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Dispersal of green turtles from Africa's largest rookery assessed through genetic markers

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Running page head: Green turtle connectivity in the Atlantic

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22 Abstract

Marine turtles are highly migratory species that establish multiple connections among distant areas, through oceanic migration corridors. To improve the knowledge on the connectivity of Atlantic green turtles, we analysed the genetic composition and contribution to juvenile aggregations of one of the world's largest rookeries at Poilão Island, Guinea-Bissau. We amplified 856bp mitochondrial DNA (mtDNA) control region sequences of this population (n=171) containing the ~490bp haplotypes used in previous studies. Haplotype CM-A8 was

- dominant (99.4%) but it divided in two variants when the whole 856 bp was considered: CM-
- 30 A8.1 (98.8%) and CM-A8.3 (0.6%). We further identified the haplotype CM-A42.1 (0.6%),
- found previously only in juvenile foraging grounds at Argentina, Brazil and Equatorial
- Guinea. The Poilão breeding population was genetically different from all others in the Atlantic (F_{ST} range 0.016-0.961, P< 0.001). An extensive 'Many-to-many' mixed-stock
- analysis (MSA) including 14 nesting populations (1,815 samples) and 17 foraging grounds
- 35 (1,686 samples) supported a strong contribution of Poilão to West Africa (51%) but also to
- Southwest Atlantic (36%). These findings, in particular the strong connectivity within West
 Africa, where illegal harvesting is still common, should motivate conservation partnerships,
- 37 Africa, where flegal harvesting is still common, should motivate conservation partnerships,
 38 so that population protection can be effectively extended through all life-stages. Our study
- expands the knowledge on migration patterns and connectivity of green turtles in the
- 40 Atlantic, evidences the importance of larger sample sizes and emphasises the need to
- 41 include more finely resolved markers in MSAs and more genetic sampling from West African
- 42 foraging grounds to further resolve the connectivity puzzle for this species.
- 43
- Key-words: connectivity, dispersal, green turtle, migration, mitochondrial DNA (mtDNA),
 mixed-stock analysis (MSA), population genetics, West Africa
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49 Introduction

Many marine species undertake migratory movements among distant geographic areas and 50 across distinct habitats, for feeding, reproduction or development. As a result they may be 51 subject to a diverse range of threats during their extensive movements. Sea birds (Catry et 52 53 al., 2011), marine mammals (Rasmussen et al., 2007), large fish (Bonfil et al., 2005, Rooker et al., 2014) and sea turtles (Hays and Scott, 2013) undertake such movements and are 54 known to play important ecological roles. Understanding their dispersal patterns and the 55 links they establish among different areas is critical to contextualize threats and inform 56 57 effective management strategies (Rees et al., 2016).

58

59 Marine turtles are long-lived organisms and their life histories are marked by ontogenic 60 habitat shifts and large-scale migrations (Bowen & Karl, 2007). Green turtles (Chelonia 61 mydas L) associate with oceanic currents after hatching and undergo an oceanic pelagic stage, which is thought to last ca. 3 – 5 years (Reich et al., 2007). After this period, often 62 referred to as 'the lost years', as the whereabouts of the turtles at this phase are poorly 63 known, they generally recruit to coastal habitats, which may change seasonally (Fukuoka et 64 65 al., 2015), and shift into benthic foraging at a straight-carapace-length of 25 – 35 cm (Bolten, 2003). These neritic zones are used as developmental habitats and turtles may spend 66 several years foraging in the same area until reaching a size or maturity stage that triggers 67 them to migrate to additional foraging areas (Patrício et al., 2011, Patrício et al., 2014, 68 Shimada et al., 2015). Upon reaching maturity, adults make periodic migrations between 69 their neritic foraging areas and natal rookeries (Bowen and Karl, 2007). This complex 70 migratory behaviour creates multiple connections among distant coastal areas through 71 oceanic migration corridors (Velez-Zuazo et al., 2008). Genetic studies have been critical in 72 enlightening such connectivity (Encalada et al., 1996; Naro-Maciel et al., 2007; Prosdocimi 73 74 et al., 2012).

75

76 Most studies have used sequences of the control region of the mitochondrial DNA (mtDNA), a maternally inherited genetic marker (Bowen and Karl, 2007). This marker shows generally 77 high levels of genetic structuring among marine turtle nesting populations worldwide, 78 79 supporting the natal homing hypothesis, in which the females of marine turtles return to the 80 beaches were they were born to reproduce as a consequence of philopatry (Meylan et al., 81 1990). In contrast, foraging aggregations are usually mixed stocks composed of individuals from different rookeries (Bowen and Karl, 2007). The high genetic structuring of nesting 82 83 populations allows the use of mixed stock analysis (MSA, Millar, 1987), to estimate 84 contributions of rookeries (stocks) to mixed foraging grounds (mixed stocks). A Bayesian 85 MSA (Pella and Masuda, 2001) has been widely applied, allowing the incorporation of 86 informative priors, such as rookery size or geographic distance. Bolker et al (2007) 87 subsequently developed a 'many-to-many' mixed stock analysis (m2m MSA), aiming to 88 simultaneously answer the questions 1) where do the individuals from a given source population go? and 2) where do individuals from a given mixed foraging ground originate? 89 90 Limitations of MSAs have been pointed out however, in particular the assumption that all 91 source populations and mixed aggregations have been adequately sampled (Proietti et al., 92 2012). The existence of orphan haplotypes at juvenile foraging grounds indicates that some stocks still lack genetic assessment or have not yet been adequately sampled; hence 93 94 estimates should be interpreted cautiously and along with meaningful ecological data.

95

One controversial result of recent MSAs of the Atlantic green turtles is the suggested 96 potential connectivity between Guinea-Bissau, West Africa, and the Southwest Atlantic. 97 Although MSAs have supported this migration (Bolker et al., 2007; Monzón-Argüello et al., 98 2010; Naro-Maciel et al., 2012), the fact that the population at Poilão, Guinea-Bissau, was 99 found to be fixed for the common South Atlantic haplotype (CMA-8, Encalada et al., 1996; 100 101 Formia et al., 2006; Godley et al., 2010) has limited the interpretations of these results. 102 Notably, the discovery of exclusive haplotypes at low frequency is highly dependent on 103 sample size. This putative migration seems to involve movements greater than expected,

