

1 **Predicting the impacts of climate change on a globally distributed species:**  
2 **the case of the loggerhead turtle**

3  
4 Short title: Marine turtles and climate change

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21

22 **Abstract**

23

24 Marine turtles utilise terrestrial and marine habitats and several aspects of their life history are tied to  
25 environmental features that are altering due to rapid climate change. We overview the likely impacts  
26 of climate change on the biology of these species, which ultimately centre upon the thermal ecology  
27 of this taxonomic group. Then, focussing in detail on three decades of research on the loggerhead  
28 turtle (*Caretta caretta*), we describe how much progress has been made to date, and how future  
29 experimental and ecological focus should be directed. Key questions include: What are the current  
30 hatchling sex ratios from which to measure future, climate induced changes? What are wild adult sex  
31 ratios and how many males are necessary to maintain a fertile and productive population? How will  
32 climate change affect turtles in terms of their distribution?

33

34 **Introduction**

35

36 *A changing world*

37

38 The earth's climate is warming: increases in average air and ocean temperatures, melting of land and  
39 sea ice, as well as rising sea levels have been observed and are likely caused by increases in  
40 anthropogenic atmospheric emissions (Hansen et al., 2006; IPCC, 2007). The observed changes in  
41 the climate since 1996 have actually been greater than anticipated (Rahmstorf et al., 2007) leading to  
42 concern regarding the future environment. Global average surface temperatures have increased by  
43 0.8 °C over the last 100 years (Hansen et al., 2006), with greater increases in temperature over the  
44 land than sea surface (IPCC, 2007). Future surface temperature increases of 2-3 °C are expected by  
45 2100 (Hansen et al., 2006). Concurrent increases in sea level have been recorded at 1.8 mm per year  
46 over the last 42 years (IPCC, 2007), or at 3.4 mm per year per degree Celsius of warming observed  
47 (Rahmstorf, 2007). The majority of sea level rise is contributed by thermal expansion (57%), with  
48 another significant contribution (28%) from surface ice melting (IPCC, 2007) and may also be  
49 increasing faster than previously predicted (Rahmstorf, 2007). In addition, although an overall  
50 decrease in average rainfall is predicted (IPCC, 2007), an increase in heavy rainfall and 'great flood'  
51 events is expected (Milly et al., 2002). Both genesis and tracks of storms are predicted to move  
52 poleward, and may increase in intensity in some regions (Bengtsson et al., 2006). Finally, the uptake  
53 of atmospheric CO<sub>2</sub> by the ocean since the industrial era has meant that ocean pH has decreased by  
54 0.1 pH units (IPCC, 2007). A further decrease of 0.35 pH units could occur over the next 100 years.

55

56 It is recognized that climate change must be incorporated into species conservation planning (Araújo  
57 et al., 2004; Hannah et al., 2002), with spatial and temporal alterations to species ranges, in  
58 accordance with climate change patterns, observed in 84% of species investigated (Parmesan and  
59 Yohe, 2003). Indeed, species extinctions as a result of climate change have been already documented  
60 (Pounds et al., 1999) and some authors have suggested that as much as one fifth to a third of  
61 terrestrial species could be at risk of extinction (Thomas et al., 2004). It has also become apparent  
62 that marine species are likely to be impacted (Croxall et al., 2005; Gremillet and Bioulinier, In press;  
63 Hawkes et al., 2007b; MacLeod, 2009; Newson et al., 2009); although far fewer studies have been  
64 conducted in comparison with terrestrial species.

65

66 *Climate change in sea turtles*

67

68 Although climate change was identified as a potential problem to sea turtles in seminal papers by  
69 Mrosovsky (1984) and Davenport (1989), it is only recently that significant research effort has been  
70 expended on the field (reviewed by Hamann et al., (2007); Hawkes et al., (2009)). Although sea

71 turtles are exposed to climate change threats both at sea and on the nesting beach, it is at the beach  
72 where the majority of research effort has been focused as it provides opportunity for more  
73 logistically feasible work. One of the primary effects of climate change on nesting beaches is sea  
74 level rise, where higher water levels will directly decrease the availability of suitable nesting sites.  
75 Recent work suggests that up to half of current available nesting area could be lost with predicted sea  
76 level rise (Fish et al., 2005; Fish et al., 2008; Mazaris et al., 2009), particularly at islands where no  
77 retreat options exist (Baker et al., 2006) or where anthropogenic coastal fortification causes ‘coastal  
78 squeeze’ (Fish et al., 2008). This coastal squeeze may be exacerbated in the forthcoming decades by  
79 a growing population whose densities at the margins of the global land mass are considerably greater  
80 than the global land average (Small and Nicolls, 2003), potentially carrying fitness consequences for  
81 nesting female turtles (Pike, 2008). On available areas of nesting beach, incubating clutches could be  
82 at risk from an increasing sea level if water tables rise, effectively flooding the nest from below.  
83 Some species could be at greater risk than others, for example green turtles (*Chelonia mydas*) lay  
84 deeper nests than loggerhead turtles (*Caretta caretta*) (Hannan et al., 2007), and leatherback turtles  
85 (*Dermochelys coriacea*) tend to nest closer to the high tide line than green turtles or loggerhead  
86 turtles nesting on the same beach (Wetterer et al., 2009; Whitmore and Dutton, 1985)

87  
88 Turtles on the nesting beach are profoundly affected by temperature, such that temperature can  
89 influence nesting phenology (Hawkes et al., 2007b; Hays et al., 2002; Pike et al., 2006; Sato et al.,  
90 1998; Webster and Cook, 2001; Weishampel et al., 2004), incubation success (Ackerman, 1997;  
91 Carthy et al., 2003), incubation duration (Matsuzawa et al., 2002; Mrosovsky et al., 1999; Pike et al.,  
92 2006) and, as sex determination is by temperature, sex of offspring (Yntema and Mrosovsky, 1980).  
93 Increasing temperatures therefore have the potential to change current nest incubation regimes as  
94 well as skew sex ratios (Hawkes et al., 2007b). Alternatively, increasing temperatures may open up  
95 areas that were previously inaccessible to nesting. Indeed, nests are now being discovered  
96 increasingly further north (see Bentivegna et al. (2005); Sénégas et al.(2008); Tomas et al. (2008)).  
97 Incubating sea turtle clutches can also be damaged or lost due to storm activity (Van Houtan and  
98 Bass, 2007), including surges, wave action and sand wash out events. The effects to the incubating  
99 nest can range from reducing hatching success to total loss of clutches on a particular beach (Snow  
100 and Snow, 2009).

