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1 **Title: The climatic debt of loggerhead sea turtle populations in a warming world**

2 Running title: The climatic debt of sea turtle populations

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28 **ABSTRACT**

29 Phenological shifts, by initiating reproductive events earlier, in response to advanced seasonal
30 warming is one of the most striking effects currently observed in wild populations. For sea
31 turtles, phenological adjustment to warming conditions could be the most effective short-term
32 adaptation option against climate change. We calculated future phenological changes required
33 in seven important loggerhead (*Caretta caretta*) nesting populations to continue achieving a
34 high hatching success and a sex ratio that lies within current ranges. Considering temperature-
35 mediated phenological changes, we found that most populations (six out of seven) will not be
36 able to keep pace with a warming climate. Under an optimistic climate warming scenario
37 (RCP4.5), these populations will face a climatic debt, that is, a difference between required
38 and expected phenological changes, and warming will substantially reduce hatching success
39 and induce a feminization of hatchlings, which may jeopardize their reproductive
40 sustainability. Our approach offers the possibility to quantify the efficiency of phenological
41 shifts in oviparous reptiles by considering physiological, developmental and phenological
42 processes.

43 **Keywords:** Climate change, phenotypic plasticity, phenology, hatching success, sex ratio,
44 embryonic development, incubation, thermal tolerance, reptile, *Caretta caretta*

45

46 **INTRODUCTION**

47 Current climatic changes affect species' abundance, distributions, phenology, physiology and
48 behavior (Bellard et al., 2012; Parmesan, 2006; Root et al., 2003). Such modifications at
49 population- and species-levels will undoubtedly scale toward community and ecosystem
50 levels, for example by disrupting trophic interactions (Walther, 2010). Assessing the
51 vulnerability of species under different climate scenarios is challenging yet it is a prerequisite

52 for developing and prioritizing conservation management strategies. Species with highly
53 heritable variability and short generation time are expected to respond rapidly to selection by
54 microevolution of determinant traits, provided that they benefit from sufficient genetic
55 diversity (Bradshaw and Holzapfel, 2006; Nogués-Bravo et al., 2018; Visser, 2008). In
56 contrast, species with long generation times might be limited in their ability to keep up with
57 the current rate of biotic and abiotic changes.

58 For these species, plasticity in behavior and physiology has the potential to
59 compensate for rapid environmental shifts, allowing them to effectively track of their climate
60 envelope (Chevin et al., 2010; Huey et al., 2012; Refsnider and Janzen, 2012). Many species
61 are already shifting spatially (to higher latitudes or altitudes) and temporally (initiating
62 reproductive events earlier or later in the season) (Parmesan, 2006; Root et al., 2003). For
63 instance, several species of birds are laying their eggs 8.8 days earlier in 25 years in the
64 United Kingdom (Crick et al., 1997). Such phenotypic plasticity may be adaptive if it enables
65 a species to match with its resources or maladaptive if it creates a mismatch with available
66 resources (Charmantier et al., 2008; Visser et al., 2012). Ectotherms are expected to be
67 especially vulnerable to changes in their thermal environment because virtually all their life
68 history traits depend on ambient temperatures, which in turn, affects fitness of individuals
69 (Deutsch et al., 2008; Tewksbury et al., 2008). Temperature can even be viewed as an
70 ecological resource for ectotherms (Magnuson et al., 1979) and especially for oviparous
71 reptiles with temperature-dependent sex determination (TSD), such as sea turtles, because it
72 allows or constrains embryonic development and directs sex ratio, which influence population
73 viability (Hulin et al., 2009; Mitchell et al., 2010).

74 Six out of the seven sea turtle species are already endangered (IUCN, 2016) and may
75 be under further threat as climate change progresses (Fuentes et al., 2013; Hamann et al.,
76 2013). In their life history, like in all oviparous reptiles, the incubation stage is particularly

77 sensitive to temperatures. Once the eggs are laid, the development of embryos is submitted to
78 environmental factors that are highly dependent on climatic conditions experienced during the
79 incubation period, without any possibility to avoid detrimental conditions. In sea turtles, both
80 the hatching success and the sex of hatchlings depend on incubation temperatures. Constant
81 temperature experiments shown that hatching occurs within a narrow thermal range (roughly
82 25-35°C) (Howard et al., 2014), with a steep threshold at lower temperatures under which
83 development fails and at higher temperatures over which embryos die. Predicting the hatching
84 success of nests in natural conditions remains challenging because temperature varies during
85 the whole incubation period. Current temperature regimes may already reach or exceed the
86 upper limit for successful development as evidenced by low incubation success observed at
87 several nesting beaches (Horne et al., 2014; Rafferty et al., 2017; Valverde et al., 2010).
88 Warming temperatures are thus expected to put the reproduction of many populations at risk.

89 In addition, sea turtles exhibit Temperature-dependent Sex Determination (TSD),
90 producing females at high incubation temperatures and males at low incubation temperatures
91 (Yntema and Mrosovsky, 1980). Many nesting sites already produce predominantly females,
92 with a bias increasing toward nearly 100% females in some of them (Hays et al., 2017; Jensen
93 et al., 2018). A further increase in incubation temperatures could dramatically jeopardize the
94 production of males, and, in turn, these populations' long-term reproductive success. An
95 adaptation to increasing temperatures could be achieved the microevolution of the pivotal
96 temperature (i.e., the temperature at which 50% of each sex may occur). However, this
97 scenario seems unlikely because (i) this trait is relatively conserved among populations (Hulin
98 et al., 2009), which suggests strong genetic constraints, (ii) long generation times should
99 hamper rapid genetic selection of individuals that might deviate, and (iii) the effective
100 heritability of pivotal temperatures in turtles is low in natural conditions (Bull et al., 1982;
101 McGaugh and Janzen, 2011; Refsnider and Janzen, 2015). Sea turtles are also known for natal

102 homing behavior and a high degree of nest site fidelity (Bowen et al., 1994b; Bowen and Karl,
103 2007; Miller, 1997). The latter trait may constrain rapid large-scale spatial shifts toward more
104 suitable thermal conditions for egg development. Without such plasticity in nest site choice,
105 low rates of embryo survival and highly female-biased sex ratios may arise in the context of
106 global warming (Fuentes et al., 2011; Poloczanska et al., 2009). Therefore, shifting the
107 nesting season might be the most efficient short-term option for sea turtles to adapt to the
108 current rate of thermal changes.

109 Earlier nesting in response to warmer environmental temperatures has been observed
110 in a fresh water turtle (*Chrysemys picta*) (Schwanz and Janzen, 2008), in loggerhead sea
111 turtles (*Caretta caretta*) (Hawkes et al., 2007; Lamont and Fujisaki, 2014; Mazaris et al.,
112 2008; Monsinjon et al., 2019; Patel et al., 2016; Pike et al., 2006; Weishampel et al., 2004;
113 Weishampel et al., 2010) and in green sea turtles (*Chelonia mydas*) (Weishampel et al., 2010).
114 However, whether this phenotypic plasticity in nesting behavior will enable sea turtles to
115 overcome warming impacts at nesting beaches remains to be investigated. Here we address
116 this issue by applying the concept of “climatic debt”, previously applied to the spatial
117 distribution of bird and butterfly communities (Devictor et al., 2012), to seven loggerhead
118 nesting populations. Briefly, the theoretical poleward range shift that a species should
119 undertake to track its thermal niche is calculated and compared to a measured real-world
120 response. In other words, a “climatic debt” can be viewed as the lag between environmental
121 changes and the species' or population's response, depending on its ability to stay
122 synchronized with previous conditions (i.e., the difference in time between required and
123 observed or expected phenological shifts). Given that sea turtle populations are unlikely to
124 fully track of suitable thermal conditions at nesting beaches by shifting spatially, we applied
125 this concept at a temporal scale by addressing the following questions: What would be the
126 “climatic prices”, that is, the phenological shifts required in the future for sea turtle

127 populations to continue producing a hatching success and a sex ratio that lie within current
128 ranges? Would expected temperature-induced phenological shifts be sufficient to reach this
129 goal (i.e., to pay the “climatic prices”) or would populations still face a “climatic debt”, that
130 is, a positive difference between the “climatic price” and the expected phenological shift?

