the start of the nesting season. There was a subsequent southerly shift in vessel 426 densities for coastal fisheries later in the nesting leatherback season. Analysis of AIS fisheries 427 data, which predominantly comprised of large Distant Water Fleet (DWF) vessels, suggested 428 that there was no activity for this category of vessel within coastal waters of Pongara National 429 Park. There was however, a hotspot of DWF vessel activity just within, and adjoining the 430 southwest/south-easterly border of Mayumba Marine Park at the start of, and during peak 431 nesting season. The coastal waters of Pongara National Park had the highest density of vessels 432 associated with shipping routes for both oil industry and cargo vessels. There were notable 433 hotspots of vessel movements both between the ports of Libreville and Port Gentil in coastal 434 waters, and offshore from these ports to the open ocean, throughout the nesting season. Seismic 435 vessel activity was primarily confined to the coastal waters south of Port Gentil and to the 436 southwest of Mayumba Marine Park. The coastal waters of Pongara National Park had high 437 levels of cumulative threat throughout the nesting season. Cumulative threat mapping indicated 438 the coastal waters from south of Port Gentil to Mayumba National Park had greatest levels of 439 cumulative threat through the peak and post-peak nesting season.

440 Several caveats must be considered when interpreting the findings of this study. Our 441 approach only uses data sourced from adult females and therefore does not consider juvenile or 442 male turtle habitat use. The distribution and density estimates of female leatherback nesting 443 activity were derived from aerial survey data sourced from seven aerial surveys (2002/03 to 444 2006/07). Inclusion of additional aerial survey data within this analysis may modify model 445 outputs; although unpublished data (Formia pers. comm.) suggests nesting patterns are similar. 446 Our method does not account for any temporal variability in nesting season that may be present 447 between the north and south of the country (Witt et al., 2009). This would be unlikely to affect 448 the modelled at-sea densities of leatherbacks, but should be considered when interpreting threat 449 mapping. Similarly, our method utilises a normally distributed nesting curve to calculate annual 450 estimates of the total number of nesting activities for each data bin, with approximations for the 451 beginning and end of the nesting season of 1st October to 30th April respectively. These 452 estimates would be slightly modified under alternative curve scenarios. To calculate the total

number of turtles nesting within each data bin for the season we applied a clutch frequency of
6.17 (Miller 1997). As our main goal was to demonstrate overlap of turtle distribution and
density with vessel activity using a relative threat index the value for clutch frequency was not
critical. However, it should be noted that clutch frequency is a critical metric in determining
population abundance (Esteban et al., 2017).

458 It is also probable that our vessel densities represent underestimations. Our analysis 459 only considers vessels that are legally required to transmit their locations by way of VMS or 460 AIS. Similarly, these systems need to be enabled and transmitting. Applying a slow speed filter 461 to all AIS data to remove vessel traffic that was not 'under-way' may have the effect of 462 removing some locations for vessels deploying purse seine gear; although, it is highly unlikely 463 that a vessel will remain motionless 'at sea' given the influence of wind and or tide and currents. 464 For coastal fisheries, we only evaluate data for the Gabon fleet. Vessel movements for DWFs 465 and artisanal fisheries are not considered; therefore, these sectors remain un-assessed. In 466 addition, our VMS data are sourced prior to September 2012. Subsequent changes to fisheries 467 management regimes within Gabon, including the definition of no-take and exclusion zones, are 468 likely to have modified vessel movement patterns in the vicinity of these zones. Finally, whilst 469 some of our component data layers do not overlap temporally, primarily due to logistical or 470 financial constraints, they represent the best available data from which to formulate this 471 analysis. Notwithstanding these temporal inconsistencies, we consider that the methodology 472 presented is sound and capable of generating realistic density estimates. However, we 473 acknowledge that these density estimates and associated threat indices may be improved with 474 temporally concurrent data.