101  
102 The effects of climate change on turtles at large in the ocean are more challenging to study, because  
103 turtles range across entire ocean basins and are late maturing and long lived (Avisé et al., 1992; Zug  
104 et al., 2002). There is compelling evidence from multiple species to suggest that the distribution and  
105 behaviour of chelonid sea turtles is influenced by temperature (Hawkes et al., 2007a; Sato et al.,  
106 1998). Leatherback sea turtles are probably affected to a lesser extent by thermal conditions due to  
107 gigantothermy (Frair et al., 1972; Paladino et al., 1990) and anatomical adaptations (Davenport et al.,

108 2009), and range further from the equator, such as into Canadian (James et al., 2005) waters and  
109 those of the Northeast Atlantic Ocean (Doyle et al., 2008; McMahon and Hays, 2006; Witt et al.,  
110 2007a). We know that ocean currents play an important role in dispersing hatchling turtles (Bolten,  
111 2003; Lohmann and Lohmann, 2003; Witherington, 2002; Witt et al., 2007b) and that these currents  
112 may change in magnitude or direction (Rahmstorf, 1997; Stocker and Schmittner, 1997), which may  
113 influence future juvenile developmental phase durations (Hamann et al., 2003). In addition, changes  
114 to the pelagic community as a result of climate change could alter trophic dynamics (Edwards and  
115 Richardson, 2004) and juvenile growth rates and further alter developmental duration (Bjorndal et  
116 al., 2000; Verity et al., 2002). For adults, changes to thermal regimes and sea surface currents could  
117 alter current adult foraging habitat as well as the location and size of home ranges and diet (Bjorndal,  
118 1997; Davenport, 1998; Meylan, 1988; Polovina et al., 2004), which has ramifications for population  
119 breeding phenology and success.

120

### 121 *The loggerhead sea turtle*

122

123 Likely as a result of extensive presence within the waters of affluent nations such as USA, Japan,  
124 Australia and those of the Mediterranean, the loggerhead turtle (*Caretta caretta*) is one of the most  
125 studied sea turtle species, and we therefore select it for the focus of this review. For the purposes of  
126 this work we have taken an Atlantic and Mediterranean wide view of this species due to the wealth  
127 of published data describing reproductive biology, feeding ecology and population trends from long  
128 term studies available for populations from these two ocean basins. We consider several aspects of  
129 the thermal biology of loggerhead sea turtles in relation to projected climate change, highlighting the  
130 progress that has been made and the steps towards predicting and understanding impacts.

131

132 The loggerhead turtle nests in tropical and sub-tropical regions. The largest known rookeries are in  
133 the southeast United States of America and Cape Verde (Figure 1a); with nesting also occurring  
134 along the Brazilian coast within the South Atlantic basin. In the Mediterranean Sea (Figure 1b),  
135 nesting is almost exclusively restricted to the eastern basin, with notable aggregations occurring in  
136 Cyprus, Greece and Turkey (Broderick et al., 2002; Margaritoulis et al., 2003).

137

138 All species of sea turtle are thought to demonstrate some degree of natal philopatry (Bowen and Karl  
139 (2007), although with some variations, see Lee (2008)) returning as adults to their natal beach  
140 regions to breed. Females typically reproduce every 2-3 years (Miller, 1997), with the seasonal  
141 magnitude of nesting in any one year dependent upon trophic conditions encountered by female  
142 turtles in the years preceding breeding and nesting (Broderick et al., 2001b; Chaloupka et al., 2008).  
143 Following reproductive activity, while some female loggerhead turtles move to oceanic areas  
144 (Hawkes et al., 2006), most will undertake migrations of varying distances to neritic foraging

145 grounds (Girard et al., 2009; Godley et al., 2003; Plotkin and Spotila, 2002; Zbinden et al., 2008)  
146 demonstrating considerable levels of site fidelity (Broderick et al., 2007). During winter periods,  
147 their range appears to be thermally constrained (Hawkes et al., 2007a) and individuals apparently  
148 hibernate during the coolest months (Broderick et al., 2007; Hawkes et al., 2007a; Hochscheid et al.,  
149 2005).

150  
151 Here we consider the thermal biology of sea turtles in relation to projected climate change,  
152 highlighting the progress that has been made and identifying the next key steps to understanding  
153 likely impacts.

#### 154 155 *Hatchling sex ratios*

156  
157 Temperature-dependent sex determination in sea turtles was first documented in loggerhead turtles  
158 by Yntema and Mrosovsky (1980), with warmer incubation temperatures producing more females,  
159 and cooler temperatures producing more males. Although early work was conducted under  
160 laboratory conditions, attention moved to field studies to assess whether hatchling sex ratios were  
161 different from 1:1 as predicted by Fisher (1930). Initial assessments of loggerhead turtle sex ratios  
162 suggested that sex ratios vary from beach to beach and also from month to month within a nesting  
163 season (Mrosovsky et al., 1984). Further work has been conducted by incubating eggs, from a variety  
164 of different populations from different latitudes, in controlled laboratory conditions, and has  
165 suggested that there is little variation in the pivotal temperature (Mrosovsky 1988, Mrosovsky and  
166 Pieau, 1991). Subsequent studies of laboratory incubation of loggerhead turtle eggs from Brazil and  
167 Greece have found similar pivotal temperatures - close to 29 °C, as have field-based estimates of  
168 pivotal temperature from the Mediterranean (Table 1). Thus variation in sex ratios observed in the  
169 wild (Figure 2) are thought to be driven largely by local environmental conditions, specifically egg  
170 temperatures during incubation (Godfrey and Mrosovsky, 2001).

171  
172 A major constraint in the study of loggerhead turtle sex ratios has been the challenge of assigning  
173 sex. Sea turtles do not have sexually dimorphic sex chromosomes, nor do they express visible  
174 external phenotypic differences between the sexes prior to adulthood. The only fully reliable method  
175 of assigning sex to hatchling loggerhead turtles has been through histological examination of the  
176 gonads (Yntema and Mrosovsky, 1980), which is labour intensive and destructive. Attempts to use  
177 dead-in-nest hatchlings for sexing are hampered by low sample sizes and possible influence of sex-  
178 biased mortality. There have been attempts to develop other, non-destructive markers of phenotypic  
179 sex, with varying degrees of success, including assessing ratios of hormone titres in the  
180 chorioallantoic fluid remaining in eggs after hatching (Gross et al., 1995) and laparoscopy of  
181 hatchlings raised in captivity for several months (Wyneken et al., 2007). Regardless of their

182 reliability, these alternative methods of directly assigning sex present logistical challenges that would  
183 hamper studies of sex ratios on a large scale in the field.