104 according to the 'closest to home' hypothesis where immature turtles tend to move to and settle in foraging grounds closest to their natal beach after recruiting to neritic habitats 105 (Bolker et al., 2007). Additionally, studies using particle dispersal modelling with major 106 oceanic currents did not support this connectivity (Godley et al., 2010; Putman and Naro-107 108 Maciel 2013). However, when Putman and Naro-Maciel (2013) estimated the origins of the 109 green turtle Atlantic mixed stocks, tracking particles back through time, this crossing seemed 110 feasible, albeit at low incidence. Lagrangian drifter data have further shown this route to be 111 possible with particle drift (Monzón-Argüello et al., 2010; Proietti et al., 2012). Finally, a 112 similarly large-scale migration of post-hatchling green turtles from Suriname to Cape Verde was supported using mtDNA (Monzón-Argüello et al., 2010). 113

114

With this is mind we investigate two questions: 1) where do the post-hatchlings from Poilão 115 116 disperse to?, and 2) do some of the juveniles found at Southwest Atlantic foraging grounds originate in Poilão? To answer these questions we greatly increased the available sample to 117 characterize the genetic composition of Poilão's nesting population, in an attempt to detect 118 rare haplotypes. We then sought to improve our understanding of the migration patterns and 119 120 connectivity among Atlantic green turtle populations by comparing our results with molecular data (n = 3,501 sequences) from 14 nesting populations and 17 foraging grounds, resulting 121 in the most extensive analysis thus far for this species in the Atlantic. 122

123

124 Methods

125 Study site and sampling

Poilão Island (N10°52', W15°43') is part of the João Vieira and Poilão Marine National Park (PNMJVP), in the Bijagós Archipelago, Guinea-Bissau. It hosts one of the major green turtle nesting populations worldwide (Catry et al., 2002, 2009). This population has been monitored yearly around the peak of the nesting season (August -September) since 2004. In 2013 and 2014 we collected skin samples from 171 nesting females. Samples were taken from the shoulder area using a 6 mm sterile biopsy punch as the females laid their eggs and stored in 96 % ethanol at room temperature. All sampled individuals were identified with unique tags on both front flippers to avoid sample duplication. Furthermore, the loss of a metal tag leaves scar marks easily recognized within, so we were certain that no previously tagged individual was mistakenly identified as 'new'. Sampling protocols were approved by the research ethics committee of the University of Exeter and the government of the Republic of Guinea-Bissau.

137

138 Sequencing and haplotype assignment

139 We extracted DNA using the QIAGEN[®] DNeasy blood & tissue kit, according to the

140 manufacturer's instructions. A fragment of ~860bp of the mtDNA control region was

141 amplified in a polymerase chain reaction (PCR) with the primers LCM15382 (5'-

142 GCTTAACCCTAAAGCATTGG-3') and H950 (5'-TCTCGGATTTAGGGGGTTT-3') (Abreu-

143 Grobois et al. 2006) which includes the short region (~486 bp) historically surveyed for green

144 turtle genetic studies (Bjorndal et al., 2006; Encalada et al., 1996; Formia et al., 2007;

Lahanas et al., 1998). Amplifications were performed in a total volume of 25 µl, containing

146 2.5 μ I of Taq buffer, 3 μ I of dNTPs, 1 μ I of MgCl₂, 0.5 μ M of each primer at 10 μ M, and 0.2 μ I

147 of Taq DNA polymerase. Cycling conditions were 94° C for 5 min, followed 35 cycles at 94°

148 C for 1 min, 55° C for 1 min and 72° C for 1 min with a final extension step at 72° C for 10

149 min. Desired PCR products were purified with a combined Exonuclease I and Shrimp

150 Alkaline Phosphatase solution (ExoSAP®). The reaction was incubated for 15 min at 37°C,

followed by 15 min incubation at 80°C to inactivate the two enzymes. Sequences of forward

and reverse DNA strands were performed at Macrogen Inc. (Netherlands). Sequences were

assembled and aligned manually using BioEdit 7.2.5 (Hall 1999). Unique haplotypes were

identified using the Basic Local Alignment Search tool (BLAST) from the National Centre for

155 Biotechnology information (<u>http://www.ncbi.nlm.nih.gov/</u>), following the nomenclature of the

156 Archie Carr Center for Sea Turtle Research, ACCSTR; <u>http://accstr.ufl.edu/ccmtdna.html</u>.

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160 **Population structure**

To assess the genetic diversity of the nesting population at Poilão compared with the other 161 Atlantic nesting populations we truncated the mtDNA fragments to 490 bp length, the 162 fragment historically explored and for which most genetic information of other locations is 163 164 currently available. We used Arlequin 3.5.1.3 (Excoffier and Lischer 2010) to estimate the 165 haplotype (h) and nucleotide (π) diversity of nesting populations, to estimate the genetic distances among population pairs (Φ st) and to test the significance of differentiations with 166 167 exact tests based on haplotype frequencies. A false discovery rate (FDR) correction (Narum, 168 2006) was applied to calculate the most fitting threshold for the P-value significance considering the number of comparisons involved in the analysis and under an expected 169 170 original threshold of P < 0.05. To contextualize our sampling location within the Atlantic region, the genetic distances were used to perform a principal coordinate analysis (PCoA) 171 172 using the package GenAIEX 6.5.0.1 (Peakall and Smouse, 2012). We tested the significance of the PCoA grouping with an AMOVA, using Arlequin 3.5.1.3 (Excoffier and Lischer 2010). 173

174

175 'Many-to-many' Mixed-stock analysis

176 We generated a dataset of 14 nesting populations (n=1,815) and 17 foraging grounds (n=1,686) when including our new mtDNA data for Poilão to the previously existing data for 177 Atlantic nesting populations and foraging grounds (see figure 1 for sites included in this 178 study and literature sources). We used only sequences generated by this study to 179 characterize the genetic composition of Poilão in order to avoid potential pseudoreplication 180 with datasets obtained in previous years. Relative contributions to foraging areas from 181 nesting populations (mixed stock-centric approach), and probable use of foraging grounds 182 from nesting populations (source-centric approach) were estimated with m2m MSA, using 183 the R package mixstock (Bolker et al., 2007) and WinBUGS (Lunn et al., 2000). We 184 conducted the MSA including the number of nesting females in each population (Seminoff et 185 al., 2015) as a weighting factor (Prosdocimi et al., 2012). We used the Gelman-Rubin 186 187 diagnostic to assess convergence of the chains to the posterior distribution, assuming that

there was no evidence of non-convergence at values < 1.2 (Pella and Masuda, 2001). As it is reasonable to assume that other African juvenile aggregations remain to be identified we simulated a juvenile foraging ground fixed for haplotype CM-A8 (similar to Naro-Maciel et al 2012), with a sample size equal to the mean of the foraging grounds sample sizes (n=99), and added this sample to the dataset to conduct another m2m MSA, as described above.