131 Combining physiological, developmental and phenological processes, we developed
132 two indices: A Hatching Success Index (HSI) that accounts for the number of nests
133 successfully laid and a Sex Ratio Index (SRI) that accounts for the number of nests
134 successfully laid and the proportion of surviving embryos. We forecasted the hatching success
135 and the sex ratio of seven important loggerhead nesting populations at a global scale (Figure
136 1) within four Regional Management Units (RMUs) (Wallace et al., 2010) under current
137 conditions and under two warming scenarios (RCP4.5 and RCP8.5) (IPCC, 2014). We first
138 assumed the timing of nesting seasons will remain unchanged until 2100 and we explored
139 how phenological shifts could buffer detrimental effects of rising temperatures by shifting the
140 nesting seasons from 0 to 365 days earlier. Finally, we calculated the climatic debts by
141 comparing the climatic prices to realistic expected phenological changes (7 days earlier per
142 degree Celsius increase in sea surface temperature) (Weishampel et al., 2004).

143

144 **MATERIALS AND METHODS**

145 **Field data**

146 Nest temperature was recorded at several nesting sites within the following Regional
147 Management Units (RMUs) (Wallace et al., 2010) of the loggerhead sea turtle:
148 Mediterranean, Northwest Atlantic, Southwest Atlantic and Southwest Indian (information
149 summarized in Supplementary material Table A1). Some data are presented here, while the
150 remaining are already published. For the latter, we used only temperature data recorded in

151 natural conditions. Temperatures were recorded within several nests for each site
152 (Supplementary material Table A1) using temperature data loggers placed in the middle of the
153 clutches while females were laying their eggs (≈ 45 cm deep). Data loggers were excavated
154 when hatchlings emerged from the nest or several days later. Temperature data recorded
155 outside the incubation period (i.e., before the laying date or after the emergence date) were
156 omitted.

157 The number of nests was surveyed daily by patrols at the seven nesting beaches during
158 a period of the year specific to each monitoring program (information summarized in
159 Supplementary material Table A2). We omitted nest attempts (false crawls) if the data set
160 contained such information. Nests were counted at Dalyan Beach, Turkey, at Blackbeard
161 Island and Wassaw Island, Georgia, at Boca Raton, Florida, at Praia do Forte and Rio de
162 Janeiro, Brazil, and at Bhanga Nek, South Africa (Figure 1).

163 **Overview of the modeling approach**

164 For the seven nesting populations studied (Figure 1, see section “Field data”), we predicted a
165 hatching success index and a sex ratio index according to scenarios for future area-specific
166 changes in air temperature and global changes in ocean temperature (IPCC, 2014)
167 (Supplementary material Table A3). Those indices were first calculated assuming that the
168 timing of nesting seasons will not shift until 2100 (Figure 2). Thereafter, we shifted nesting
169 seasons each day from 0 to 365 days earlier and we calculated the resulting hatching success
170 and sex ratio indices, which enabled quantifying respective climatic prices (i.e., phenological
171 shifts, in number of days earlier, required for projected indices to reach the lower limit of
172 current ranges, Figure 2). Finally, we calculated the climatic debts (in number of days) by
173 subtracting expected future temperature-induced phenological shifts from climatic prices. To
174 project future temperature-induced phenological shifts, we assumed that a 1°C increase in sea
175 surface temperature will shift a nesting season 7 days earlier (Weishampel et al., 2004). Based

176 on this linear relationship, $+1.19^{\circ}\text{C}$ and $+2.89^{\circ}\text{C}$ increases in ocean temperature (two
177 warming scenarios: respectively, RCP4.5 and RCP8.5) (IPCC, 2014) (Supplementary material
178 Table A3) would advance the whole nesting seasons 8.3 and 20.2 days earlier, respectively.
179 Negative climatic debts indicate that phenological shifts can effectively offset detrimental
180 effects of warming temperatures whereas positive climatic debts indicate that phenological
181 shifts do not allow populations to track of their thermal niche (Figure 2). Hatching success
182 and sex ratio indices resulting from future temperature-induced phenological shifts were
183 calculated (Figure 2).

184 Following an elaborate modeling approach, it is possible to predict the temperature
185 within the nest, the incubation duration, the hatching success, and the sex ratio (Figure 3).
186 First, nest temperature was reconstructed based on a correlative model that links the
187 temperature recorded within natural nests and environmental temperatures, such as air
188 temperature and sea surface temperature, at nesting beaches (Figure 3.1). This step enables
189 production of long-term time series of nest temperatures using projections from global climate
190 models. We accounted for metabolic heating (i.e., the temperature difference between the nest
191 and the adjacent incubation substratum), which is a characteristic of sea turtle nests due to
192 their large clutch sizes (Booth and Astill, 2001; Broderick et al., 2001; Godfrey et al., 1997;
193 Godley et al., 2001), and we reconstructed natural daily thermal fluctuations because they
194 affect sex determination (Georges, 2013; Georges et al., 2005; Georges et al., 1994). Second,
195 embryonic growth (in terms of carapace size) was modeled based on the Thermal Reaction
196 Norm (TRN) for growth rate inferred from nest temperatures, incubation durations and
197 hatchling measurements (straight carapace length of hatchlings), combined with a growth
198 function (Figure 3.2). When iteratively applied to time series of reconstructed nest
199 temperatures, this approach provides information about embryonic development such as the
200 incubation period and the location of the ThermoSensitive Period (TSP) of development for

201 sex determination (i.e., the period during which temperature influences sex determination).
202 Third, hatching success was estimated by a model linking the average nest temperature to the
203 Thermal Tolerance Curve (TTC) inferred using constant temperature experiments (Figure
204 3.3). Fourth, Constant Temperature Equivalents (CTEs) were converted into sex ratio
205 estimates based on the TRN for sex ratio inferred using constant temperature experiments
206 (Figure 3.4). Fifth, the dynamics of nesting activity was inferred based on the number of nests
207 counted during monitoring surveys (Figure 3.5), which enabled including the temporal
208 window within which nests are incubating. Finally, we calculated hatching success and sex
209 ratio indices per season by including the number of nests laid per day (Figure 3.6).

210 **Reconstructing nest temperatures**

211 We modeled past Nest Temperatures (NT) based on a previously published method (Girondot
212 and Kaska, 2014b; Monsinjon et al., 2017a; Monsinjon et al., 2017b). Nest temperature
213 correlates with Air Temperature (AT) and Sea Surface Temperature (SST) in front of the
214 beach (Girondot and Kaska, 2014b). We collected such data from the European Centre for
215 Medium-Range Weather Forecasts (ECMWF) data sets, which provide temperature every 6
216 hrs (UTC) for several decades at 0.125° resolution (Dee et al., 2011). Sea Surface
217 Temperature (SST) and Air Temperature (AT) at a height of 2 m were extracted from the 1st
218 January 1979 to the 31st December 2016 at geographic coordinates closest to the location of
219 nesting sites (distances between these geographic coordinates and the exact position of
220 nesting sites ranged from 1.2 to 19 km, Supplementary material Table A4). We modeled the
221 daily mean temperature and the metabolic heating using a generalized linear mixed model
222 with Gaussian distribution and identity link function (Monsinjon et al., 2017b) with the mixed
223 effect being the nest identity. Natural daily thermal fluctuations were reconstructed as they
224 can strongly affect sex determination (Georges, 2013; Georges et al., 2005; Georges et al.,
225 1994). We calculated the average daily amplitudes of temperatures (AmpT) using daily

226 maximum (from noon to noon) and daily minimum (from midnight to midnight) (Eccel, 2010)
227 for all days and all nests, independently for each nesting sites. We also calculated the average
228 time of the day when daily maxima and daily minima occur (respectively, Ti.Max and
229 Ti.Min). After site-specific long-term time series of mean nest temperatures were
230 reconstructed, we replaced daily mean by daily maximum ($\text{mean} + \text{AmpT}/2$) and daily
231 minimum ($\text{mean} - \text{AmpT}/2$) that we set at Ti.Max and Ti.Min respectively. Site-specific
232 parameters used to predict NT are presented in Supplementary material Table A4 (see also
233 Supplementary material Note A1). This modeling approach allowed for an accurate prediction
234 of nest temperature (Supplementary material Note A1, Figure A1).