Although the presented analysis focuses on a single species, much of the associated
threats will apply to other air-breathing mobile marine vertebrates in Gabonese coastal waters.
These species include olive ridley sea turtles (Maxwell et al., 2011; Metcalfe et al., 2015),
humpback dolphins (*Sousa teuszii*) (Collins, 2015; Weir and Collins, 2015) and humpback
whales (*Megaptera novaeangliae*) (Rosenbaum et al., 2014); although mitigation and
management measures would undoubtedly be species specific. Such an approach to monitoring

481 key activities of relevance to conservation is considered among the key global priorities for 482 cetacean research (Parsons et al 2015). This is especially salient given the emerging evidence 483 that some baleen whales have limited potential for vessel avoidance (McKenna et al 2015). 484 Historically, Mayumba Marine Park was the only designated MPA within the Gabon 485 EEZ: confined to a 15 x 60 km strip of coastal waters to the far south of the Gabonese EEZ. 486 Typically, small protected areas offer limited conservation benefits (Gaines et al., 2010) 487 particularly to mobile species. A recent comprehensive marine spatial planning review has been 488 made of Gabon's territorial waters which integrated data from this analysis. This review has led 489 to, approximately 23% of Gabon's territorial waters and EEZ being designated as MPAs, in 490 which commercial fishing will be excluded. For leatherback turtles, this is likely to result in 491 increased protection of inter-nesting at-sea habitat in waters adjacent to Mayumba National 492 Park, in near-shore waters to the south of Port Gentil and to the north, at Pongara (Fig. 5). 493 Indeed, associated management strategies protecting marine habitats and improving fisheries 494 management, including improved surveillance and enforcement of fisheries, as well as 495 designation of exclusion zones around maritime oil and gas infrastructure, likely already 496 influence some vessel movements in key areas identified in this study. Ultimately, with 497 increased spatio-temporal understanding of threat (gleaned from continued collection and 498 analysis of vessel movements) and species/vessel interactions (collected by way of boat 499 observer programs and post-mortems), together with better temporal understanding of impacts 500 (e.g. deployment of season-specific gear types), MPA design and management strategies may be 501 tailored and fine-tuned to deliver a holistic network of protected areas that provide protection 502 for a suit of Gabon's biodiversity rich marine species.

503

504 ACKNOWLEDGEMENTS

505

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
- 510 Research Centre at the University of Massachusetts (Boston), NERC, Vaalco Energy and the
- 511 Wildlife Conservation Society. We are sincerely grateful to the field teams and logistics staff
- 512 who assisted in the aerial and ground surveys and with field-site assistance. BJG and MJW
- 513 receive funding from the Natural Environment Research Council (NE/J012319/1), the European
- 514 Union and the Darwin Initiative. The authors would like to acknowledge the constructive input
- 515 from three anonymous referees, the Editor and the Associate Editor.