193

194 Results

195 Genetic composition of Poilão

196 Genetic variability of the Poilão nesting population was the lowest of all Atlantic populations 197 $(h \pm SD = 0.012 \pm 0.011, \pi \pm SD = 0.0001 \pm 0.0003, table 1)$. The haplotype CM-A8 was 198 dominant as suggested by previous studies (Formia et al., 2006). However the use of longer 199 sequences (856bp sequences) distinguished two variants of this haplotype: CM-A8.1 (98.8 200 %) and CM-A8.3 (0.6%). We also identified the haplotype CM-A42.1 (0.6%), a previously orphan haplotype found to date only in juveniles from West Africa and South American 201 202 foraging aggregations (see Table S1 for haplotype frequencies of nesting populations). Because this is a rare haplotype and not previously detected in the population we performed 203 204 two independent PCRs, and sequenced the amplified fragment in two independent occasions, to confirm that this result was not a product of genotyping error. 205

206

207 **Population Structure**

The nesting population at Poilão was significantly different from all other Atlantic green turtle 208 rookeries (Table S2). All other nesting populations were distinct from each other except 209 when comparing Ascension Island with Bioko Island, Aves with Suriname, and Aves with 210 211 Buck Island. The comparisons between Suriname and Buck Island, and between Sao Tome and Principe and Bioko became non-significant after FDR correction. Populations pairs 212 where genetic differentiation was not detected were kept as discrete sources for the m2m 213 214 MSA, based on their divergence in population size and geographic position (Monzón-215 Argüello et al., 2010; Putman and Naro-maciel, 2013). The PCoA separated rookeries by

region and evidenced three major groups: South Atlantic, Southeast Caribbean and Northwest Caribbean (Fig. 2), each group defined by a major haplotype(s): CM-A8, CM-A5 and CM-A3/A1, respectively. An accumulated 85.5% of the genetic variability was explained by the two principal coordinates of the PCoA. Although located in the North Atlantic, Poilão clustered within the South Atlantic group. Using this *a-priori* grouping in the AMOVA, highly significant structure was observed among the three groups (F_{ST} = 0.691, P <0.001), with 55.9% of the variation found among groups.

223

224 'Many-to-many' Mixed-stock analysis

225 The source-centric m2m MSA indicated that most of Poilão's hatchlings recruit to African 226 foraging grounds (51.4%), but 36.2% would reach juvenile aggregations in the Southwest 227 Atlantic and 8.6% reached North Atlantic aggregations (Fig. 3). A small proportion of the 228 Poilão rookery was attributed to an 'unknown' foraging area (3.7%). The foraging groundcentric m2m MSA estimated that at Sao Tome, Corisco Bay and 'West Africa' (Liberia to 229 230 Benin) foraging grounds, over 60% of the juveniles originate at Poilão, as do 31% of the green turtles foraging at Cape Verde (Fig. 4). Notably, at the Southwest Atlantic foraging 231 232 aggregations proportions ranging from 16 – 41% were attributed to Poilão (Fig. 4). Adding the simulated West African foraging ground did not change contributions at a regional scale, 233 but the relative contributions to the Gulf of Guinea were significantly lower (8 to 14 % lower, 234 Fig. S1), to accommodate a large contribution to this putative aggregation. Because CM-A42 235 is a rare haplotype and therefore difficult to detect when sampling a population, we decided 236 to run two additional MSAs using simulated datasets, each of these including haplotype CM-237 A42 in one of the other two major green turtle rookeries in the Atlantic (i.e. Costa Rica and 238 239 Ascension Island), and observed no significant changes (Fig. S1).

240

241 Discussion

One of the principal techniques that can offer insight into the migratory connectivity of

243 species with complex life cycles is genetics. The robustness of subsequent inferences,

244 however, are highly dependent on the amount of information available, including the number of populations and foraging grounds analysed, and the strength of the signal, including 245 sample sizes at each site and length of the genetic sequence and number of genetic 246 markers analysed. Here we substantially increased the sampling effort at one of the largest 247 248 Atlantic green turtle rookeries, in Poilão, Guinea-Bissau, in order to resolve the uncertainties surrounding the connectivity between this nesting population and distant juvenile 249 aggregations. We successfully found the origin of a previously orphan haplotype, present in 250 251 West Africa but also in South American foraging grounds, giving strength to the hypothesis 252 of east-to-west connectivity.

253

254 **Post-hatchling dispersal to east and west**

The contributions estimated by the m2m MSA confirm a strong connectivity within West 255 256 Africa, as previously hypothesized (Godley et al., 2010), particularly with foraging grounds in the Gulf of Guinea (i.e. 'Sao Tome', 'West Africa' and 'Corisco'). This dispersal was also 257 predicted under an ocean circulation model and through passive drifting associated with the 258 Guinea current (Putman and Naro-Maciel, 2013). Due to the large size of the nesting 259 260 population at Poilão, it is likely however that significant proportions of other African juvenile aggregations originate there. In Guinea-Bissau there are at least two known aggregations of 261 immature green turtles; i) at Unhocomo and Unhocomozinho Islands, in the Bijagós 262 Archipelago, ca. 100 km NE from Poilão Island, and ii) at Varela beach, ca. 200 km NE from 263 Poilão, that have not been genetically described. The same is true for a foraging ground in 264 Mauritania, mentioned in Godley et al (2010), and in Congo. We have shown that the 265 estimated proportions of post-hatchlings distributed among West African foraging grounds 266 depend on the inclusion of new juvenile aggregations. To fully understand the connectivity of 267 the large nesting population at Poilão it is essential that investigation into identifying and 268 genetically characterizing these aggregations is undertaken. The MSA also suggests the 269 270 existence of a transatlantic developmental migration for the green turtle, from east to west,

potentially associated with the Equatorial currents, and continuing south, reaching foraginggrounds in the south of Brazil and in Argentina.

273

Studies using estimations of passive drift with major oceanic currents to predict the 274 275 movements of post-hatchlings have suggested that dispersal from Guinea-Bissau to Southwest Atlantic is unlikely (Godley et al., 2010; Putman and Naro-Maciel, 2013). 276 277 However, marine turtle hatchlings are capable of oriented swimming significantly impacting 278 trajectories (Putman et al., 2012a, 2012b; Scott et al., 2012), and able to swim against 279 currents (Booth, 2014). Indeed, recent research has shown that drifter tracks can diverge 280 substantially from those of young turtles (Putman and Mansfield, 2015) and it is likely that 281 this process is contributing to observed divergence between genetic- and drift-based 282 predictions (Naro-Maciel et al., 2016). Because CM-A42 is a rare haplotype and therefore 283 difficult to detect, we ran additional MSAs using simulated datasets, including this haplotype in each of the two other major green turtle rookeries in the Atlantic (i.e. Costa Rica and 284 285 Ascension Island), and observed no significant changes (Fig. S1).