235 We forecasted NT based on region-specific scenarios of changes in air temperature
236 and a global scenario of changes in ocean temperature (IPCC, 2014) (Supplementary material
237 Table A3). We chose an optimistic scenario of Representative Concentration Pathway (RCP)
238 in greenhouse gas concentration that predicts a rising radiative forcing that will stabilize at
239 $+4.5 \text{ W.m}^{-2}$ after 2100 as compared to preindustrial values, assuming a decrease in emissions
240 of CO_2 after 2040 (RCP4.5) (Moss et al., 2010). We also chose to make predictions under a
241 more pessimistic scenario. This extreme scenario predicts a radiative forcing that will reach
242 $+8.5 \text{ W.m}^{-2}$ by 2100 as compared to preindustrial values and will keep rising afterward
243 assuming no decrease in emissions of CO_2 (RCP8.5) (Moss et al., 2010). These data were
244 extracted from the KNMI (Koninklijk Nederlands Meteorologisch Instituut) Climate Explorer
245 website (https://climexp.knmi.nl/plot_atlas_form.py). Briefly, the KNMI interface allows the
246 user to select the region (here defined by IPCC Working Group 1), the data set (here Coupled
247 Model Intercomparison Project 5 for IPCC's Fifth Assessment Report), the variable (here
248 near-surface temperature), the scenario of RCP in greenhouse gas concentration (here RCP4.5
249 and RCP8.5) and the periods to be compared to obtain anomalies (here anomalies as
250 compared with the 1979-2016 period). Projected temperature anomalies were extracted for the

251 following regions: North-East Brazil, Eastern-North-America, Southern-Africa and South-
252 Europe-Mediterranean (summarized in Supplementary material Table A3). We added
253 projected (region-specific) increases in temperature to AT time series previously extracted
254 from ECMWF data sets. We also extracted the projected increase in ocean temperature at the
255 scale of the world, which was added to SST time series previously extracted from ECMWF
256 data sets. Future NT is then reconstructed following the method described above but this time
257 using modified time series of AT and SST. These new NT time series are forecasts for the
258 2062-2100 period while considering the 1979-2016 period as a baseline.

259 **Modeling embryonic development**

260 The size of an embryo according to the temperature experienced within the nest can be
261 modeled based on the Thermal Reaction Norm (TRN) for growth rate using an equation that
262 describes the effect of temperature on the growth rate along with an equation that describes
263 the progression of embryo size during incubation (Girondot and Kaska, 2014a). This method
264 has been implemented to estimate the TRN for the growth rate of three loggerhead nesting
265 populations (Fuentes et al., 2017; Girondot and Kaska, 2014a; Monsinjon et al., 2017b). The
266 components form a thermodynamic description of the effect of temperature on the rate of
267 biological reactions applied to a Gompertz model for the growth of an embryo (Girondot and
268 Kaska, 2014a). Here, we applied this method following recent upgrades (Girondot et al.,
269 2018). The model requires (i) temperature time series recorded within nests from the moment
270 when eggs were laid to the moment when hatchlings emerged from the nest and (ii)
271 measurements of the Straight Carapace Length (SCL) of hatchlings (SCL data used to infer
272 TRNs are summarized in Supplementary material Table A5).

273 To detect potential differences in TRNs for growth rate among nesting populations
274 from the same Regional Management Unit (RMU), we applied a similar approach as per
275 Monsinjon et al. (2017b). Briefly, the TRN for growth rate was estimated for two populations

276 (i) independently for both populations (hypothesis 1: the populations exhibit different TRNs)
277 and (ii) after data sets of nest temperature were grouped together (hypothesis 2: the
278 populations exhibit similar TRNs). We calculated the Akaike Information Criterion corrected
279 for finite sample size (AICc) and the Akaike weight, i.e. the relative support of both
280 hypotheses (Burnham and Anderson, 2002). The sum of AICc of each model estimated
281 independently (hypothesis 1) were then compared with the AICc of the model estimated with
282 both data sets grouped together (hypothesis 2). Before comparing the populations closest to
283 one another within the same RMU, we first grouped those which belonged to the same
284 “subdivided” management unit (i.e., demographically isolated but not genetically different)
285 (Shamblin et al., 2014). The model selection procedure is presented in Supplementary
286 material Table A6.

287 Once population-specific TRNs for growth rate were estimated (Supplementary
288 material Note A2, Figure A2), we modeled embryonic development at nesting sites based on
289 long-term time series of reconstructed nest temperatures (NT). If we consider a nest being laid
290 at a date i , the progression of embryo size (SCL) is modeled until it reaches, at the date $i+n$,
291 the final SCL of a completely developed embryo (i.e., a freshly emerged hatchling) known for
292 the nesting population. This allowed the extraction of information such as the incubation
293 duration (n), the nest temperature within the whole incubation period, and the nest
294 temperature within the TSP (see section “Estimating sex ratio” for defining TSP boundaries
295 within incubation). The model was run again at the date $i+1$ and so on for the period when NT
296 is available (i.e., each day between 1979 and 2016).

297 **Estimating hatching success**

298 Here, we introduce a new mathematical description of the thermal tolerances of sea turtle
299 embryos. This model is fitted here for the loggerhead sea turtle using data obtained at constant
300 temperatures in laboratory conditions. The Thermal Tolerance Curve (TTC) is described by a

301 model composed of the product of two logistic equations and a term defining the average
302 hatching success within the optimal range of temperatures (equation 1):

$$303 \quad HS = \frac{1}{1 + \exp\left(\frac{1}{|S_L|}(P_L - t)\right)} \times \frac{1}{1 + \exp\left(\frac{1}{-|S_H|}(P_H - t)\right)} \times H \quad \text{equation 1}$$

304 With S_L and P_L being the logistic parameters defining the lower part of the curve, S_H and P_H
305 being the logistic parameters defining the higher part of the curve and H being the average
306 hatching success within the optimal range of temperatures. This method accounts for both the
307 upper and the lower thermal limits for embryo survival, which is a prerequisite when making
308 projections according to extremes scenarios of thermal changes.

309 To infer the TTC, we used data for the loggerhead sea turtle from five Regional
310 Management Units (RMUs) (Supplementary material Table A7). For each constant
311 temperature experiment, the hatching success is calculated as being the number of embryos
312 that successfully hatched divided by the total number of eggs (of which we subtracted the
313 number of undeveloped embryo if specified in the original publication). The model is fitted
314 using maximum likelihood with a binomial distribution for error. As most of the data come
315 from different populations, we assessed potential similarities among RMUs. To detect
316 potential differences, we estimated the TTCs (i) independently (making the hypothesis that
317 RMUs exhibit different TTCs) and (ii) after all data were grouped together (making the
318 hypothesis that RMUs exhibit similar TTCs). Based on the AICc and the Akaike weight,
319 TTCs were found similar among RMUs (Supplementary material Note A3).

320 The model described here allows for predicting the hatching success for any nest that
321 incubated at constant temperatures (Supplementary material Figure A3). However,
322 temperature is not constant under natural conditions and it is poorly known how fluctuating
323 thermal regimes influence hatching success (Howard et al., 2014). Using published data of

324 hatching success from natural nests (Godley et al., 2001; Horne et al., 2014; Read et al.,
325 2013), we searched for an equivalent at constant temperature (i.e., the mean nest temperature
326 during incubation plus a correction parameter) that best describes hatching success in natural
327 conditions. This correction parameter aims to adjust data from natural conditions so they can
328 be compared with data from constant temperature experiments. Data were extracted from
329 figures in respective original publications using the software WebPlotDigitizer version 4.1
330 (<https://automeris.io/WebPlotDigitizer/>) when tables were not provided. We predicted the
331 hatching success from mean nest temperatures with a correction parameter varying from -
332 1.5°C to +1.5°C each 0.01°C and we kept the value that minimizes the dispersion (sum of
333 squares) of residuals (here +0.32°C, see Supplementary material Note A3).