516 References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., Matthiopoulos, J., 2008. Estimating
 space- use and habitat preference from wildlife telemetry data. Ecography 31, 140–
 160.
- Aerts, L.A.M., McFarland, A.E., Watts, B.H., Lomac-MacNair, K.S., Seiser, P.E., Wisdom,
 S.S., Kirk, A.V., Schudel, C.A., 2013. Marine mammal distribution and abundance
 in an offshore sub-region of the northeastern Chukchi Sea during the open-water
 season. Cont. Shelf Res. 67, 116–126. doi:10.1016/j.csr.2013.04.020
- Alfaro-Shigueto, J., Dutton, P.H., Van Bressem, M., Mangel, J., 2007. Interactions between
 leatherback turtles and Peruvian artisanal fisheries. Chelonian Conserv. Biol. 6,
 129–134.
- Becker, E.A., Forney, K.A., Foley, D.G., Smith, R.C., Moore, T.J., Barlow, J., 2014.
 Predicting seasonal density patterns of California cetaceans based on habitat models. Endanger. Species Res. 23, 1–22.
- Briscoe, D.K., Maxwell, S.M., Kudela, R., Crowder, L.B., Croll, D., 2016. Are we missing
 important areas in pelagic marine conservation? Redefining conservation hotspots
 in the ocean. Endanger. Species Res. 29, 229–237.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D., Thomas, L.,
 2001. Introduction to distance sampling estimating abundance of biological
 populations. Oxford University Press, Oxford.
- 536 CLS, 2011. Argos user's manual. 537 http://www.argossystem.or
 - http://www.argossystem.org/documents/userarea/argos_manual_en.pdf.
- Casale, P., Abitsi, G., Aboro, M.P., Agamboue, P.D., Agbode, L., Allela, N.L., Angueko,
 D., Nguema, J.N.B.B., Boussamba, F., Cardiec, F., 2017. A first estimate of sea
 turtle bycatch in the industrial trawling fishery of Gabon. Biodivers. Conserv. 1–13.
- 541 Collins, T., 2015. Chapter Three-Re-assessment of the Conservation Status of the Atlantic
 542 Humpback Dolphin, Sousa teuszii (), Using the IUCN Red List Criteria. Adv. Mar.
 543 Biol. 72, 47–77.
- 544 Coyne, M.S., Godley, B.J., 2005. Satellite Tracking and Analysis Tool (STAT): an
 545 integrated system for archiving, analyzing and mapping animal tracking data. Mar.
 546 Ecol. Prog. Ser. 301, 1–7.
- 547 Cronin, M., Pomeroy, P., Jessopp, M., 2013. Size and seasonal influences on the foraging
 548 range of female grey seals in the northeast Atlantic. Mar. Biol. 160, 531–539.
- Billes, A., Fretey, J., Mourndembe, J., 2003. Monitoring of leatherback turtles in Gabon.
 Presented at the Proceedings of the 22nd Annual Symposium of Sea Turtle Biology and Conservation, pp. 131–132.
- Denkinger, J., Parra, M., Muñoz, J.P., Carrasco, C., Murillo, J.C., Espinosa, E., Rubianes,
 F., Koch, V., 2013. Are boat strikes a threat to sea turtles in the Galapagos Marine
 Reserve? Ocean Coast. Manag. 80, 29–35. doi:10.1016/j.ocecoaman.2013.03.005
- Edrén, S., Wisz, M.S., Teilmann, J., Dietz, R., Söderkvist, J., 2010. Modelling spatial
 patterns in harbour porpoise satellite telemetry data using maximum entropy.
 Ecography 33, 698–708.
- Esteban, N., Mortimer, J.A., Hays, G.C., 2017. How numbers of nesting sea turtles can be
 overestimated by nearly a factor of two. Presented at the Proc. R. Soc. B, The Royal
 Society, p. 20162581.
- Evans, P.G., Hammond, P.S., 2004. Monitoring cetaceans in European waters. Mammal
 Rev. 34, 131–156.
- Follett, L., Genschel, U., Hofmann, H., 2014. A graphical exploration of the Deepwater
 Horizon oil spill. Comput. Stat. 29, 121–132.
- Forney, K.A., Becker, E.A., Foley, D.G., Barlow, J., Oleson, E.M., 2015. Habitat-based
 models of cetacean density and distribution in the central North Pacific. Endanger.
 Species Res. 27, 1–20.