286

287 Expanded sample size and geographic coverage

Formia et al (2006) assessed the genetic composition of Poilão nesting females (n=51) and 288 found it was fixed for the South Atlantic dominant mtDNA haplotype CM-A8. By extending 289 this previous sample size, we were able to detect a rare haplotype, CM-A42, which to date 290 had only been reported from juvenile green turtles foraging in South America, and in West 291 Africa. This enabled the differentiation of Poilão from other Atlantic rookeries, agreeing with 292 the high philopatry, characteristic of the green turtle, and the fine scale differentiation 293 existent in other places. Increasing sample size has previously been shown to improve 294 295 statistical power of detection of structure among populations, through the finding of rare 296 haplotypes (Formia et al., 2007).

298 The existence of non-significant comparisons among certain population pairs could result from i) recent isolation, such that haplotype frequencies did not have time to differentiate, or 299 300 ii) current gene flow, mediated by incidental deviations from natal homing. Lack of 301 differentiation between Bioko and Ascension Island has been attributed to recent 302 colonization of the former (Formia et al., 2006). Likewise, Aves and Buck Island may be 303 more recent than the more diverse population in Suriname. Alternatively, the proximity between Aves and Buck Island (<300 km), and between Bioko and Sao Tome (<400 km), 304 305 may be more likely to result in occasional migrants preventing substantial differentiation at 306 an evolutionary timescale (Formia et al., 2006).

307

308 Our study further expands the geographic coverage of previous MSAs of the green turtle in 309 the Atlantic, incorporating 14 nesting populations and 17 foraging grounds in our dataset. In 310 particular the inclusion of African foraging grounds (i.e. Corisco Bay, Sao Tome and 'West Africa') improved the estimates for the distribution of hatchlings from Poilão, significantly 311 reducing the estimate of the putative "unknown" foraging site (here 3.7%) compared to a 312 recent MSA (14.3% in Putman and Naro-Maciel, 2013), as well as substantially reducing the 313 314 confidence intervals. In a previous m2m MSA a high contribution of Ascension Island to Corisco Bay was estimated (ca. 40%, Bolker et al., 2007). Here that contribution drops to 315 9.2%, and we predict a much stronger connectivity between Poilão and Corisco. By including 316 more foraging grounds in our analyses, we show that Ascension rookery contributes 317 primarily to juvenile aggregations along the Southwest Atlantic (71.6%), also seen in Putman 318 and Naro-Maciel (2013). Analogously, the foraging ground-centric MSA in Bolker et al (2007) 319 attributes most of the Corisco Bay foraging ground to Ascension Island (>70%), while we 320 321 estimate that 60.5% of the aggregation origins at Poilão, and only 27.7% would come from 322 Ascension. Additionally, the contributions of Aves Island and NE Brazil to Corisco Bay estimated before (ca. 15% each, Bolker et al., 2007) were considerably lower in our study 323 (2.7% and 4.8%, respectively), and these populations also seem to contribute more to the 324 325 Southwest Atlantic. See tables S3 and S4 for m2m MSA summary results.

327 Limitations of MSA and future directions

Although increasing the available sample size at Poilão and expanding the dataset for 328 329 Atlantic green turtles has improved MSA estimates, this analysis is based on a single marker 330 and on a short fragment of the mtDNA. To further unveil the green turtle connectivity puzzle 331 in the Atlantic (and elsewhere) the strength of the genetic signal can be enhanced, at a 332 lesser cost than substantially increasing sample sizes. Data from the longer mtDNA 333 sequences should be obtained from existing samples and made available, to be 334 incorporated in MSAs. Additionally, a new marker consisting of four AT short tandem repeats (STRs) in the 3' end of the mtDNA, the mtSTR, had been shown to add information on the 335 336 genetic variability within unique mtDNA haplotype classes and to contribute to improve the 337 knowledge on population connectivity and evolutionary relationships (Shamblin et al., 2015, 338 Tikochinski et al., 2012). Recent research using nuclear markers have found significant structure among sea turtle rookeries, supportive of male phylopatry (Carreras et al., 2011; 339 340 Naro-Maciel et al., 2012; Naro-Maciel et al., 2014; Roden et al., 2013). Finally, new genomic approaches are have the potential to greatly increase the signal resolution and detect fine-341 342 scale population structure (Benestan et al., 2015; Funk et al., 2012; Milano et al., 2014). Some of the above information is now becoming available at local scales. Hopefully future 343 collaborations among research groups at wider scales will lead to significant advances in our 344 understanding of the dispersal and distribution of marine turtles. 345

346

347 Adult linkage

Godley et al (2010) recorded the trajectories of eight post-nesting females from Poilão using satellite transmitters, finding that they foraged either locally, at the Bijagós Archipelago (n = 4), or regionally (n = 4), at the Banc d'Arguin National Park, Mauritania (> 1000 km distant). This aspect of investigation would clearly benefit from enhanced sampling effort, preferably across multiple seasons, at different points of the season and across a range of size classes, to avoid inter-annual (Witt et al., 2011), seasonal (Rees et al., 2010) and phenotypic

(Hawkes et al., 2006) biases in dispersal. Future satellite tracking should be conducted in
tandem with stable isotope analysis to facilitate the posterior assignment of turtles to these
areas, facilitating the analyses of larger sample sizes, more relevant for population studies
(Zbinden et al., 2011).

358

If nesting females from Poilão are limited to the East Atlantic it does not necessarily 359 360 contradict our suggestion of transatlantic dispersal as post-hatchlings. Post-hatchling turtles 361 forage during their developmental migration (Reich et al., 2007), which allows them to travel 362 much longer distances than adults that typically fast during their reproductive migrations (Hays and Scott, 2013; Scott et al., 2014). According to Scott et al (2014), if the 363 364 developmental foraging area is so far as to be too costly to be repeatable during the cyclic reproductive migrations, adults may forage locally, as observed at the Bijagós, instead of 365 366 returning to the sites experienced when younger. This mechanism reduces the consumption of reproductive energy utilized, potentially increasing fecundity, however it is dependent on 367 368 the availability of foraging areas.