184  
185 Other researchers have pursued methods that indirectly estimate sex ratios of hatchlings, most  
186 commonly by using environmental parameters such as sand and air temperature (Hawkes et al.,  
187 2007b; Matsuzawa et al., 2002; Mrosovsky and Provancha, 1992). Some researchers have also used  
188 the incubation period of loggerhead nests as an indirect measure of sex ratio, because the rate of  
189 embryonic development is linked to temperature (Godfrey and Mrosovsky, 1997; Godley et al.,  
190 2001b; Marcovaldi et al., 1997). While these methods of indirectly estimating sex ratios have helped  
191 generate larger datasets (Hawkes et al., 2007a), few have been validated (Mrosovsky et al., (1999)).  
192 Validation is especially important as most of these studies use pivotal temperature or pivotal  
193 incubation data from laboratory studies that also are based on few clutches using constant incubation  
194 temperatures. To date, there have been published pivotal temperature studies for only six different  
195 loggerhead nesting beaches in the Atlantic and Mediterranean Sea, with most pivotal values based on  
196 just two clutches (Table 1). More studies are needed to increase reliability of these values and  
197 illuminate the individual variation and capacity for adaptation in this trait. Indeed, pivotal  
198 temperature studies of freshwater turtles using many clutches suggest that pivotal temperatures are  
199 much more variable within a particular species, due either to intrinsic differences between and/or  
200 variability of maternal contributions (e.g. hormones) in the eggs (Bowden et al., 2000; Dodd et al.,  
201 2006). The development of a non-destructive but accurate marker of phenotypic sex of hatchlings  
202 would also greatly facilitate the generation of hatchling sex ratio datasets, both directly and  
203 indirectly, although to date there has been little success in this endeavour (Wibbels, 2003).

204  
205 Despite the logistical challenges of accurately assigning sex to hatchling sea turtles, loggerhead  
206 turtles have been the focus of a number of sex ratio studies, based on either direct or indirect  
207 assessments of offspring sex. Within the Atlantic Ocean there is a general trend, although  
208 statistically insignificant, of more female biased hatchling sex ratios for rookeries located closer to  
209 the equator and more balanced sex ratios (i.e. closer to 1:1) at rookeries that are further away from  
210 the equator (Figure 3a, Spearman rank-order correlation using absolute latitude versus arc-sine  
211 transformed percentage of females produced at each rookery,  $n = 10$ ,  $\rho = -0.22$ ,  $p = 0.54$ ). In the  
212 case of the south-east USA, the more southerly rookeries in eastern Florida are estimated to produce  
213 nearly 90% female hatchlings (Hanson et al., 1998; Mrosovsky and Provancha, 1992), while more  
214 northerly rookeries in Georgia, South Carolina and North Carolina are thought to produce closer to  
215 55-60% female hatchlings (Hawkes et al., 2007b; Mrosovsky et al., 1984). There are exceptions to  
216 this trend, including reported 1:1 hatchling sex ratios on some smaller, vegetated beaches in western  
217 Florida (Foley et al., 2000). A similar latitudinal trend exists south of the equator in Brazil, where the  
218 more northerly populations of Sergipe and Bahia produce nearly all female hatchlings (Marcovaldi et

219 al., 1997; Naro-Maciel et al., 1999), while the more southerly rookery in Espirito Santo produce  
220 closer to 1:1 hatchling sex ratios (Baptistotte et al., 1999; Marcovaldi et al., 1997). Note that  
221 hatchling sex ratios studies have not been randomly designed, and there remain many nesting  
222 beaches both north and south of the equator, some of them major rookeries, that have not been  
223 adequately studied for hatchling sex ratio production (e.g. Yucatan Peninsula in Mexico, Rio de  
224 Janeiro state in Brazil). Therefore, caution is needed in interpreting large spatial scale trends based  
225 on limited available information.

226  
227 In the Mediterranean Sea most loggerhead nesting occurs in the eastern basin (Figure 1b), and  
228 loggerhead hatchling sex ratios (Figure 3b) are estimated to be female biased on most beaches  
229 (Godley et al., 2001b; Oz et al., 2004; Zbinden et al., 2006), with beaches of southerly latitude  
230 showing a general trend towards a greater female bias (Spearman rank-order correlation,  $n = 7$ ,  $\rho =$   
231  $-0.75$ ,  $p = 0.06$ ). Exceptional loggerhead nests laid on beaches of the central and western  
232 Mediterranean Sea (Sénégas et al., 2008; Tomas et al., 2008) may experience cooler incubation  
233 environments, and thus may produce male-biased hatchling sex ratios, although relative numbers of  
234 these nests are quite small.

235  
236 There are several issues that hamper our understanding of this important population parameter,  
237 including a) the lack of long-term datasets, which are needed to discern overall trends instead of  
238 short-term studies that may reflect temporary variations only; b) the lack of systematic sampling for  
239 sex ratios across nesting populations that encompass the entire nesting season, making it difficult to  
240 interpret available data; and c) a reliable, simple and non-destructive marker of phenotypic sex of  
241 hatchlings. More concentrated effort on issue c) would contribute towards resolving issues a) and b).  
242 In the meantime, more work should be focused on better refining currently employed techniques of  
243 indirectly estimating the sex of hatchlings, including temperature and duration of incubation. For  
244 instance, more pivotal temperature experiments, to capture (or rule out) spatio-temporal variability  
245 both within and among nesting beaches (e.g. variation with latitude), are needed, and should include  
246 information on the transitional range of temperature that produces both sexes (Hulin et al., 2009).  
247 Additionally, validation of indirect estimates against direct estimates (histological examination of the  
248 gonads) within the same study will help define rates of error associated with indirect estimates  
249 (Mrosovsky et al., 2009). Finally, long-term monitoring of index sites should be set up as soon as  
250 possible, to establish baselines against which to measure possible future changes to hatchling sex  
251 ratio induced by climate change.

252



253 *Predicting future hatchling sex ratios and nest death*

254

255 It is commonly acknowledged that average global air and sea surface temperatures will rise, and with  
256 them so will sand temperatures at nest depth on loggerhead nesting beaches. More effort is urgently  
257 needed to predict how such changes may impact future hatchling sex ratios of populations (Fuentes  
258 et al., In press). If sea turtles do not adapt by shifting their geographic ranges, phenology of breeding  
259 or pivotal temperatures, sex ratios, many of which are already highly female biased, will become  
260 further skewed. Some studies have recorded an earlier onset of loggerhead turtle nesting (e.g. Pike et  
261 al., (2006), Weishampel et al., (2004)) others have not (e.g. Hawkes et al., (2007b), Pike (2009)).  
262 Given that females may select cooler sites (e.g. shaded) to lay their clutch at existing or new  
263 locations, the recording of clutch temperatures will be the main indicator for monitoring adaptation  
264 (or lack thereof) to rising temperatures.