334 **Estimating sex ratio**

335 The loggerhead sea turtle exhibits a cool male/warm female pattern of Temperature-
336 dependent Sex Determination (TSD) (Yntema and Mrosovsky, 1980). We inferred the
337 Thermal Reaction Norm (TRN) for sex ratio of loggerhead populations nesting in
338 Mediterranean, Northwest Atlantic, Southwest Atlantic and Southwest Indian Regional
339 Management Units (RMUs) based on constant temperature experiments previously carried out
340 in laboratory conditions. Data for Mediterranean were from Greece (Mrosovsky et al., 2002).
341 Data for Northwest Atlantic were from Florida (Mrosovsky, 1988), North Carolina
342 (Mrosovsky, 1988) and Georgia (Yntema and Mrosovsky, 1980, 1982). Data for Southwest
343 Atlantic were from Brazil (Marcovaldi et al., 1997). Data for Southwest Indian ocean were
344 from South Africa (Maxwell, 1987). We estimated TRNs for sex ratio using a logistic
345 equation (Girondot, 1999).

346 The simple mean temperature during either periods of incubation typically is a poor
347 predictor of sex ratio because the effect of temperature on sex determination may vary with
348 gonadal growth which also depends on temperature (Georges et al., 2005; Neuwald and

349 Valenzuela, 2011). A Constant Temperature Equivalent (CTE) was developed to account for
350 such effect by calculating the temperature at which half of the development occurred
351 (Georges, 1989; Georges et al., 1994). Here, we used a recent update that accounts for a
352 nonlinear development within incubation (Fuentes et al., 2017). Basically, this CTE is the
353 mean temperature weighted by the differential growth within the TSP. We produced sex ratio
354 estimates based on population-specific TRNs for sex ratio (Supplementary material Note A4,
355 Figure A4) using this proxy.

356 The ThermoSensitive Period (TSP) of development occurs between embryonic stages
357 21 and 26 for sea turtles (Miller, 1985) which roughly corresponds to the middle third of
358 incubation at constant temperature as generally observed in most reptiles with TSD (Bull,
359 1987; Desvages et al., 1993; Girondot et al., 2018; Pieau and Dorizzi, 1981; Woolgar et al.,
360 2013). The Straight Carapace Length (SCL) at the onset of the TSP and the SCL at the end of
361 the TSP are respectively 21% and 71% of the SCL of a completely developed embryo for the
362 loggerhead sea turtle (Girondot et al., 2018).

363 **Unraveling the dynamics of nesting activity**

364 We used a set of equations that describe the underlying dynamics of a nesting season based on
365 time series of nest counts (Girondot, 2017). Basically, a nonlinear function with seven
366 parameters was fitted using maximum likelihood with negative-binomial distribution for each
367 ordinal day of the year. These parameters describe adequately the pattern of a nesting season:
368 a minimum number of nests when turtles are not active before and after the active season and
369 a maximum number of nests at the ordinal day when the peak of activity occurs around which
370 the curve can flatten out. The dispersion around the mean was controlled by a negative-
371 binomial parameter (Girondot, 2017). Here we assumed that the curve was not flat around the
372 peak because a visual examination of nest counts showed a bell-shaped distribution. First, we
373 allowed all parameters to vary across seasons to obtain a “season-specific” description of

374 nesting activity at any nesting site. Second, we fitted parameters without allowing them to
 375 vary across seasons to obtain a “global” description of nesting activity. The global description
 376 of nesting activity was used in Figure 4 to provide a visual picture of the dynamics of nesting
 377 activity along with within-year variations in hatching success and sex ratio. The season-
 378 specific description of nesting activity was used to capture the actual interseasonal variability
 379 of current hatching success and sex ratio indices while the global description of nesting
 380 activity was used to project future indices, assuming the overall pattern of nesting seasons will
 381 remain unchanged until 2100.

382 **Calculating hatching success and sex ratio indices**

383 We calculated a Hatching Success Index (HSI) as being the average hatching success during a
 384 nesting season weighted by the number of nests laid (equation 2).

$$385 \quad HSI = \frac{\sum_{i=k}^N HS_i \times Nest_i}{\sum_{i=k}^N Nest_i} \quad \text{equation 2}$$

386 HS_i is the hatching success (survival proportion) for nests laid at the day i of the season with
 387 k being the first date of the season. $Nest_i$ is the number of nests laid at the day i of the
 388 season. N is the last date of the season.

389 We calculated a Sex Ratio Index (SRI) as being the average sex ratio during a nesting
 390 season corrected by the hatching success and weighted by the number of nests laid, which is
 391 the sex ratio of surviving hatchlings (equation 3).

$$392 \quad SRI = \frac{\sum_{i=k}^N SR_i \times Nest_i \times HS_i}{\sum_{i=k}^N Nest_i \times HS_i} \quad \text{equation 3}$$

393 SR_i is the sex ratio (male proportion) for nests laid at the day i of the season with k being the
 394 first date of the season. $Nest_i$ is the number of nests laid at the day i of the season. HS_i is the
 395 hatching success for nests laid at the day i of the season. N is the last date of the season.

396 Current indices (between 1979 and 2016) were calculated only for seasons when nests
397 were surveyed (see Supplementary material Table A2) and using the season-specific
398 description of nesting activity. Future indices (i.e., forecasts for the 2062-2100 period) were
399 calculated for all future seasons (n = 38) using the global description of nesting activity (see
400 section “Unraveling the dynamics of nesting activity” for the descriptions of nesting activity).

401

402 **RESULTS**

403 **Current nesting activity, hatching success and sex ratio**

404 Currently, the nesting seasons occur when the hatching success is optimal at Dalyan Beach,
405 Blackbeard Island, Wassaw Island, Rio de Janeiro, and Bhanga Nek (respectively, Figure 4a,
406 b, c, f and g). A different situation is observed at Boca Raton and Praia do Forte, where the
407 hatching success decreases slightly around the peak of nesting (respectively, Figure 4d and e).

408 The nesting seasons occur when both sexes are produced in variable proportions (with
409 a peak of nesting when mostly female hatchlings are expected) at Dalyan Beach, Blackbeard
410 Island, Wassaw Island, Rio de Janeiro, and Bhanga Nek (respectively, Figure 4h, i, j, m and
411 n). A different situation is observed at Boca Raton and Praia do Forte, where the whole
412 nesting seasons occur when a nearly 100% female-biased sex ratio is expected (respectively,
413 Figure 4k and l).

414 **Warming temperatures may reduce hatching success and induce a feminization of** 415 **hatchlings**

416 Current Hatching Success Indices (HSIs) are optimal for all nesting populations studied here
417 except at Boca Raton and Praia do Forte (Figure 5a). Under an optimistic warming scenario
418 (RCP4.5), all nesting populations are expected to face a reduction in hatching success, except

419 at Dalyan Beach (Figure 5a). According to this scenario, the population nesting at Boca Raton
420 should face a very low hatching success (<20%). Under a pessimistic warming scenario (RCP
421 8.5), all nesting populations should face a hatching success lower than 50%, except at Dalyan
422 Beach (Figure 5a). In this extreme warming situation, expected phenological shifts can
423 effectively buffer reductions in hatching success, except for populations nesting at Boca
424 Raton and Praia do Forte which may face a very low hatching success (<10%) either ways
425 (Figure 5a).

426 Current Sex Ratio Indices (SRIs) are highly female-biased at Praia do Forte and Boca
427 Raton (>95% females) whereas it is less skewed toward females at other nesting sites (<85%
428 females) (Figure 5b). Under an optimistic warming scenario (RCP4.5), the sex ratio might
429 become increasingly female-biased in all nesting populations studied here (with only female
430 hatchlings expected at Praia do Forte), except at Boca Raton where the proportion of males is
431 expected to increase slightly (Figure 5b). Under a pessimistic warming scenario (RCP8.5), all
432 nesting populations should experience a highly female-biased sex ratio (>95% females),
433 except at Boca Raton where the proportion of males might increase substantially (Figure 5b).
434 In both warming situations, only the population nesting at Dalyan Beach may benefit from a
435 buffering effect of expected phenological shifts while the opposite situation is observed at
436 Boca Raton (Figure 5b).

437 **Most populations could face a climatic debt in the future**

438 Phenological shifts required in the future (2062-2100 as compared to 1979-2016) for HSIs
439 and SRIs to remain within current ranges (i.e., climatic prices) range from 0 day earlier (for
440 HSI at Dalyan Beach under an optimistic warming scenario: RCP4.5) to 118 days earlier (for
441 HSI at Rio de Janeiro under a pessimistic warming scenario: RCP8.5) (Table 1,
442 Supplementary material Figure A5). Six out of the seven nesting populations studied here
443 could face a climatic debt in the future under both warming scenarios and for both the HSI

444 and the SRI (Table 1). Only the population nesting at Dalyan Beach might not face a climatic
445 debt in the future for the HSI to remain within its current range and only under the RCP4.5
446 scenario (Table 1).