369

370 **Conservation implications**

In this study we show the importance of Poilão rookery for the recruitment of juvenile green 371 turtles in West Africa, and also that the link with the Southwest Atlantic is very likely. In 372 Guinea-Bissau, despite marine turtles being fully protected by the national fisheries law, 373 illegal take continues to occur without much law enforcement effort (Catry et al., 2009), 374 particularly at the Bijagós Archipelago, where turtles are frequently harvested at the nesting 375 beaches, mostly for local consumption (Catry et al., 2009). The nesting population at Poilão 376 is one exception, thanks to the Bijagós traditional 'law' (reinforced by state authorities), 377 restricting access to the island on very rare ceremonies of social and religious significance 378 379 (Catry et al., 2009). Off Guinea-Bissau and along the coast of West Africa however, vast artisanal fleets and many industrial fishing fleets operate, using trawlers without turtle 380 381 excluder devices (Catry et al., 2009; Zeeberg et al., 2006), and longlining (Moore et al.,

382 2010). Unfortunately there is a scarcity of quantitative data in the region, either on bycatch or on targeted harvesting of marine turtles, particularly from artisanal fisheries (Moore et al., 383 2010). The foraging grounds in the Southwest Atlantic to which Poilão seems to contribute 384 to, on the other hand, are mostly protected from illegal harvesting (Marcovaldi and dei 385 386 Marcovaldi, 1999), although bycatch may be a problem (Wallace et al., 2010). Despite the existing threats, major green turtle populations are recovering globally following decades of 387 conservation efforts (Bourjea et al., 2015, Broderick et al., 2006, Catry el at., 2009). It may 388 389 be that the long term enhanced protection in South America and the efforts in Poilão itself 390 are the principle factors involved in the recovery of this population.

391

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Table 1. Haplotypic and genetic diversity of Atlantic green turtle (*Chelonia mydas*) nesting populations (n = 14) included in a many-to-many

641 mixed stock analysis (Bolker et al., 2007), using the control region of the mitochondrial DNA as a marker (490bp). The number of females

refers to the total number of reproductive females in each population. The study population is represented in bold.

Nesting Population	short name	sample size	no. of females*	no. of haplotypes	haplotypic diversity (<i>h</i>)	nucleotide diversity (π)
East central Florida	EcFL	311	4490	9	0.512 ± 0.020	0.0016 ± 0.0013
South Florida	SFL	174	3302	10	0.444 ± 0.043	0.0022 ± 0.0016
Southwest Cuba	CUB	28	2226	7	0.648 ± 0.089	0.0053 ± 0.0033
Quintana Roo, Mexico	MEX	20	18257	7	0.816 ± 0.058	0.0051 ± 0.0032
Tortuguero, Costa Rica	CR	433	131751	5	0.163 ± 0.023	0.0033 ± 0.0022
Matapica/Galibi, Suriname	SUR	73	13067	4	0.132 ± 0.053	0.0013 ± 0.0011
Buck Island	BUC	49	63	2	0.153 ± 0.065	0.0030 ± 0.0020
Aves Island	AV	67	2833	2	0.140 ± 0.055	0.0029 ± 0.0020
Rocas/Fernando Noronha	RC/FN	69	345	7	0.463 ± 0.071	0.0026 ± 0.0018
Trindade Island	TRI	99	2016	7	0.505 ± 0.052	0.0012 ± 0.0011
Ascension Island	ASC	245	1417	13	0.303 ± 0.038	0.0008 ± 0.0008
Poilão, Guinea-Bissau	GB	171	29016	2	0.012 ± 0.011	0.0001 ± 0.0003
Bioko Island, Eq. Guinea	BIO	50	850	2	0.184 ± 0.068	0.0004 ± 0.0006
Sao Tome and Principe	STP	26	376	7	0.569 ± 0.110	0.0026 ± 0.0019

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644 * Seminoff et al., (2015)



Figure 1. a) Atlantic green turtle (*Chelonia mydas*) nesting populations (n=14) and foraging grounds (n=17) used many-to-many
mixed stock analysis (m2m MSA), and results of foraging ground-centric MSA (pie charts: proportion of each foraging site that origins
from the study population in black). Nesting populations: EcFL, East central Florida, SFL, South Florida, USA (Shamblin et al., 2014); CUB:
Southwest Cuba (Ruiz-Urquiola et al., 2010); MEX: Quintana Roo, Mexico (Encalada et al., 1996); CR: Tortuguero, Costa Rica (Bjorndal et al.,

650 2005; Encalada et al., 1996); SUR: Matapica and Galibi, Suriname (Encalada et al., 1996; Shamblin et al., 2012); AV: Aves Island (Lahanas et al., 1998, 1994; Shamblin et al., 2012), Venezuela; BUC: Buck Island (Shamblin et al., 2012); RC/FN: Rocas Atol and Fernando de Noronha 651 (Bjorndal et al., 2006; Encalada et al., 1996), Brazil; ASC: Ascension Island (Encalada et al., 1996; Formia et al., 2007); TRI: Trindade Island, 652 Brazil (Bjorndal et al., 2006); POI: Poilão, Guinea-Bissau (study population); BIO: Bioko Island, Equatorial Guinea (Formia et al., 2006); STP: 653 654 Sao Tome and Principe (Formia et al., 2006). Foraging grounds: NC: North Carolina (Bass et al., 2006), EcFL: East central Florida (Bagley, 655 2003; Bass and Witzell, 2000), BHM: Bahamas (Lahanas et al., 1998), BRB: Barbados (Luke et al., 2004), ALF: Almofala, Brazil (Naro-Maciel 656 et al., 2007), RC: Rocas Atoll, Brazil (Naro-Maciel et al., 2012), FN: Fernando de Noronha, Brazil (Naro-Maciel et al., 2012), BA: Bahia, Brazil (Naro-Maciel et al., 2012), ES: Espirito Santo, Brazil (Naro-Maciel et al., 2012), UB: Ubatuba, Brazil (Naro-Maciel et al., 2007), AI: Arvoredo 657 658 Island, Brazil (Proietti et al., 2012), CB: Cassino Beach, Brazil (Proietti et al., 2012), BuA, Buenos Aires, Argentina (Prosdocimi et al., 2012), CV: Cape Verde (Monzón-Argüello et al., 2010), COR: Corisco Bay, Equatorial Guinea (Formia, 2002), WA: 'West Africa' (Liberia to Benin, 659 Formia, 2006). GfC: Gulf Current, NEC: North Equatorial Current, SEC: South Equatorial Current, BrC: Brazil Current, GC: Guinea Current, 660 BgC: Benguela Current; b) Region map with study site, Poilão, and three juvenile foraging grounds likely to partly originate at Poilão, to date 661 662 genetically uncharacterized: Unhocomo/Unhocomozinho and Varela at Guinea Bissau, and Banc d'Arguin at Mauritania. Dashed arrow illustrates the direction of four green turtle females tracked from Poilão to Banc d'Arguin (Godley et al., 2010). (Maps created using 663 www.seaturtle.org/maptool). 664