265

266 Although some have inferred past sex ratios from historic air temperature (Hawkes et al., 2007b;  
267 Hays et al., 2003), there have been surprisingly few studies that have attempted to predict how future  
268 climate change may impact hatchling production of sea turtles and those that have addressed this  
269 issue have predicted sex ratios and hatching success at set elevated temperatures (Hawkes et al.,  
270 2007b) as opposed to estimating future sex ratios under modelled climate change scenarios (IPCC,  
271 2000). For those clutches that normally produce at least some males, a rise in temperature within a  
272 clutch will most likely increase the proportion of females produced. If temperatures rise above the  
273 threshold for successful development for extended periods (~33°C) embryonic death will increase  
274 (Miller, 1997).

275

276 To illustrate how variable predictions of hatchling sex ratios might be, we examined temporal trends  
277 in historic and global circulation model forecasts of sea surface temperature for the month of peak  
278 incubation at six loggerhead turtle nesting colonies (Figure 4). From this information alone one  
279 might predict that regions that are currently experiencing higher incubation temperatures might be  
280 most at risk from further increases, potentially leading to complete feminisation in hatchling  
281 production. From detailed studies in Cyprus we know, for example, that mean clutch temperatures  
282 during 1996 to 1999 (Godley et al., 2001a) were ~4 °C warmer than sea surface temperature, likely,  
283 at least in part, a result of sand albedo (Hays et al., 2001). In addition, other variables such as depth  
284 of clutch and clutch size have been shown to influence clutch temperature (Broderick et al., 2001a)  
285 but have been the focus of few sex ratio studies to date. Understanding how these variables influence  
286 clutch temperature is crucial for predicting nest fate for future climate scenarios. For sites at risk (i.e.  
287 those that are currently experiencing extreme bias in sex ratios and near-lethal temperatures),  
288 accurate predictions are needed and monitoring strategies with intervention plans put into place in  
289 case limited or no adaptation to climate change occurs.

290 *Sex ratios in advanced demographic groups*

291

292 Less well understood are sex ratios of pelagic stage neonate turtles, older juveniles and adults  
293 (Blanvillain et al., 2008; Hawkes et al., 2009). Sex ratios of older size classes are an important  
294 component of population dynamics (Frankham, 1995), affecting both genetic variation within the  
295 population and mating systems. Given that effective population size ( $N_e$ ) will seldom be twice that of  
296 the rarer sex (Milner-Gulland et al., 2003), populations with highly skewed sex ratios are likely to  
297 suffer negative impacts through random drift and loss of genetic variation, compromising their  
298 ability to respond to selection pressures and impeding population recovery. In order to understand  
299 juvenile and adult sex ratios, at-sea surveys to catch and sex wild turtles either laparoscopically:  
300 Blanvillain et al.,(2008), by hormonal assay (possible in individuals >2-3 years age): Braun-McNeill  
301 et al., (2007), or by secondary sexual features in mature individuals, have to be undertaken.  
302 Notwithstanding cost, such studies require expertise and need to be undertaken over a long period  
303 (>10 years). It is not surprising therefore that there exist few data in the peer-reviewed literature to  
304 elucidate whether skewed hatchling sex ratios are reflected in the wider population.

305

306 Work that has been published for loggerhead turtles however, suggests that a female bias remains in  
307 the juvenile and adult population (approximately 2 females to 1 male; Table 2). A lag between  
308 hatchling sex ratio and older life stage turtles (large juveniles and adults) however, would be  
309 approximately 30 years (based on age to maturity estimates in Casale et al., (2009) and Heppell et  
310 al., (2003)), such that future juvenile and adult sex ratios could be more female biased than at  
311 present. Although marine turtle fertility levels remain quite robust even at very low rookery size  
312 (Bell et al., In press) it is conceivable that there will be a critical adult sex ratio beyond which  
313 fertility will become reduced.

314

315 *Distribution*

316

317 As satellite tracking data have become more widely integrated with oceanographic data (Godley et  
318 al., 2008), the parameters describing preferable habitat for loggerhead sea turtles (e.g. seabed depth  
319 preference, surface current strength, upper and lower thermal preference) have become clearer.  
320 Habitat suitability models, utilising some of these parameters (Hawkes et al., 2007a; McMahon and  
321 Hays, 2006), are now being developed and these will provide the foundation to which global  
322 circulation models, used to build climate change predictions, might be applied. The predominant  
323 variable used in bioclimatic envelope modelling is temperature, and as ectotherms it is likely a good  
324 descriptor of the fundamental niche of sea turtles. However, the realised niche may be somewhat  
325 smaller, as augmented by prey and predator distribution and inter and intra-specific competition.  
326 Therefore with further characterisation of these variables (Witt et al., 2007a), models might predict

327 available habitat under future climate change scenarios with greater specificity. In the absence of  
328 such data for loggerhead turtles, we limit our discussion to modelling the fundamental (thermal)  
329 niche.

330  
331 In order to investigate how climate change may alter current thermal ranges for loggerhead sea  
332 turtles, we integrated oceanographic habitat preferences for adult loggerhead turtles (temperatures  
333 warmer than 15°C) with historic and forecast monthly mean sea surface temperatures. For the  
334 Atlantic Ocean these data were used to model the past, present and future thermally accessible range  
335 (1970 to 2089, Figure 5). For the Mediterranean Sea we took an alternative approach, displaying the  
336 mean March 15°C isotherm over successive 20-y periods (Figure 6). Within the annual cycle of sea  
337 surface temperature in the Mediterranean Sea, March represents the coldest month when cheloniid  
338 sea turtles are most likely to be spatially constrained by temperature. Broadly, these simple thermal  
339 envelope (niche) models describe an increase in available habitat through time. For the Atlantic  
340 Ocean we see the 90% habitat suitability contour migrating poleward with greatest range extension  
341 in the mid North Atlantic and some 75 to 100 km poleward extension along the US Atlantic coast.  
342 This model represents habitat suitability using a year-round approach; however, during warmer  
343 summer months loggerhead turtle distribution regularly extends further north than the annualised  
344 90% habitat suitability contours. In the Mediterranean Sea, we see the western basin becoming  
345 increasing favourable to occupation during winter months, by 2089 only a small area of the  
346 Mediterranean Sea, south of France, will remain inaccessible to year round occupation.