568 Fossette, S., Witt, M., Miller, P., Nalovic, M., Albareda, D., Almeida, A., Broderick, A., 569 Chacón-Chaverri, D., Coyne, M., Domingo, A., 2014. Pan-Atlantic analysis of the 570 overlap of a highly migratory species, the leatherback turtle, with pelagic longline 571 fisheries. Proc. R. Soc. B Biol. Sci. 281. doi:DOI: 10.1098/rspb.2013.3065 572 Freitas, C., 2010. argosfilter: Argos locations filter. R package version 0.62. 573 Freitas, C., Lydersen, C., Fedak, M.A., Kovacs, K.M., 2008. A simple new algorithm to 574 filter marine mammal Argos locations. Mar. Mammal Sci. 24, 315–325. 575 Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve 576 networks for both conservation and fisheries management. Proc. Natl. Acad. Sci. 577 107, 18286-18293. doi:10.1073/pnas.0906473107 578 Grecian, W.J., Inger, R., Attrill, M.J., Bearhop, S., Godley, B.J., Witt, M.J., Votier, S.C., 579 2010. Potential impacts of wave- powered marine renewable energy installations on 580 marine birds. Ibis 152, 683-697. 581 Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, 582 J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., 583 Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 584 2008. A Global Map of Human Impact on Marine Ecosystems. Science 319, 948-585 952. 586 Hammond, P., Berggren, P., Benke, H., Borchers, D., Collet, A., Heide- Jørgensen, M., 587 Heimlich, S., Hiby, A., Leopold, M.F., Øien, N., 2002. Abundance of harbour 588 porpoise and other cetaceans in the North Sea and adjacent waters. J. Appl. Ecol. 589 39, 361–376. 590 Hart, K.M., Lamont, M.M., Fujisaki, I., Tucker, A.D., Carthy, R.R., 2012. Common coastal 591 foraging areas for loggerheads in the Gulf of Mexico: Opportunities for marine 592 conservation. Biol. Conserv. 145, 185-194. Hintzen, N.T., Bastardie, F., Beare, D., Piet, G.J., Ulrich, C., Deporte, N., Egekvist, J., 593 594 Degel, H., 2012. VMStools: open-source software for the processing, analysis and 595 visualisation of fisheries logbook and VMS data. Fish. Res. 115, 31-43. 596 Hitipeuw, C., Dutton, P.H., Benson, S., Thebu, J., Bakarbessy, J., 2007. Population Status 597 and Internesting Movement of Leatherback Turtles, Dermochelys coriacea, Nesting 598 on the Northwest Coast of Papua, Indonesia. Chelonian Conserv. Biol. 6, 28-36. 599 doi:10.2744/1071-8443(2007)6[28:PSAIMO]2.0.CO;2 600 Huang, H.-W., 2015. Conservation Hotspots for the Turtles on the High Seas of the Atlantic 601 Ocean. PloS One 10, e0133614. Hyrenbach, K.D., Forney, K.A., Dayton, P.K., 2000. Marine protected areas and ocean 602 603 basin management. Aquat. Conserv. Mar. Freshw. Ecosyst. 10, 437-458. 604 doi:10.1002/1099-0755(200011/12)10:6<437::AID-AQC425>3.0.CO;2-Q 605 Lauriano, G., Panigada, S., Casale, P., Pierantonio, N., Donovan, G., 2011. Aerial survey 606 abundance estimates of the loggerhead sea turtle Caretta caretta in the Pelagos 607 Sanctuary, northwestern Mediterranean Sea. Mar Ecol Prog Ser 437, 291–302. 608 Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelis, R., McDonald, 609 S., DiMatteo, A., Dunn, D.C., Kot, C.Y., 2014. Global patterns of marine mammal, 610 seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna 611 hotspots. Proc. Natl. Acad. Sci. 111, 5271-5276. 612 Lewison, R.L., Freeman, S.A., Crowder, L.B., 2004. Quantifying the effects of fisheries on 613 threatened species: the impact of pelagic longlines on loggerhead and leatherback 614 sea turtles. Ecol. Lett. 7, 221-231. 615 Lum, L.L., 2006. Assessment of incidental sea turtle catch in the artisanal gillnet fishery in 616 Trinidad and Tobago, West Indies. Appl. Herpetol. 3, 357–368. 617 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2015. cluster: Cluster 618 Analysis Basics and Extensions. R package version 1.15.2.