447

448 **DISCUSSION**

449 For ectotherms, such as fishes, amphibians and non-avian reptiles, temperature is a major
450 driver of population distribution and viability (Angilletta et al., 2010; Deutsch et al., 2008;
451 Huey et al., 2009; Maffucci et al., 2016). Our results highlight differences among loggerhead
452 nesting populations in their capacity to keep pace with the rate of thermal changes and suggest
453 that only a subset of populations may be able to offset detrimental effects by shifting their
454 nesting phenology. A growing number of studies have suggested that phenological changes
455 may, to some extent, buffer detrimental effects of warming temperatures on reptile embryos
456 (Almpanidou et al., 2018; Mitchell et al., 2008; Mitchell et al., 2016; Stubbs et al., 2014). For
457 many sea turtle populations, whether climate-induced phenological shifts confer the potential
458 to buffer detrimental effects on their progeny remains unclear. Here we took a step forward in
459 the prediction of warming impacts on sea turtles' hatching success and sex ratio using an
460 elaborate modeling approach and comparing distant populations, which should inform new
461 strategies for prioritizing conservation efforts at a global scale. Importantly, our model offers
462 a process-based framework to quantify the sex ratio of sea turtle hatchlings during a nesting
463 season by considering (i) the number of nests laid and (ii) the proportion of surviving embryos
464 under both cold and warm conditions.

465 **Nesting activity, hatching success and sex ratio**

466 Loggerhead populations nesting at the lowest latitudes of our data sets (Boca Raton, Florida,
467 and Praia do Forte, Brazil) are already at the edge of thermal limits for embryo survival

468 (Figure 4d and e) and nest during the period when mostly female hatchlings are produced.
469 Conversely, other populations studied here, which nest at relatively higher latitudes, may
470 experience optimal incubation temperatures for embryo survival and produce a more balanced
471 sex ratio. Overall, male hatchlings are more likely to hatch during the first part of the nesting
472 season while mostly females are produced during the rest of the nesting season. This may
473 explain why future sex ratio at Boca Raton is expected to be less skewed toward females,
474 because remaining male-producing clutches would experience more suitable temperatures at
475 the beginning of the nesting season than middle and late clutches that may experience 100%
476 failure, as currently suspected at female-producing nesting sites (Figure 4d and e).

477 Whether a highly female-biased primary sex ratio is likely to persist through age
478 classes may vary within and among sea turtle species (Hamann et al., 2013; Hamann et al.,
479 2010). If feminization of the primary sex ratio persists in the adult sex ratio, detrimental
480 effects at population level can occur such as (i) reduced fertility rates (Bell et al., 2009) and/or
481 (ii) loss of genetic diversity through reduction of effective population size (Hamann et al.,
482 2010). Concerning these threats, males can breed annually with multiple females while
483 females do not breed every year. This sex-specific difference in reproductive behavior can be
484 somewhat compensatory and balance the operational sex ratio, thus buffering current or future
485 negative effects of female-biased adult sex ratios on fertility rates (Hays et al., 2010; Wright
486 et al., 2012). According to some authors, temperature-dependent sex determination can confer
487 a short-term demographic advantage by producing more females at increasing temperatures,
488 which could first enhance population growth (Hays et al., 2017). However, such a positive
489 effect on population dynamics does not seem sufficient to offset the current rate of climatic
490 changes in the long term (Laloë et al., 2014, 2017; Saba et al., 2012; Santidrián Tomillo et al.,
491 2015a). A decrease in effective population size finally seems inevitable, which in turn can
492 induce genetic erosion and thus lower potential to respond to selection pressures (Hamann et

493 al., 2010). There is a strong need for further research into population dynamics, and
494 particularly modeling, that integrates genetic Allee effects linked to potential biases in sex
495 ratio (Mitchell et al., 2010).

496 Nesting phenology and hatching success both influence the number of male and
497 female hatchlings that may reach the sea. Only a few studies have attempted to account for
498 differential survival of both sexes accounting for temperature-mediated hatching success or
499 emergence rate (Hays et al., 2017; Santidrián Tomillo et al., 2014) and none have accounted
500 for the number of nests before the present study. Here we provide reliable quantitative
501 predictions of temperature-mediated hatching success based on the thermal tolerance curve of
502 loggerhead embryos, which accounts for both lower and upper critical limits. This novel
503 model should now be calibrated in other sea turtle species to make accurate predictions under
504 both cold and warm extreme conditions, which is particularly relevant for populations nesting
505 at high latitudes where seasons are more pronounced. Nevertheless, this method can still be
506 improved. In natural conditions, embryo survival depends on the magnitude of the thermal
507 stress and the time spent over a critical threshold (Howard et al., 2014, 2015). Therefore, new
508 methods to predict hatching success should be deployed to capture biologically-determined
509 thermal variation. Recent studies about heat tolerance of loggerhead embryos will probably
510 help in refining models that incorporated cellular processes underlying embryo survival in
511 response to temperature (Bentley et al., 2017; Tedeschi et al., 2016). Precipitations and
512 moisture levels within nests are other factors that influence hatching success, either directly or
513 indirectly through an evaporative cooling effect (Montero et al., 2018a; Montero et al., 2018b;
514 Pike, 2013; Santidrián Tomillo et al., 2015b). Further studies must integrate this parameter
515 into a more comprehensive model to forecast the hatching success of sea turtles as the rate of
516 precipitation is also expected to change in the future (IPCC, 2014).

517 **Phenological shifts: adaptive potential and implications for conservation**

518 Sea turtles have been around for more than 110 million years (Hirayama, 1998) and have
519 survived dramatic thermal changes (Hamann et al., 2007; Hawkes et al., 2009). However, the
520 mechanisms by which sea turtles adapted and whether they will be able to adapt in the future
521 remains an open question. Shifting the nesting season is one key response to rising
522 environmental temperatures. In a freshwater turtle, it appears that shifting the nesting season
523 may not be effective enough to offset warming impacts on sex ratio (Schwanz and Janzen,
524 2008; Telemeco et al., 2013). The opposite conclusion reached for tuataras (Nelson et al.,
525 2018). Our results highlight differences in the efficiency of phenological shifts among
526 loggerhead populations to buffer detrimental effects of warming temperatures, with
527 populations nesting at the edge of lethal thermal limits being likely at greater risks (i.e., low
528 hatching success and female-biased sex ratio). Following this, several management strategies
529 can be proposed: (i) nest relocation, artificial nest shading and watering to cool the nests
530 (Esteban et al., 2018; Hill et al., 2015), (ii) preservation, restoration and enrichment of native
531 coastal vegetation to increase available shaded areas (Kamel, 2013), (iii) assisted migration
532 (or colonization) of nesting sites by moving eggs to colder beaches (Bowen et al., 1994a) and
533 (iv) foster international collaborations and agreements for safeguarding sea turtles worldwide
534 (Carr, 1956; Wold, 2002) to allow for a better protection of resilient nesting populations, like
535 the one nesting at Dalyan Beach, Turkey, identified in the present study. The first strategy
536 requires long-term human resources, which are not always available depending on the
537 country. Moreover, this strategy could slow down or prevent potential local adaptations by
538 lowering natural selection pressures (Mrosovsky, 2006). The second strategy could be
539 sustainable but further research is needed to anticipate potential detrimental effects of highly
540 vegetated beaches on egg incubation and female nesting success (Wood et al., 2014). The
541 third strategy, here based on sea turtles' natal homing behavior, is still controversial and
542 requires, among others, an extensive ecological understanding of the species and a careful

543 characterization of new intended habitats (Dade et al., 2014; McLachlan et al., 2007). We
544 urge further research to evaluate the risks and benefits associated with assisted migration and
545 we recommend following the last proposed strategy, while further identifying other resilient
546 nesting populations and potentially suitable beaches for nesting based on the application and
547 development of our approach.