Figure 2. PCoA of the 14 Atlantic green turtle (Chelonia mydas) populations using ϕ_{st} 666 and considering the 490bp fragment. The percentage of the variability explained by each 667 coordinate is shown in brackets. ASC: Ascension Island; AV: Aves Island, Venezuela; BIO: 668 Bioko Island, Equatorial Guinea; BUC: Buck Island; CR: Tortuguero, Costa Rica; CUB: 669 Southwest Cuba; EcFL: East central Florida, MEX: Quintana Roo, Mexico; POI: Poilão, 670 Guinea-Bissau (this study); RC/FN: Rocas Atol and Fernando Noronha, Brazil; SFL: South 671 Florida, USA; STP: Sao Tome and Principe; SUR: Matapica and Galibi, Suriname; TRI: 672 Trindade Island, Brazil. 673



Figure 3. Mean relative contribution of Poilão (Guinea-Bissau) nesting population to 17 Atlantic
green turtle (*Chelonia mydas*) foraging grounds, estimated by a many2many mixed stock analysis
(Bolker et al 2007). Error bars show 95 % confidence intervals. WA: 'West Africa' – Liberia to Benin, ST:
Sao Tome, COR: Corisco Bay, CV: Cape Verde, BuA: Buenos Aires, UB: Ubatuba, ALF: Almofala, CB:
Cassino Beach, FN: Fernando de Noronha, ES: Espírito Santo, BA: Bahia, AI: Arvoredo Island, RC: Rocas
Atol, BRB: Barbados, BHM: Bahamas, NC: North Carolina, EcFL: East central Florida. Dashed lines
separate geographic regions.

683 Supplementary material:

- **Table S1.** mtDNA control region haplotype frequencies (490 bp), at 14 Atlantic green turtle
- nesting populations with total no. of samples per area. See Fig. 1 for site abbreviations. Long

haplotypes (856bp) for study area are shown in the table below.

Hanlotype	Nesting Populations EcFL ^{a,b} SFL ^b MEX ^a CR ^{c,d} CUB ^e BUC ^f AV ^{d,f,g} SUR ^{a,f} RC/N ^{a,h} TRI ^h ASC ^{a,i,j} POI ^k BIO ⁱ													
паріотуре	EcFL ^{a,b}	SFL⁵	MEX ^a	CR ^{c,d}	CUB ^e	BUC ^f	AV ^{d,f,g}	SUR ^{a,f}	RC/N ^{a,h}	TRI ^h	ASC ^{a,i,j}	POI ^k	BIO ⁱ	
CM-A1	197	27	7		3									
CM-A2	7	4												
CM-A3	92	127	5	395	16		5	1						
CM-A4				1		16								
CM-A5	2	4	1	32		45	62	68						
CM-A6								3			11		5	
CM-A7								1						
CM-A8	1								50	67	204	170*	45	
CM-A9									7	19	9			
CM-A10									2		5			
CM-A11									1	1				
CM-A12									5					
CM-A13	7	2												
CM-A15			1											
CM-A16	2	1	1											
CM-A17	_	2	2											
CM-A18	1	1	3											
CM-A20	•	•	Ũ	2										
CM-A21				3										
CM-A23				Ũ						6	1			
CM-A24										1	7			
CM-A25									3	•	1			
CM-A27					1				0					
CM-A28	2	3			1									
CM-A32	2	0							1	4	1			
CM-A33										1				
CM-A35										•				
CM-A36														
CM-437														
CM-438														
CM-A39											1			
CM-442												1*		
CM-444											1	•		
CM-445											1			
CM-A46											2			
CM-A48					5						~			
CM-A50					U						1			
CM-A53		3												
CM-A56		Ŭ			1									
CM-A57					1									
n	311	174	20	433	28	61	67	73	69	gg	245	171	50	
^a Encolodo o	tal 1006	bShom	blin at a	1 201 /	Giorna		2005 di	abanac	ot al 1000	eD		ot ol C	0010	
^f Shamblin e	t al. 2012,	^g Lahan	as et al.	1994, ^h	Bjornda	l et al. 2	2005, ^s L 2006, ⁱ Fo	rmia et a	l. 2006, ^j Fo	, rruiz prmia e	t al. 2007	, ^k This s	study	
* Long haple	otypes (85	66bp): C	MA8.1 (n=169)	, CMA8.	3 (n=1),	CMA42	.1 (n=1)						

Table S2. Pairwise exact test P-values (above diagonal) and pairwise F_{ST} values (below diagonal) among the 14 Atlantic green turtle (*Chelonia mydas*) nesting populations, based on ~490bp sequences of the control region of the mtDNA. The study site is in grey and in bold, and abbreviations follow those in Figure 1. Asterisks indicate statistically significant comparisons (*P < 0.05, **P < 0.01, ***P < 0.001) i) prior to corrections, in the low diagonal, ii) after false discovery rate (FDR) correction, in the above diagonal. Non-significant values, after FDR (Narum, 2006) correction, are marked in bold (for a P< 0.05 FDR = 0.0098, P< 0.01 FDR = 0.0020, P< 0.001 FDR = 0.0002).

	MEX	EcFL	SFL	CR	AV	BUC	CUB	SUR	TRI	RC/FN	ASC	POI	BIO	STP
MEX	-	0.009*	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
EcFL	0.082**	-	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
SFL	0.182***	0.197***	-	0.000***	0.000***	0.000***	0.009*	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
CR	0.202***	0.254***	0.033***	-	0.000***	0.000***	0.009*	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
AV	0.796***	0.895***	0.872***	0.820***	-	0.342	0.000***	0.108	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
BUC	0.783***	0.897***	0.873***	0.822***	0.000	-	0.000***	0.045	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
CUB	0.104***	0.243***	0.131**	0.154***	0.822***	0.811***	-	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
SUR	0.880***	0.920***	0.905***	0.849***	0.021	0.031*	0.887***	-	0.000***	0.000***	0.000***	0.000***	0.000***	0.000***
TRI	0.860***	0.899***	0.885***	0.820***	0.657***	0.659***	0.873***	0.759***	-	0.009*	0.000***	0.000***	0.000***	0.000***
RC/FN	0.787***	0.886***	0.863***	0.810***	0.567***	0.554***	0.812***	0.666***	0.031**	-	0.000***	0.000***	0.000***	0.009*
ASC	0.913***	0.918***	0.914***	0.852***	0.728***	0.735***	0.922***	0.795***	0.060***	0.037***	-	0.000***	0.243	0.000***
POI	0.953***	0.931***	0.929***	0.855***	0.805***	0.823***	0.950***	0.895***	0.146***	0.070***	0.016***	-	0.000***	0.000***
BIO	0.877***	0.909***	0.894***	0.824***	0.640***	0.646***	0.878***	0.789***	0.093***	0.037***	0.003	0.106***	-	0.036
STP	0.766***	0.895***	0.870***	0.811***	0.522***	0.505***	0.792***	0.671***	0.083***	0.036*	0.067***	0.201***	0.045*	-