619 Matthiopoulos, J., McConnell, B., Duck, C., Fedak, M., 2004. Using satellite telemetry and 620 aerial counts to estimate space use by grey seals around the British Isles. J. Appl. 621 Ecol. 41, 476-491. 622 Maxwell, S.M., Ban, N.C., Morgan, L.E., 2014. Pragmatic approaches for effective 623 management of pelagic marine protected areas. Endanger. Species Res. 26, 59-74. 624 Maxwell, S.M., Breed, G.A., Nickel, B.A., Makanga-Bahouna, J., Pemo-Makaya, E., 625 Parnell, R.J., Formia, A., Ngouessono, S., Godley, B.J., Costa, D.P., Witt, M.J., 626 Coyne, M.S., 2011. Using satellite tracking to optimize protection of long-lived 627 marine species: olive ridley sea turtle conservation in central Africa. PloS One 6, 628 e19905. 629 Metcalfe, K., Agamboué, P.D., Augowet, E., Boussamba, F., Cardiec, F., Fay, J.M., Formia, A., Kema, J.R.K., Kouerey, C., Mabert, B.D.K., 2015. Going the extra mile: 630 Ground-based monitoring of olive ridley turtles reveals Gabon hosts the largest 631 632 rookery in the Atlantic. Biol. Conserv. 190, 14-22. Miller, J.D., 1997. Reproduction in sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology 633 634 of Sea Turtles. CRC Press, Boca Raton, p. 432. 635 Nabavi, S.M.B., Zare, R., Vaghefi, M.E., 2012. Nesting Activity and Conservation Status of 636 the Hawksbill Turtle(Eretmochelys imbricata) in Persian Gulf. J. Life Sci. 6, 74–79. Natale, F., Gibin, M., Alessandrini, A., Vespe, M., Paulrud, A., 2015. Mapping Fishing 637 Effort through AIS Data. PloS One 10, e0130746. 638 639 Nel, R., Punt, A.E., Hughes, G.R., 2013. Are coastal protected areas always effective in 640 achieving population recovery for nesting sea turtles? PloS One 8, e63525. 641 Nelms, S.E., Piniak, W.E., Weir, C.R., Godley, B.J., 2016. Seismic surveys and marine 642 turtles: An underestimated global threat? Biol. Conserv. 193, 49-65. 643 Pikesley, S.K., Agamboue, P.D., Bonguno, E.A., Boussamba, F., Cardiec, F., Fay, J.M., 644 Formia, A., Godley, B.J., Laurance, W.F., Mabert, B.D.K., others, 2013. Here 645 today, here tomorrow: Beached timber in Gabon, a persistent threat to nesting sea 646 turtles. Biol. Conserv. 162, 127-132. 647 Pikesley, S.K., Broderick, A.C., Cejudo, D., Coyne, M.S., Godfrey, M.H., Godley, B.J., Lopez, P., López-Jurado, L.F., Elsy Merino, S., Varo-Cruz, N., Witt, M.J., Hawkes, 648 649 L.A., 2014. Modelling the niche for a marine vertebrate: a case study incorporating 650 behavioural plasticity, proximate threats and climate change. Ecography 38, 803-651 812. doi:10.1111/ecog.01245 652 Roe, J.H., Morreale, S.J., Paladino, F.V., Shillinger, G.L., Benson, S.R., Eckert, S.A., 653 Bailey, H., Tomillo, P.S., Bograd, S.J., Eguchi, T., 2014. Predicting bycatch 654 hotspots for endangered leatherback turtles on longlines in the Pacific Ocean. Proc. 655 R. Soc. B Biol. Sci. 281, 20132559. 656 Rosenbaum, H.C., Maxwell, S.M., Kershaw, F., Mate, B., 2014. Long- Range Movement 657 of Humpback Whales and Their Overlap with Anthropogenic Activity in the South 658 Atlantic Ocean. Conserv. Biol. 28, 604-615. 659 Scheidat, M., Verdaat, H., Aarts, G., 2012. Using aerial surveys to estimate density and 660 distribution of harbour porpoises in Dutch waters. J. Sea Res. 69, 1–7. 661 Seminoff, J.A., Eguchi, T., Carretta, J., Allen, C.D., Prosperi, D., Rangel, R., Gilpatrick Jr, J.W., Forney, K., Peckham, S.H., 2014. Loggerhead sea turtle abundance at a 662 663 foraging hotspot in the eastern Pacific Ocean: implications for at-sea conservation. 664 Endanger. Species Res. 24, 207-220. 665 Sharples, R.J., Moss, S.E., Patterson, T.A., Hammond, P.S., 2012. Spatial variation in 666 foraging behaviour of a marine top predator (Phoca vitulina) determined by a largescale satellite tagging program. PLoS One 7, e37216. 667 Shelmerdine, R.L., 2015. Teasing out the detail: how our understanding of marine AIS data 668 669 can better inform industries, developments, and planning. Mar. Policy 54, 17-25.