548 Here we assumed that 1°C increase in sea surface temperature will shift nesting
549 seasons 7 days earlier (Weishampel et al., 2004). However, this relationship could vary
550 among populations and whether temperature affects nesting phenology at foraging, breeding,
551 and/or nesting areas remains unclear (Mazaris et al., 2009; Monsinjon et al., 2019). One of the
552 steepest responses was found in Mediterranean where loggerheads start nesting 8.5 days
553 earlier in response to 1°C increase in sea surface temperature at breeding areas (Mazaris et al.,
554 2008). Conversely, the slope of this relationship seems to be weaker for populations nesting at
555 low latitudes (Mazaris et al., 2013), which may jeopardize even more their ability to adapt to
556 rising temperatures. Moreover, we do not know whether the general pattern of nesting activity
557 will remain the same in the future. There is limited advancement of nesting phenology in
558 some loggerhead populations but no evidence for delayed initiation of nesting in response to
559 warmer temperatures, as observed in leatherback sea turtles (*Dermochelys coriacea*) (Neeman
560 et al., 2015). Some loggerhead populations have shortened their nesting season in response to
561 warmer temperatures (Pike et al., 2006; Weishampel et al., 2010) while the opposite response
562 was also found in other populations (Hawkes et al., 2007; Lamont and Fujisaki, 2014). Better
563 understanding of the timing of sea turtle reproduction is a gap that needs further research.

564 **Thermal heterogeneity, spatial shifts and other threats**

565 In the present study, we reproduced thermal heterogeneity at a fine temporal and geographical
566 scale through modeling, but we did not account for thermal heterogeneity occurring at other
567 spatial scales: inside a nest and between nests of the same nesting beach. Within a nesting

568 beach, in the context of global warming, eggs developing at cooler temperatures could suffer
569 less mortality than those developing at warmer temperatures, such that our model could
570 underestimate the proportion of male hatchlings. Further studies are required to provide
571 biologically-relevant characterization of thermal heterogeneity at these finer spatial scales.
572 Here, we projected nest temperatures based on a correlative model that involves air
573 temperature and sea surface temperature. Nevertheless, the temperature within a nest depends
574 on soil properties (e.g., thermal conductivity, soil reflectance) and other external forcing (e.g.,
575 wind speed, solar radiation, water content) that must be considered. Much effort is warranted
576 for assessing the environmental conditions at nesting sites and the physical properties of
577 beaches to better predict nest temperatures, possibly using a (mechanistic) microclimate
578 model (Fuentes and Porter, 2013; Kearney and Porter, 2017; Mitchell et al., 2016; Porter et
579 al., 2010).

580 Such micro-environmental variability may provide reptiles with a way for buffering
581 the effects of climate change. Females might modify the placement of their nests in order to
582 compensate for rising temperatures (Doody et al., 2006; Doody and Moore, 2010). For
583 instance, shade cover may provide sufficient thermal variation for a freshwater turtle to select
584 thermal microhabitats for nesting (Refsnider et al., 2013). Variation in sand color at nesting
585 beaches can also provide thermal microhabitats (Hays et al., 2001). This adaptive mechanism
586 may be effective as long as nesting sites with different available thermal conditions remain
587 accessible (Doody and Moore, 2010; Refsnider and Janzen, 2012).

588 Rapid spatial shift of nesting sites at a regional scale is unlikely for sea turtles due to
589 their natal homing behavior and, for some species, high degree of nest site fidelity (reviewed
590 in Miller, 1997). However, a few loggerhead females were found to attempt nesting hundreds
591 of kilometers distant from their former nesting sites in Australia (Limpus, 2008) and tens of
592 kilometers in South Africa (Nel et al., 2013). These wanderers have the potential to forge

593 range extensions. Establishment of new nesting sites may compensate the loss of current
594 nesting sites (Fuentes et al., 2013; Hawkes et al., 2009), provided that other suitable nesting
595 beaches are still available (Katselidis et al., 2012; Pike, 2013). For example, the population
596 nesting at Bhanga Nek, South Africa, may benefit from the availability of suitable nesting
597 beaches farther South along the East coast of Africa which provides sandy beaches within a
598 wide range of latitudes.

599 In any case, other environmental changes will soon threaten or are already threatening
600 the viability of sea turtles populations: (i) the availability of nesting sites may decrease as the
601 sea level rises (Fuentes et al., 2010), (ii) coastal development may further disturb these
602 nesting habitats (Fuentes et al., 2016; Sella and Fuentes, 2019), (iii) changes in precipitation
603 regimes may affect incubation success and hatchling sex ratio (Montero et al., 2019;
604 Santidrián Tomillo et al., 2015b), (iv) increasing intensity of extreme climatic events may
605 cause a high number of nest destruction (Fuentes and Abbs, 2010), and finally (v) adults can
606 be affected by other threats such as bycatch in fisheries and pollution (Hawkes et al., 2009;
607 Patrício et al., 2018).

608 **Conclusions**

609 By assessing the adaptive potential of phenological shifts under two plausible warming
610 scenarios, our study enabled the identification of loggerhead nesting populations that might
611 face detrimental thermal conditions at nesting beaches in the future. Within the locations
612 studied, we found that the population nesting at Dalyan Beach, Turkey, will be able to keep
613 track of suitable thermal conditions under an optimistic scenario of future changes in
614 environmental temperatures. Under a pessimistic warming scenario, only this population
615 nesting at Dalyan Beach would be able to buffer, but not utterly offset, the effect of warming
616 temperatures. We also identified two populations that might experience low embryo survival
617 and mostly females being produced under both warming scenarios, which are those nesting at

618 Boca Raton, Florida, and Praia do Forte, Brazil. These results show the importance of
619 modeling the long-term site-specific effects of climate change at a local scale to be able to
620 evaluate the sustainability of diverse populations. Other sea turtle species already face or will
621 soon face such warming impacts at their nesting sites and thus warrant further investigations.

622 The use and development of our approach should prove useful for assessing the
623 viability of sea turtle populations as well as other ectotherms. Combining thermal tolerances,
624 physiological and phenological processes, our conceptual approach can be applied to other
625 ectotherm species spatially-constrained by their natal homing behavior and their high degree
626 of nest site fidelity, such as salmon and other anadromous fish species, to explore the potential
627 of phenological shifts in thermal niche tracking. Species can adapt to environmental changes
628 by shifting their spatial and temporal distribution (i.e., habitat range and phenological shifts,
629 respectively) simultaneously (Chuine, 2010), so that phenological shifts can buffer or
630 neutralize range shifts (Socolar et al., 2017). Future research should now combine resource-
631 driven and climate-driven shifts in phenology and geography in a single framework to explore
632 the adaptive potential of species in response to contemporary climate change.

633

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654

655 **AUTHOR CONTRIBUTIONS**

656 J.M. initiated the project and performed the data analysis. J.W., K.R., M.L., P.L., A.S.,
657 M.A.G.d.M., M.M.P.B.F, Y.K., J.T., R.N., K.L.W., A.-M.L. and D.R. compiled the data. J.M
658 and J.-M.G. conceived the manuscript. M.G. built mathematical models. J.M. wrote the
659 manuscript with contributions from all authors.

660

661 **CONFLICTS OF INTEREST**

662 The authors declare no competing interests.

663

664 **PERMITS**

665 Data collection at Bhanga Nek took place under the Research Agreement with iSimangalio
666 Wetland Authority, with animal ethics clearance (A09-SCI-ZOO-005) and Dept of
667 Environmental Affairs Permits (RES2010/55 & 2011/41). Data collection in Georgia was
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669 permit No. 41620-02018; and approved by the Georgia Southern University IACUC. Data
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671 073, and USFWS permits.

672

673 **SUPPLEMENTARY MATERIAL**

674 Supplementary material includes four notes, five figures and seven tables and can be found
675 with this article online. Correspondence and requests for materials should be addressed to
676 M.G. Statistical analyses were performed using R (R Core Team, 2019). Mathematical
677 models used in this study are available in the following R packages: ‘phenology’ (Girondot,
678 2019b) and ‘embryogrowth’ (Girondot, 2019a).