347  
348 Despite the obvious utility of models such as ours in predicting and managing for future range  
349 changes, it should be noted that insufficient data describing the oceanographic parameters of habitat  
350 occupation have been published for the seven species of sea turtles. In particular, the habitat  
351 preferences of juvenile turtles and adult males are largely unknown and future tracking efforts need  
352 to address this shortcoming (Godley et al., 2008). These data are fundamental to both the  
353 development and accuracy of future models and at present it has not been possible to develop robust  
354 models for many major rookeries. These models do not, as yet, factor in potential habitat losses, if  
355 any, to exceptionally warm waters. Furthermore, they can not reasonably factor in predicted changes  
356 in prey distribution, given the generalist diet of the loggerhead turtle. Truly holistic predictive  
357 modelling for these species is far from trivial. However, when available, future habitat suitability  
358 models could be integrated with climate change predictions, using methodologies such as ours, to  
359 make and test predictions about range alterations.

360

361 ***Conclusion***

362

363 In this review we have highlighted some of the primary threats from climate change faced by these  
364 species, the current knowledge of sex ratios, temperature-dependent sex determination, and species  
365 distribution and recommend future studies that will provide critical information for the prediction of  
366 the potential effects of climate change, which will inform possible adaptive management practices.  
367 These practices might include artificial nest shading or watering of nests to reduce incubation  
368 temperatures (e.g. Naro-Maciel et al. (1999)), translocation of clutches to cooler sites on current  
369 nesting beaches or reseeded populations to new locations (Hoegh-Guldberg et al., 2008). We do,  
370 however, urge that robust experiments be conducted to test the effectiveness of such practices (Pintus  
371 et al., 2009). In addition, further empirical studies, in particular the development of a non-destructive  
372 marker to identify hatchling sex, are urgently needed to aid accurate prediction of sex ratios and  
373 hence identify populations that may require mitigation activities. Finally, the threats from climate  
374 change experienced by these species of conservation concern are only part of a suite of other threats  
375 such as direct exploitation, fisheries bycatch and habitat loss that potentially hinder marine turtle  
376 population recovery. Targeting these latter threats will better engender resilience in marine turtle  
377 stocks while they adjust to changes in conditions as they have done in the past.

378

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380

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## Legends

**Figure 1. Distribution and abundance of loggerhead sea turtle nesting in (a) Atlantic Ocean and (b) Mediterranean Sea.** Sources: USA and Bahamas (Conant et al., 2009); Brazil (Marcovaldi and Chaloupka, 2007); other Atlantic locations (Ehrhart et al., 2003); Mediterranean (Margaritoulis et al., 2003).

**Figure 2. Estimated proportion of male (black) and females (white) hatchling production at selected loggerhead sea turtle nesting rookeries in (a) Atlantic Ocean and (b) Mediterranean sea.** Sources: 1. Hawkes et al., (2007b); 2. Bell (2003); 3. Mrosovsky et al., (1984); 4. Mrosovsky and Provancha (1992); 5. Hanson et al., (1998); 6. Schmid et al., (2008); 7. Foley et al., (2000); 8-10. Marcovaldi et al., (1997); 11. Houghton and Hays (2001); 12. Zbinden et al., (2006); 13. Rees and Margaritoulis (2004); 14. Godley et al., (2001b); 15. Kaska et al., (1998); 16 and 17. Oz et al., (2004).

**Figure 3. Relationship between latitude and percentage of female hatchlings produced at nesting rookeries in (a) Atlantic Ocean and (b) Mediterranean Sea.** The latitudes of nesting rookeries with sex ratio data were expressed as absolute values. Arabic numbers indicate source literature as described in Figure 2.

**Figure 4. Historic and forecast near-shore sea surface temperature for loggerhead sea turtle nesting (a-f) rookeries for the predominant month of incubation.** Historic sea surface temperature (filled squares, Jan. 1870 to May 2009; Hadley Ice and Sea Surface Temperature (HadISST) dataset; Rayner et al., (2003)). Forecast sea surface temperature (open squares, Jun. 2009 to Nov. 2089; Hadley Global Earth Model 1 (HadGEM1) using IPCC SRES A2 scenario (IPCC, 2000; Johns et al., 2006) available from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Meehl et al., 2007). Monthly gridded HadGEM1 data were spatially resampled and variance and trend adjusted (Sheppard, 2003) according to the temporal and spatial structure of HadISST data using Matlab (Version 7.8.0, MathWorks Inc, Natick, Massachusetts, US). Robust locally weighted scatter plot smooth (Cleveland, 1979) (solid line,  $r = 0.5$ ). Reference line to aid visual interpretation ( $28^{\circ}\text{C}$ , broken line). In Cyprus, nest temperatures are typically  $4^{\circ}\text{C}$  greater than sea surface temperatures (see text for details).

**Figure 5. Historic and forecast loggerhead turtle habitat suitability for the Atlantic Ocean.** Forecast sea surface temperature data (HadGEM1) were variance and trend adjusted and merged with historic (HadISST) data. Six 20-y duration sea surface temperature datasets were constructed. Each 20-y dataset comprised of 240 months of spatially gridded mean monthly SST data. Each pixel of each 20-y gridded SST dataset was scored as 0 or 1 according to thermal suitability (i.e.  $< 15^{\circ}\text{C} = 0$  &  $\geq 15^{\circ}\text{C} = 1$ ), following the method of Hawkes et al., (2007a). The temporal availability of habitat was calculated by dividing the number of months that each cell was suitable against the total number of months analysed. The proportion of time that each cell(pixel) was thermally accessible was subsequently expressed as percentage. Isolines of 90% habitat suitability were derived using cubic interpolation using Matlab.

**Figure 6. Historic and forecast 20-y mean March sea surface temperature for the Mediterranean Sea with 20-y mean  $15^{\circ}\text{C}$  isotherm.** Forecast sea surface temperature data (HadGEM1) were variance and trend adjusted and merged with historic (HadISST) data. Six 20-y duration sea surface temperature datasets were constructed. For each 20-y dataset the mean March position of the  $15^{\circ}\text{C}$  isotherm was identified (solid line) using cubic interpolation.