- 670 Stapleton, S., Peacock, E., Garshelis, D., 2015. Aerial surveys suggest long- term stability
 671 in the seasonally ice- free Foxe Basin (Nunavut) polar bear population. Mar.
 672 Mammal Sci.
- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L.,
 Bishop, J.R., Marques, T.A., Burnham, K.P., 2010. Distance software: design and
 analysis of distance sampling surveys for estimating population size. J. Appl. Ecol.
 47, 5–14.
- Tiwari, M., Wallace, B.P. & Girondot, M. 2013. Dermochelys coriacea (Southeast Atlantic
 Ocean subpopulation). The IUCN Red List of Threatened Species 2013.
- 679 Vermard, Y., Rivot, E., Mahévas, S., Marchal, P., Gascuel, D., 2010. Identifying fishing trip
 680 behaviour and estimating fishing effort from VMS data using Bayesian Hidden
 681 Markov Models. Ecol. Model. 221, 1757–1769.
- Wedding, L., Maxwell, S., Hyrenbach, D., Dunn, D., Roberts, J., Briscoe, D., Hines, E.,
 Halpin, P., 2016. Geospatial approaches to support pelagic conservation planning
 and adaptive management. Endanger. Species Res. 30, 1–9.
- Weir, C.R., Collins, T., 2015. Chapter Four-A Review of the Geographical Distribution and
 Habitat of the Atlantic Humpback Dolphin (Sousa teuszii). Adv. Mar. Biol. 72, 79–
 117.
- 688 Whittock, P.A., Pendoley, K.L., Hamann, M., 2014. Inter-nesting distribution of flatback
 689 turtles Natator depressus and industrial development in Western Australia.
 690 Endanger. Species Res. 26, 25–38.
- Witt, M.J., Akesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C.,
 Luschi, P., Stroud, S., Godley, B.J., 2010. Assessing accuracy and utility of
 satellite-tracking data using Argos-linked Fastloc-GPS. Anim. Behav. 80, 571–581.
- Witt, M.J., Baert, B., Broderick, A.C., Formia, A., Fretey, J., Gibudi, A., Mounguengui,
 G.A.M., Moussounda, C., Ngouessono, S., Parnell, R.J., 2009. Aerial surveying of
 the world's largest leatherback turtle rookery: a more effective methodology for
 large-scale monitoring. Biol. Conserv. 142, 1719–1727.
- Witt, M.J., Bonguno, E.A., Broderick, A.C., Coyne, M.S., Formia, A., Gibudi, A.,
 Mounguengui, G.A.M., Moussounda, C., NSafou, M., Nougessono, S., 2011.
 Tracking leatherback turtles from the world's largest rookery: assessing threats
 across the South Atlantic. Proc. R. Soc. B Biol. Sci. 278, 2338–2347.
- Witt, M.J., Broderick, A.C., Coyne, M.S., Formia, A., Ngouessono, S., Parnell, R.J.,
 Sounguet, G.-P., Godley, B.J., 2008. Satellite tracking highlights difficulties in the
 design of effective protected areas for Critically Endangered leatherback turtles
 Dermochelys coriacea during the inter-nesting period. Oryx 42, 296–300.
- Witt, M.J., Godley, B.J., 2007. A Step Towards Seascape Scale Conservation: Using Vessel
 Monitoring Systems (VMS) to Map Fishing Activity. PloS One 2, e1111.
- 708
- 709