Necting Population	Foraging grounds																	
Nesting Population	NC	EcFL	BHM	BRB	ALF	RC	FN	BA	ES	UB	AI	СВ	BuA	CV	COR	ST	WA	Х
Poilão, Guinea Bissau																		
Mean	0.01	0.01	0.03	0.03	0.04	0.02	0.04	0.04	0.04	0.05	0.03	0.04	0.06	0.06	0.10	0.17	0.18	0.04
CI: 97.5%	0.04	0.05	0.09	0.10	0.10	0.06	0.09	0.10	0.09	0.14	0.08	0.10	0.13	0.13	0.20	0.31	0.32	0.13
CI: 2.5%	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.01	0.01	0.01	0.02	0.02	0.03	0.07	0.08	0.00
Bioko, Eq.Guinea																		
Mean	0.05	0.05	0.05	0.05	0.05	0.06	0.05	0.06	0.07	0.05	0.05	0.05	0.05	0.06	0.07	0.05	0.06	0.05
CI: 97.5%	0.17	0.17	0.19	0.19	0.18	0.20	0.19	0.20	0.22	0.19	0.19	0.18	0.19	0.20	0.22	0.19	0.21	0.18
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sao Tome and Principe																		
Mean	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.05	0.06	0.09	0.08	0.06	0.05
CI: 97.5%	0.17	0.18	0.18	0.19	0.17	0.17	0.17	0.17	0.17	0.18	0.17	0.22	0.16	0.19	0.31	0.27	0.19	0.20
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ascension Island, UK																		
Mean	0.01	0.01	0.02	0.05	0.09	0.09	0.05	0.05	0.08	0.11	0.09	0.08	0.07	0.02	0.09	0.03	0.04	0.02
CI: 97.5%	0.04	0.05	0.06	0.12	0.17	0.18	0.12	0.14	0.16	0.21	0.18	0.16	0.16	0.06	0.17	0.09	0.10	0.07
CI: 2.5%	0.00	0.00	0.00	0.00	0.03	0.03	0.01	0.00	0.02	0.04	0.03	0.02	0.02	0.00	0.03	0.00	0.00	0.00
Trindade, Brazil																		
Mean	0.03	0.03	0.04	0.04	0.04	0.08	0.04	0.12	0.08	0.05	0.10	0.09	0.08	0.03	0.03	0.04	0.03	0.04
CI: 97.5%	0.11	0.12	0.14	0.14	0.13	0.21	0.13	0.29	0.21	0.16	0.24	0.22	0.23	0.12	0.10	0.14	0.12	0.14
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Rocas/F.Noronha, Brazil																		
Mean	0.05	0.05	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.06	0.05	0.07	0.05	0.05	0.05	0.06	0.05	0.05
CI: 97.5%	0.20	0.19	0.19	0.20	0.19	0.22	0.19	0.19	0.20	0.20	0.19	0.23	0.18	0.19	0.16	0.19	0.18	0.19
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Suriname																		
Mean	0.01	0.03	0.05	0.07	0.07	0.05	0.14	0.07	0.08	0.03	0.04	0.04	0.05	0.17	0.01	0.02	0.03	0.04
low C.I.	0.04	0.09	0.15	0.16	0.15	0.11	0.25	0.15	0.15	0.07	0.09	0.09	0.12	0.31	0.03	0.06	0.09	0.12
upper C.I.	0.00	0.00	0.00	0.01	0.02	0.01	0.05	0.01	0.02	0.00	0.01	0.01	0.01	0.06	0.00	0.00	0.00	0.00

696 Table S3. Co	ontinuation
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Nosting Population	Foraging grounds																	
Nesting Population	NC	EcFL	BHM	BRB	ALF	RC	FN	BA	ES	UB	AI	СВ	BuA	CV	COR	ST	WA	Х
Aves Island, VNZ																		
Mean	0.04	0.05	0.06	0.07	0.07	0.06	0.07	0.06	0.05	0.06	0.06	0.05	0.06	0.07	0.03	0.04	0.05	0.05
CI: 97.5%	0.13	0.19	0.20	0.20	0.21	0.20	0.21	0.21	0.18	0.17	0.20	0.16	0.19	0.25	0.09	0.15	0.15	0.18
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Buck Island																		
Mean	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.05	0.05	0.06	0.05	0.05	0.06	0.06	0.05	0.05	0.06	0.06
CI: 97.5%	0.21	0.19	0.21	0.20	0.20	0.20	0.18	0.19	0.18	0.20	0.17	0.18	0.19	0.18	0.20	0.18	0.19	0.20
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tortuguero, CR																		
Mean	0.01	0.15	0.53	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.28
CI: 97.5%	0.04	0.33	0.84	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.64
CI: 2.5%	0.00	0.04	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Mexico																		
Mean	0.16	0.42	0.13	0.06	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.17
CI: 97.5%	0.42	0.72	0.38	0.18	0.02	0.01	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.04	0.00	0.02	0.03	0.49
CI: 2.5%	0.03	0.11	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Southeast Cuba																		
Mean	0.27	0.11	0.11	0.07	0.03	0.03	0.03	0.03	0.01	0.02	0.01	0.01	0.02	0.05	0.01	0.03	0.04	0.12
CI: 97.5%	0.53	0.34	0.34	0.24	0.14	0.10	0.10	0.11	0.05	0.07	0.05	0.06	0.06	0.18	0.03	0.12	0.13	0.37
CI: 2.5%	0.06	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
South Florida, USA																		
Mean	0.21	0.16	0.12	0.11	0.04	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.05	0.01	0.02	0.03	0.12
CI: 97.5%	0.51	0.48	0.39	0.36	0.14	0.10	0.10	0.09	0.04	0.05	0.04	0.04	0.05	0.17	0.02	0.09	0.10	0.40
CI: 2.5%	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
East central Florida, USA																		
Mean	0.30	0.20	0.12	0.09	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.04	0.00	0.02	0.02	0.11
CI: 97.5%	0.57	0.51	0.39	0.27	0.05	0.05	0.06	0.06	0.02	0.04	0.02	0.03	0.04	0.14	0.02	0.07	0.07	0.39
CI: 2.5%	0.04	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Foraging grounds	Nesting populations													
Foraging grounds	EcFL	SFL	MX	CR	CUB	BUC	AV	SUR	RC/N	TRI	ASC	GB	Bio	STP
North Carolina, USA														
Mean	0.19	0.10	0.35	0.16	0.08	0.00	0.01	0.02	0.00	0.01	0.02	0.05	0.01	0.00
CI: 2.5%	0.02	0.00	0.14	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CI: 97.5%	0.41	0.26	0.59	0.36	0.18	0.00	0.05	0.06	0.01	0.03	0.06	0.11	0.02	0.01
East central Florida, USA														
Mean	0.03	0.02	0.26	0.63	0.01	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00
CI: 2.5%	0.00	0.00	0.12	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CI: 97.5%	0.11	0.08	0.43	0.78	0.03	0.00	0.02	0.04	0.00	0.01	0.03	0.04	0.01	0.00
Bahamas														
Mean	0.01	0.01	0.03	0.92	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00
CI: 2.5%	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CI: 97.5%	0.03	0.02	0.08	0.97	0.01	0.00	0.01	0.04	0.00	0.01	0.01	0.03	0.00	0.00
Barbados														
Mean	0.06	0.06	0.15	0.28	0.02	0.00	0.03	0.14	0.00	0.01	0.09	0.13	0.01	0.00
CI: 2.5%	0.00	0.00	0.02	0.08	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.01	0.00	0.00
CI: 97.5%	0.18	0.19	0.31	0.46	0.09	0.00	0.11	0.25	0.01	0.05	0.22	0.28	0.03	0.01
Almofala, Brazil														
Mean	0.01	0.03	0.02	0.14	0.02	0.00	0.04	0.19	0.00	0.02	0.26	0.25	0.01	0.00
CI: 2.5%	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.08	0.00	0.00	0.10	0.09	0.00	0.00
CI: 97.5%	0.04	0.09	0.07	0.23	0.06	0.00	0.15	0.29	0.02	0.07	0.43	0.41	0.04	0.02
Rocas Atol, Brazil														
Mean	0.02	0.03	0.02	0.05	0.02	0.00	0.06	0.21	0.01	0.05	0.37	0.16	0.02	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.15	0.01	0.00	0.00
CI: 97.5%	0.06	0.09	0.06	0.12	0.07	0.00	0.20	0.33	0.03	0.15	0.57	0.35	0.06	0.02