## Tables

Location	Pivotal °C	Latitude	Longitude	Source
Cumberland Is., GA, USA	28.5	30.86	-81.42	Mrosovsky (1988) <sup>1</sup>
Turkey / Cyprus	29.0	35.93	32.35	Kaska et al., (1998) <sup>2,3</sup>
Jupiter Island, FL, USA	29.2	27.07	-80.12	Mrosovsky (1988) <sup>1</sup>
Bald Head Is., NC, USA	29.2	33.84	-77.97	Mrosovsky (1988) <sup>1</sup>
Bahia Brazil	29.2	-10.38	-37.67	Marcovaldi et al., (1997) <sup>1</sup>
Kyparissia, Greece	29.3	37.25	21.66	Mrosovsky et al., (2002) <sup>1</sup>

**Table 1.** Pivotal temperatures for loggerhead sea turtles in the Atlantic Ocean and Mediterranean Sea. <sup>1</sup>Study used 2 clutches; <sup>2</sup>Field-based; <sup>3</sup>Two study clutches from one beach in Cyprus and six from four different beaches in Turkey combined to calculate pivotal.

Location	Life stage	% ♀	Method	Source
Atlantic, USA	Juvenile	67.7	LAP	Braun-McNeill et al., (2007)
Atlantic, USA	Juvenile	74.5	RIA	Braun-McNeill et al., (2007)
Atlantic, USA	Juvenile	66.0	OBS	Stabenau et al., (1996)
Atlantic, USA	Juvenile	65.3	OBS	Shoop et al., (1998)
Mediterranean	Adult	76.5	OBS	Casale et al., (2005)
Mediterranean	Juvenile	54.2	OBS	Casale et al., (2006)

**Table 2:** Reported juvenile and adult sex ratios for loggerhead turtles. Method of sexing: laparoscopy (LAP), radioimmunoassay (RIA) or observation of gross anatomical features (OBS).