711 Legends

712 Fig. 1. Location data (black circles) of satellite tracked inter-nesting leatherback turtles tracked 713 from, (a) Pongara National Park (n = 18) and (b) Mayumba National Park (n = 14). Tagging 714 locations (white stars). (c) Modelled leatherback turtle density at-sea October-April. Densities 715 (turtles 100 km⁻² apportioned by percentiles) are drawn in accordance with the figure legend. 716 200 m continental shelf isobath (broken line) and EEZ maritime boundaries (broken line 717 polygon). In part (c) coastal National Parks (dark-grey polygons) and reserves (mid-grey 718 polygons) and the ports of Libreville and Port Gentil are labelled. Mayumba National Park 719 (Marine Protected Area (MPA)), broken white polygon. Part (c) is located according to the 720 inset. All parts drawn to differing spatial scales. Map drawn to Projected Coordinate System: 721 Africa Albers Equal Area Conic. 722 723 Fig. 2. Density mapping of fisheries activity derived from Vessel Monitoring System (VMS) 724 and Automatic Identification System (AIS) data. (a-d) VMS data for leatherback nesting 725 seasons 2010/11 and 2011/12. A speed rule was applied to distinguish fishing from steaming or 726 near-stationery movement (Witt & Godley 2007); only data with speeds ≥ 1 or ≤ 5 knots were 727 retained. (e-h) AIS data for leatherback nesting seasons 2012/13 and 2013/14. A speed rule was 728 applied to remove near-stationery movement; only data with speeds ≥ 1 knot were retained. For 729 each dataset, data for the complete nesting season (a,e) were apportioned into three seasonal 730 groups: (b,f) October and November, (c,g) December to February and (d,h) March and April. 731 Location data were summarised (counts) to a 10 x 10 km resolution raster with only the first 732 location per day per cell being counted. Annual averaged seasonal density rasters were then 733 divided by the respective numbers of days of the season. This provided a surface that described 734 the average (mean) number of unique vessels day⁻¹ within each 10 x 10 km raster pixel. Parts 735 (a,b,c,d) and (e,f,g,h) are drawn to differing spatial scales. All other map features are drawn and 736 labelled in accordance with Fig. 1. Map drawn to Projected Coordinate System: Africa Albers

737 Equal Area Conic.

739 Fig. 3. Density mapping of vessel activity categorised as, (a-d) oil support vessels, including 740 tankers carrying crude/refined oil and other petrochemical related products, (e-h) seismic 741 research vessels and (i-l) cargo vessels, derived from Automatic Identification System (AIS) 742 data for leatherback nesting seasons 2012/13 and 2013/14. A speed rule was applied to remove 743 near-stationery movement; only data with speeds ≥ 1 knot were retained. Data for the complete 744 nesting season (a,e,i) were then apportioned into three seasonal groups: (b,f,j) October and 745 November, (c,g,k) December to February and (d,h,i) March and April. Location data were 746 summarised (counts) to a 10 x 10 km resolution raster with only the first location per day per 747 cell being counted. Annual averaged seasonal density rasters were then divided by the 748 respective numbers of days of the season. This provided a surface that described the average 749 (mean) number of unique vessels day⁻¹ within each 10 x 10 km raster pixel. All parts drawn to 750 the same spatial scale. All other map features are drawn and labelled in accordance with Fig. 1. 751 Map drawn to Projected Coordinate System: Africa Albers Equal Area Conic. 752 753 Fig. 4. Cumulative seasonal vessel densities (a,c,e,g). Vessel density rasters were re-scaled 0-1 754 and summed. Threat index for inter-nesting leatherback turtles (b,d,f,h). Cumulative vessel 755 density rasters were multiplied by leatherback density rasters. To provide for data at the same 756 spatial resolution leatherback turtle at-sea density raster were re-sampled to the same resolution

757 (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 Fig. 1. Map

761 drawn to Projected Coordinate System: Africa Albers Equal Area Conic.

762

Fig. 5. Leatherback turtle density at-sea and Marine Protected Areas. Leatherback turtle

densities (turtles 100 km⁻² apportioned by percentiles: October-April) are drawn in accordance

765 with the figure legend. Mayumba National Park (Marine Protected Area (MPA)), broken white

766 polygon, all other MPAs, black hatched polygons. All other map features are drawn and labelled

- 767 in accordance with Fig. 1. Map drawn to Projected Coordinate System: Africa Albers Equal
- 768 Area Conic.
- 769

- 770 Figure(s)
- 771 Fig. 1.