Table S4. Continuation

Foraging grounds	Nesting populations													
	EcFL	SFL	MX	CR	CUB	BUC	AV	SUR	RC/N	TRI	ASC	GB	Bio	STP
Fernando Noronha, Brazil														
Mean	0.02	0.02	0.03	0.02	0.01	0.00	0.04	0.40	0.00	0.02	0.16	0.26	0.01	0.00
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.02	0.09	0.00	0.00
CI: 97.5%	0.05	0.06	0.08	0.06	0.05	0.00	0.15	0.50	0.02	0.06	0.33	0.42	0.04	0.02
Bahia, Brazil														
Mean	0.02	0.02	0.02	0.03	0.02	0.00	0.06	0.25	0.01	0.08	0.21	0.27	0.02	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.01	0.02	0.03	0.00	0.00
CI: 97.5%	0.07	0.08	0.08	0.09	0.07	0.00	0.19	0.39	0.02	0.21	0.48	0.51	0.06	0.02
Espirito Santo, Brazil														
Mean	0.01	0.01	0.01	0.01	0.01	0.00	0.05	0.26	0.01	0.04	0.29	0.29	0.02	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.09	0.06	0.00	0.00
CI: 97.5%	0.03	0.03	0.03	0.04	0.03	0.00	0.16	0.36	0.02	0.12	0.52	0.47	0.07	0.02
Ubatuba, Brazil														
Mean	0.01	0.01	0.01	0.02	0.01	0.00	0.04	0.08	0.01	0.03	0.40	0.36	0.01	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.16	0.08	0.00	0.00
CI: 97.5%	0.04	0.04	0.04	0.05	0.04	0.00	0.13	0.17	0.02	0.10	0.68	0.60	0.05	0.02
Arvoredo Island, Brazil														
Mean	0.01	0.01	0.01	0.01	0.01	0.00	0.06	0.16	0.01	0.07	0.37	0.27	0.01	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.17	0.07	0.00	0.00
CI: 97.5%	0.03	0.03	0.04	0.04	0.03	0.00	0.18	0.27	0.02	0.16	0.59	0.47	0.06	0.02
Casino Beach, Brazil														
Mean	0.01	0.01	0.01	0.01	0.01	0.00	0.05	0.15	0.01	0.06	0.31	0.35	0.01	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.12	0.15	0.00	0.00
CI: 97.5%	0.03	0.04	0.04	0.04	0.03	0.00	0.16	0.26	0.03	0.15	0.53	0.55	0.06	0.03

Forgaing grounds	Nesting populations													
i oraging grounds	EcFL	SFL	MX	CR	CUB	BUC	AV	SUR	RC/N	TRI	ASC	GB	Bio	STP
Buenos Aires, Argentina														
Mean	0.01	0.01	0.01	0.01	0.01	0.00	0.04	0.17	0.00	0.05	0.25	0.41	0.01	0.00
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.08	0.20	0.00	0.00
CI: 97.5%	0.04	0.04	0.04	0.04	0.03	0.00	0.16	0.27	0.02	0.14	0.48	0.58	0.05	0.02
Cape Verde														
Mean	0.03	0.03	0.04	0.04	0.02	0.00	0.04	0.40	0.00	0.01	0.04	0.31	0.01	0.00
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.14	0.00	0.00
CI: 97.5%	0.10	0.09	0.13	0.14	0.07	0.00	0.16	0.54	0.02	0.05	0.16	0.47	0.04	0.02
Corisco Bay, Eq. Guinea														
Mean	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.01	0.28	0.60	0.01	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.37	0.00	0.00
CI: 97.5%	0.02	0.01	0.02	0.02	0.01	0.00	0.05	0.08	0.02	0.04	0.47	0.77	0.07	0.04
Sao Tome, Sao Tome and Principe														
Mean	0.01	0.01	0.01	0.01	0.01	0.00	0.02	0.04	0.00	0.01	0.07	0.77	0.01	0.01
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.62	0.00	0.00
CI: 97.5%	0.04	0.04	0.05	0.05	0.04	0.00	0.07	0.10	0.01	0.05	0.19	0.87	0.04	0.03
West Africa: Liberia to Benin														
Mean	0.01	0.01	0.02	0.02	0.01	0.00	0.02	0.06	0.00	0.01	0.08	0.75	0.01	0.00
CI: 2.5%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.58	0.00	0.00
CI: 97.5%	0.05	0.05	0.06	0.07	0.04	0.00	0.07	0.13	0.01	0.04	0.22	0.86	0.03	0.01

Table S4. Continuation