Figure 1

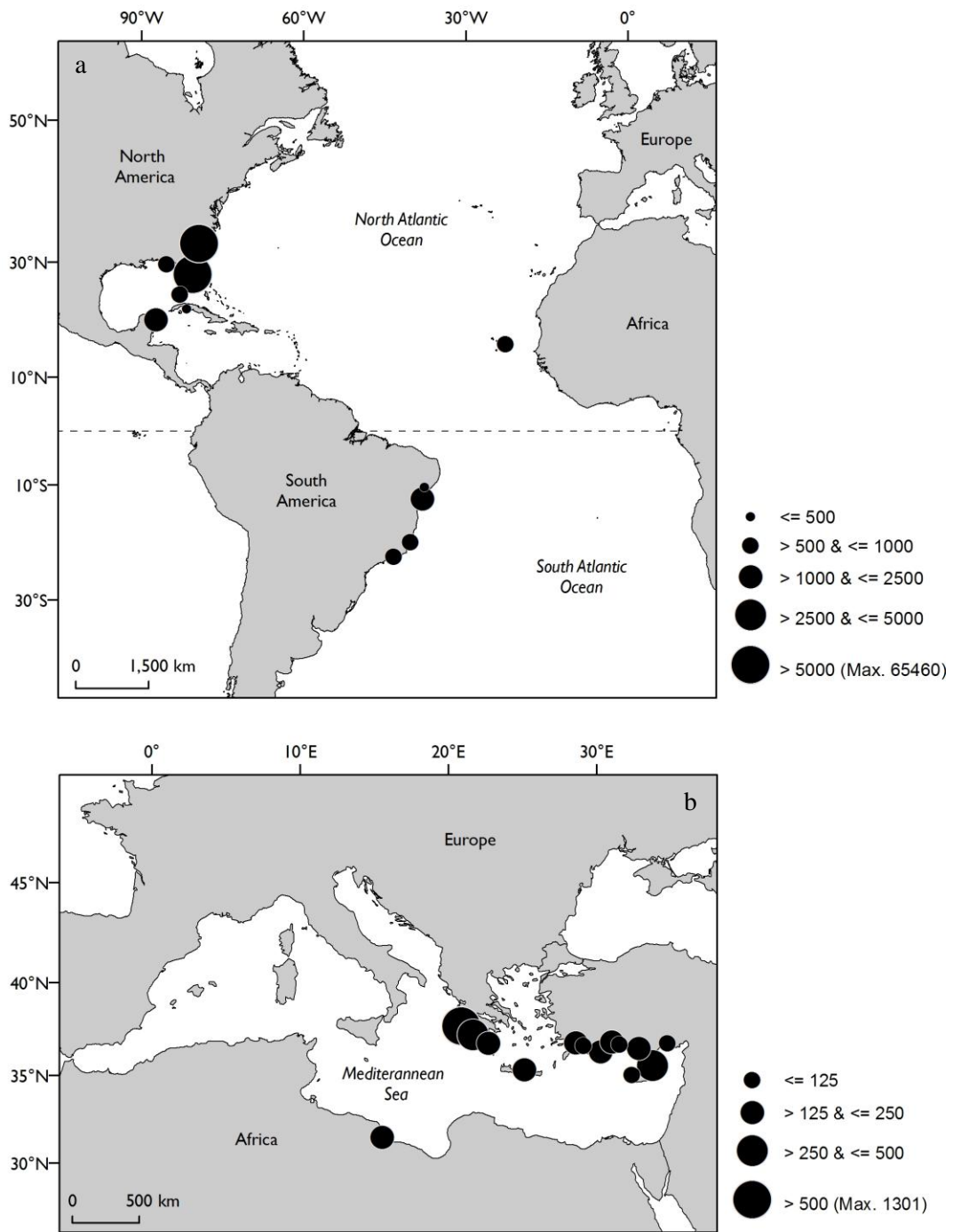


Figure 2

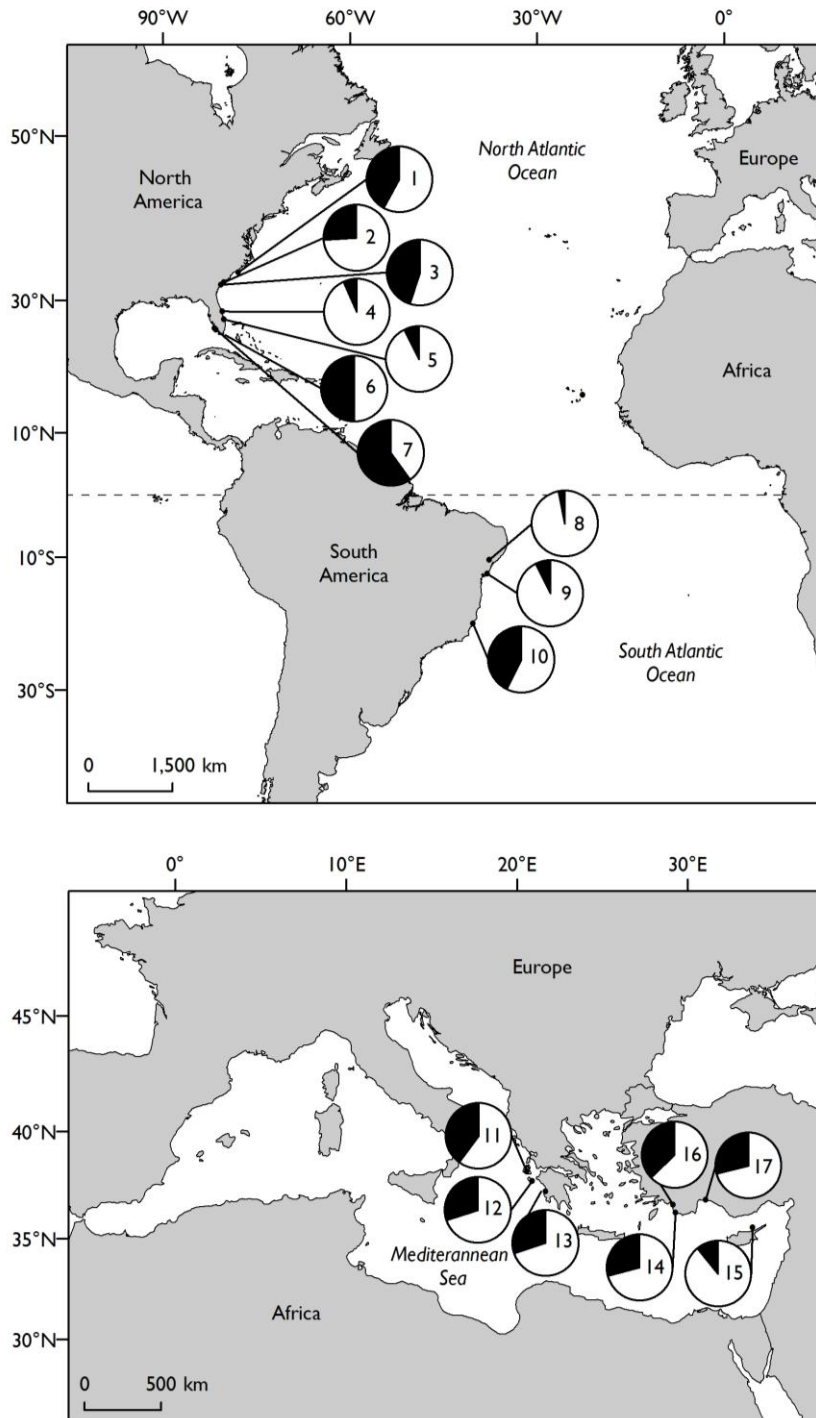




Figure 3

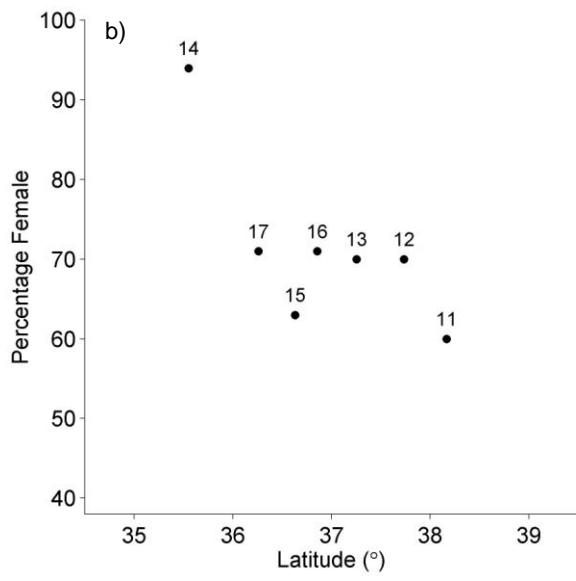
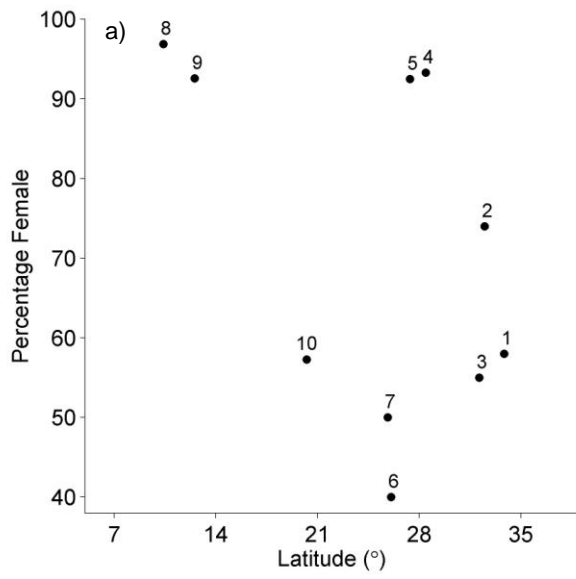