679

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1089

1090 **FIGURES**

1091 **Figure 1. Location of nesting sites**

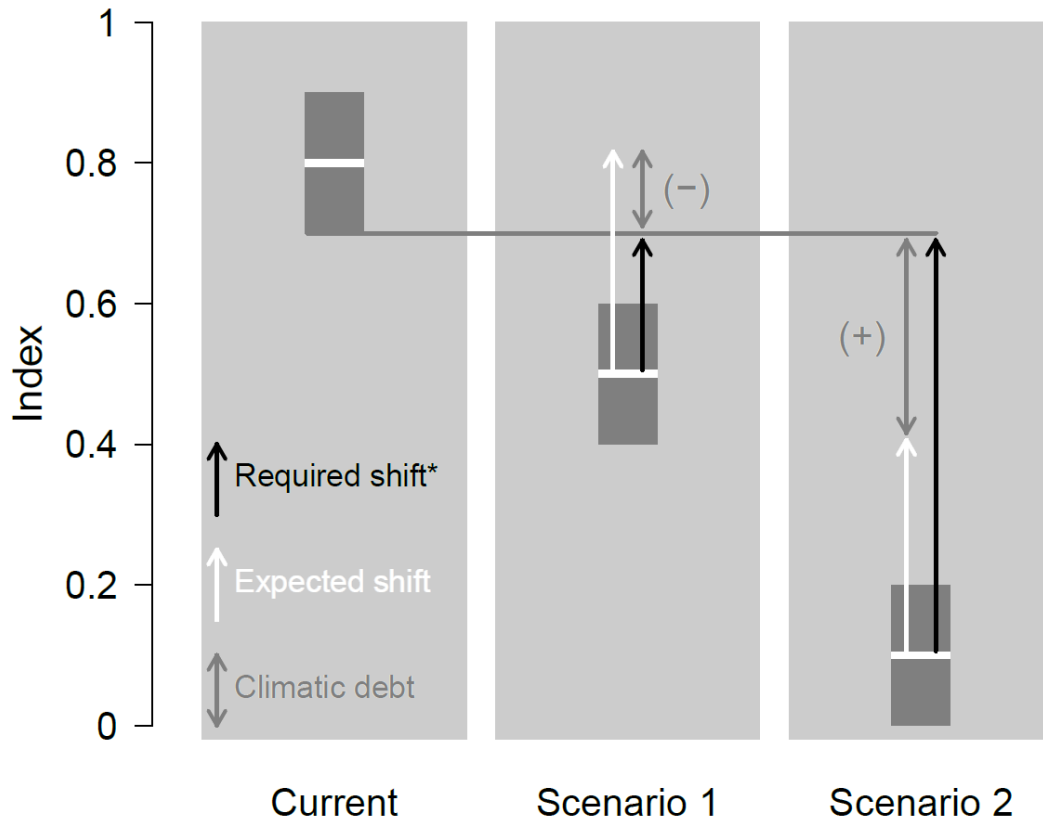


1092

1093 **Legend:** Locations of the seven nesting sites studied (red dots) within four Regional
 1094 Management Units (RMUs): Mediterranean (Dalyan Beach, Turkey), Northwest Atlantic
 1095 (Boca Raton, Florida, USA, Wassaw Island and Blackbeard Island, Georgia, USA),
 1096 Southwest Atlantic (Praia do Forte and Rio de Janeiro, Brazil) and Southwest Indian (Bhanga
 1097 Nek, South Africa).

1098

1099 **Figure 2. Conceptual approach to calculating the climatic debt**

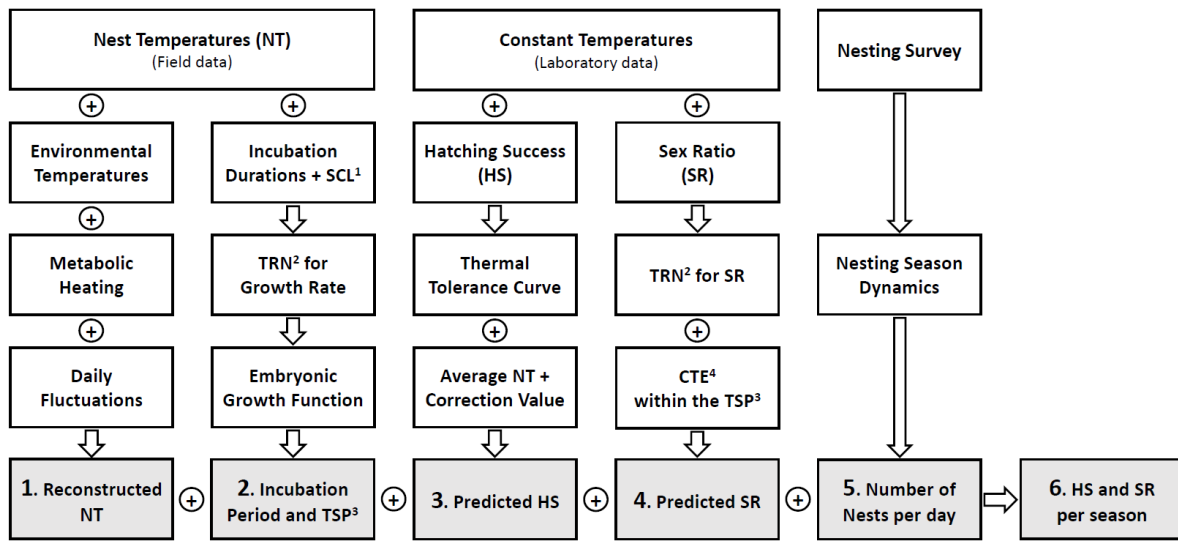


1100

1101 **Legend:** Grey bars represent the range of current and projected indices (quantiles at 25% and
 1102 75%) assuming no phenological shifts (under two warming scenarios) and white dashes
 1103 represent quantiles at 50%. Black arrows represent the change in the index value required for
 1104 the quantile at 50% of projected indices to reach the lower limit of current indices (*i.e., shift
 1105 required to “pay” what we define as the climatic price). White arrows represent the change in
 1106 the index value resulting from expected temperature-induced phenological shifts. Grey
 1107 double-headed arrows represent the change in the index values according to the climatic
 1108 scenario, after considering the expected phenological shift (i.e., the effect of what we define
 1109 as the climatic debt). A negative climatic debt (-) is a situation where the expected
 1110 phenological shift can effectively offset future climatic change, whereas a positive climatic
 1111 debt (+) is the opposite situation.