779 Fig. 3.



781 Fig. 4.



784 Fig. 5.



786 Supplementary material

Nesting	Survey	Aerial survey dates		
season		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 A.1. Aerial survey schedule for the Gabonese coast 2002/03, 2005/06 and 2006/07.

789 Table A.2. Summary of PTT data for female leatherback turtles, detailing: PTT Id., nesting

season, release location, deployment date, inter-nesting periods (n), PTT manufacturer and

- 791 model.
- 792

Id	PTT	Nesting season	Release location	Deployment date	Inter-nesting periods (n)	Inter-nesting duration (mean) (days)	PTT make	Model
1	57666	2005/06	М	2005-12-10	1	11	Sirtrack	KiwiSat 101
2	57383		М	2005-12-11	0	no data	Sirtrack	KiwiSat 101
3	57381		М	2006-02-23	0	no data	Sirtrack	KiwiSat 101
4	57378		М	2006-02-24	1	10	Sirtrack	KiwiSat 101
5	57390		М	2006-02-24	1	13	Sirtrack	KiwiSat 101
6	65693		М	2006-03-09	0	no data	SMRU*	SRDL
7	57663		М	2006-03-19	0	no data	Sirtrack	KiwiSat 101
8	65694		М	2006-03-22	1	11	SMRU*	SRDL
9	68562	2006/07	М	2007-02-03	2	10	SMRU*	SRDL
10	68563		М	2007-02-09	1	11	SMRU*	SRDL
11	80621	2007/08	М	2008-02-12	0	no data	Sirtrack	KiwiSat 202
12	80622		М	2008-02-12	1	7	Sirtrack	KiwiSat 202
13	80623		М	2008-02-12	2	10	Sirtrack	KiwiSat 202
14	80620		М	2008-02-12	2	12	Sirtrack	KiwiSat 202
15	80624		М	2008-02-12	1	11	Sirtrack	KiwiSat 202
16	89072	2008/09	Р	2008-12-08	3	12	Wildlife Computers	MK10-AF
17	89071		Р	2008-12-09	6	12	Wildlife Computers	MK10-AF
18	89075		Р	2008-12-11	5	11	Wildlife Computers	MK10-A
19	89073		Р	2008-12-15	4	11	Wildlife Computers	MK10-AF
20	89074		Р	2008-12-16	3	10	Wildlife Computers	MK10-AF
21	89076		Р	2008-12-16	7	10	Wildlife Computers	MK10-A
22	92577		М	2009-02-18	3	10	Wildlife Computers	MK10-A
23	92578		М	2009-02-18	2	10	Wildlife Computers	MK10-A
24	92579		М	2009-02-21	1	10	Wildlife Computers	MK10-A
25	92580		М	2009-02-21	1	12	Wildlife Computers	MK10-A
26	92581	2009/10	Р	2009-12-07	5	11	Wildlife Computers	MK10-A
27	92582		Р	2009-12-07	7	10	Wildlife Computers	MK10-A
28	122425	2012/13	Р	2012-10-25	7	10	Wildlife Computers	SPLASH10-AF
29	122426		Р	2012-10-26	6	11	Wildlife Computers	SPLASH10-AF
30	122427		Р	2012-10-26	7	11	Wildlife Computers	SPLASH10-AF
31	122428		Р	2012-10-27	7	10	Wildlife Computers	SPLASH10-AF
32	122429		Р	2012-10-27	6	9	Wildlife Computers	SPLASH10-AF
33	122430		Р	2012-10-28	1	9	Wildlife Computers	SPLASH10-AF
34	122431		Р	2012-10-28	5	10	Wildlife Computers	SPLASH10-AF
35	122432		Р	2012-10-28	7	11	Wildlife Computers	SPLASH10-AF
36	122433		Р	2012-10-28	8	10	Wildlife Computers	SPLASH10-AF
37	122434		Р	2012-10-28	7	11	Wildlife Computers	SPLASH10-AF
				mean	3	10	-	
				total	121			

793 * Sea Mammal Research Unit

- Table A.3. 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
- 796 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
Offshore distance	0.91	0.36	16.37	19.03