Figure 4

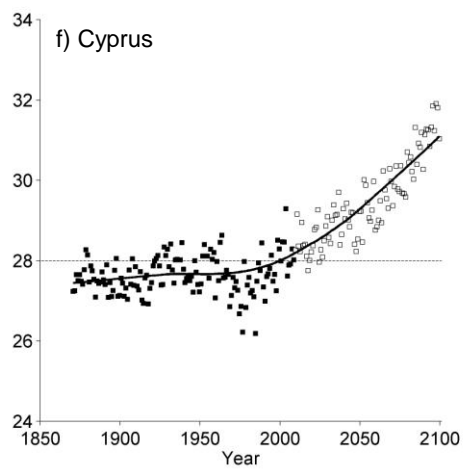
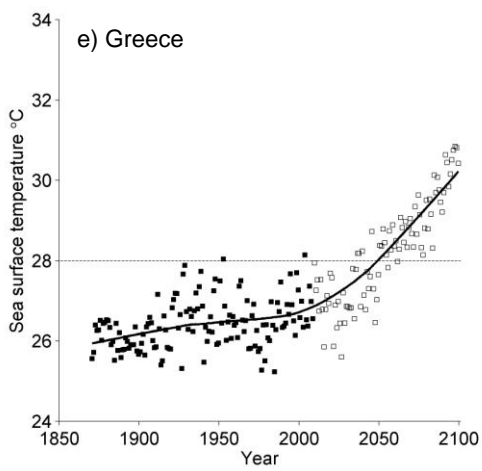
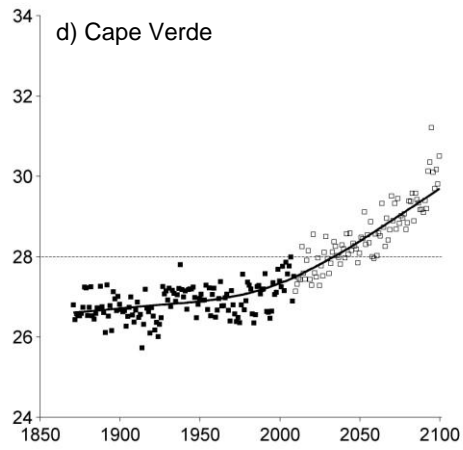
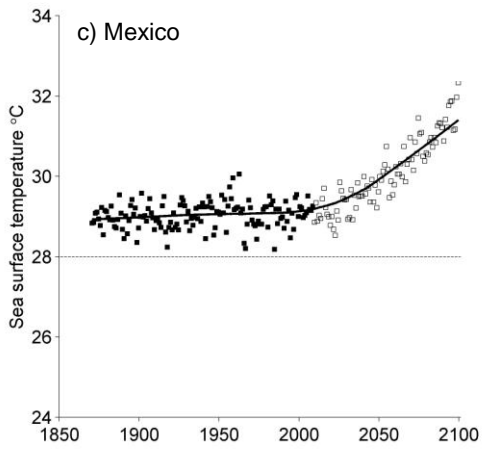
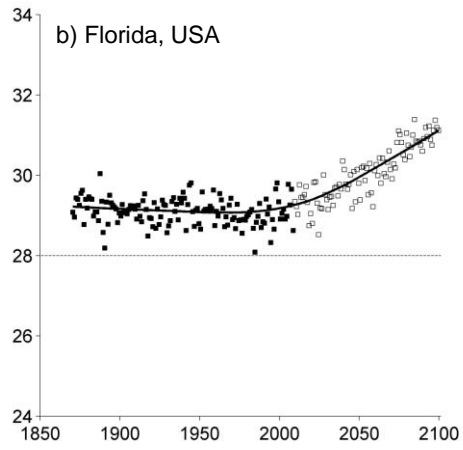
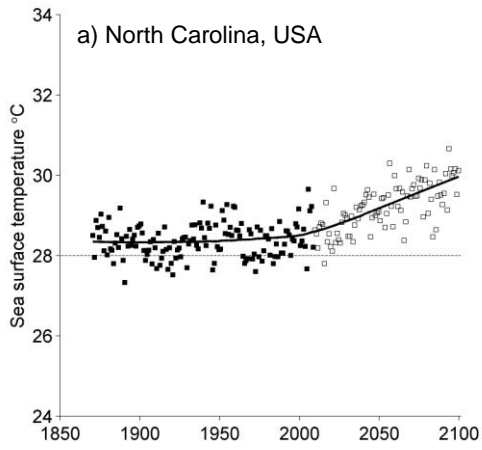


Figure 5

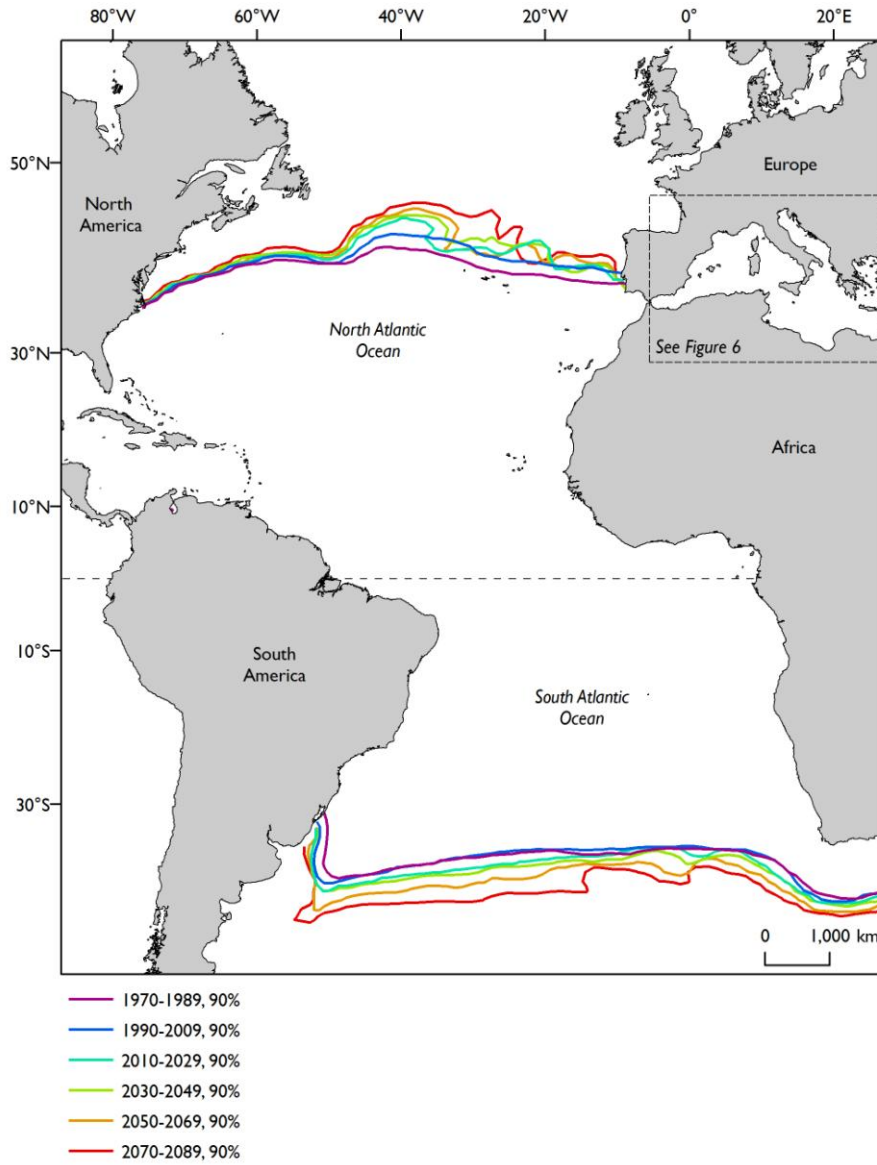


Figure 6