1112

1113 **Figure 3. Modeling Framework**

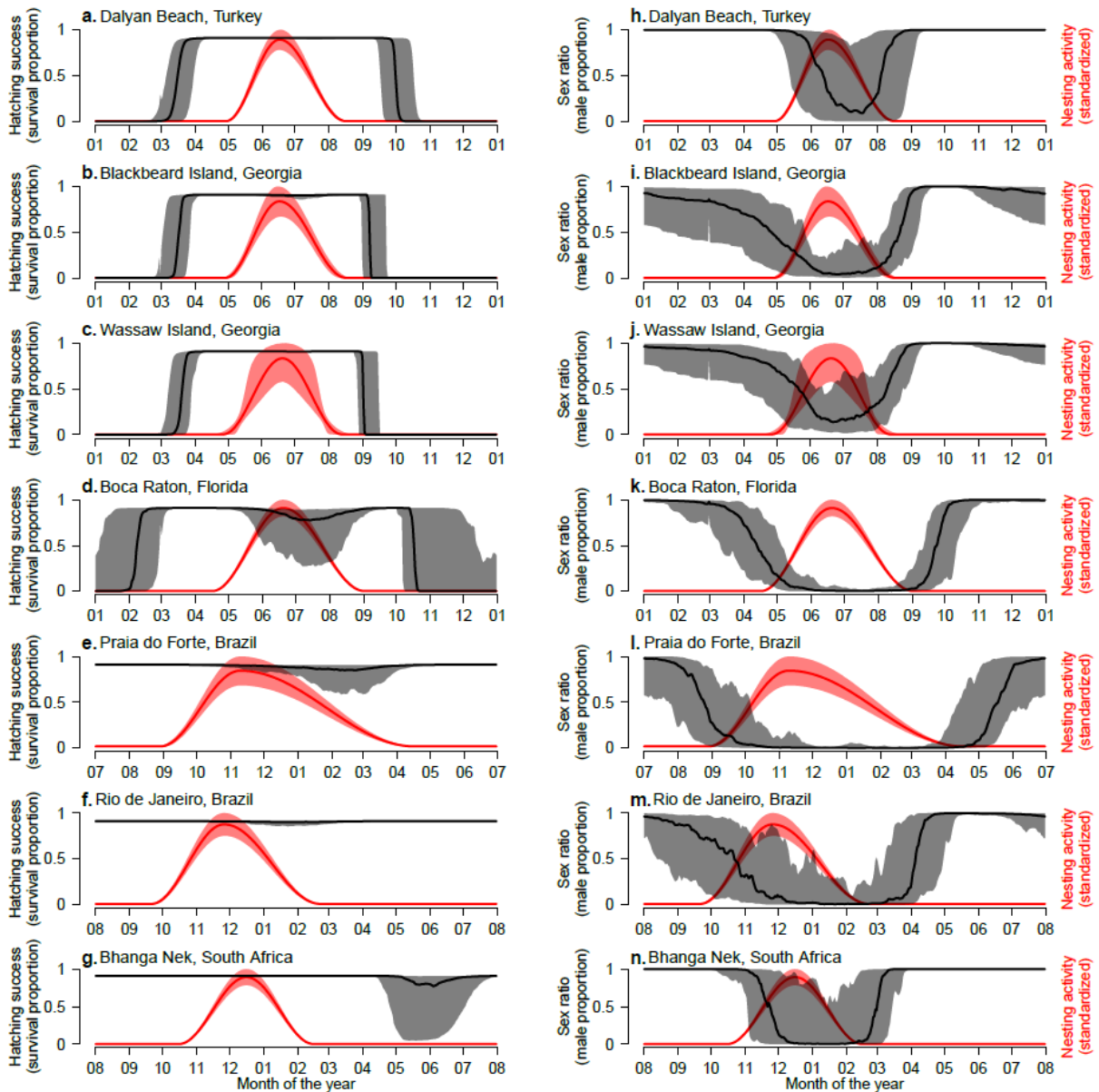


1114

1115 **Legend:** (1) Reconstructing nest temperature, (2) Modeling embryonic development, (3)
 1116 Estimating hatching success, (4) Estimating sex ratio, (5) Unraveling the dynamics of nesting
 1117 activity and (6) Calculating hatching success and sex ratio indices (see Methods).
 1118 Abbreviations: ¹Straight Carapace Length (SCL) of hatchlings, ²Thermal Reaction Norm
 1119 (TRN), ³ThermoSensitive Period (TSP) of development for sex determination and ⁴Constant
 1120 Temperature Equivalent (CTE). Plus marks (+) indicate data required to infer a model and
 1121 arrows lead to a result.

1122

1123 **Figure 4. Nesting activity, hatching success and sex ratio**



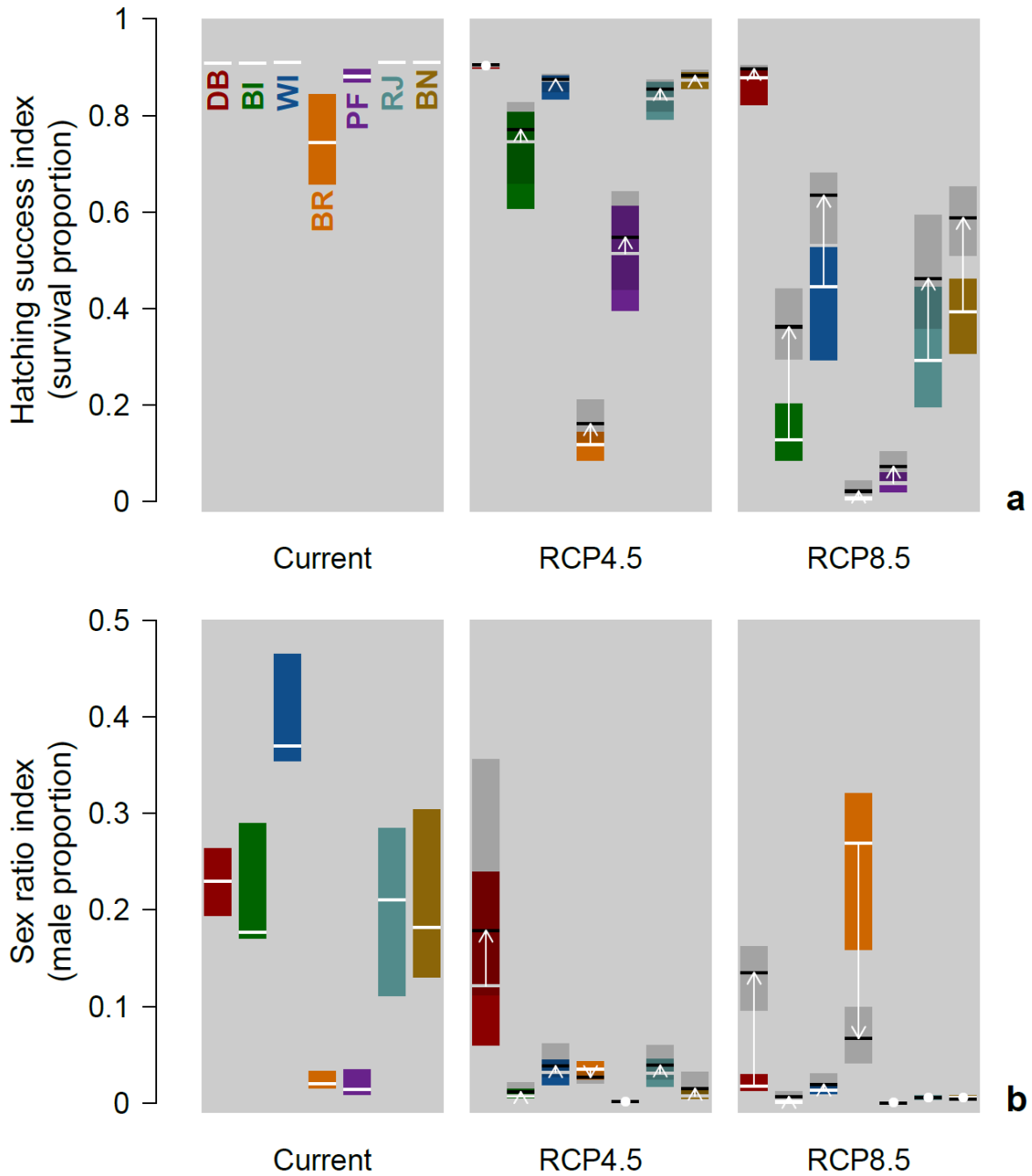
1124

1125 **Legend:** Current hatching success and sex ratio (quantiles at 50%, black lines) for any days
 1126 throughout the season with lower and upper quantiles (respectively, at 2.5% and 97.5%, grey
 1127 areas) are shown for populations nesting at Dalyan Beach, Turkey (respectively, **a** and **h**), at
 1128 Blackbeard Island, Georgia, USA (respectively, **b** and **i**), at Wassaw Island, Georgia, USA
 1129 (respectively, **c** and **j**), at Boca Raton, Florida, USA (respectively, **d** and **k**), at Praia do Forte,
 1130 Brazil (respectively, **e** and **l**), at Rio de Janeiro, Brazil (respectively, **f** and **m**) and at Bhanga
 1131 Nek, South Africa (respectively, **g** and **n**). Quantiles were calculated based on 1979-2016 time
 1132 series. Standardized nesting activity (number of nests laid throughout the season based on the

1133 global description of nesting activity) is indicated by red lines and the confidence interval at
1134 95% is indicated by red shaded areas. Note that the first month on the x-axis differs according
1135 to the nesting site.

1136

1137 **Figure 5. Warming temperatures may reduce hatching success and induce a**
1138 **feminization of hatchlings**



1139

1140 **Legend:** Current hatching success (a) and sex ratio (b) indices are shown (left panels) with
 1141 projected ones (middle [RCP4.5] and right [RCP8.5] panels): (i) assuming no phenological
 1142 shift (colored bars and white dashes) and (ii) considering expected phenological shifts (grey
 1143 shaded bars and black dashes). Colored or grey shaded areas show lower and upper quantiles
 1144 (respectively, at 25% and 75%), which give a measure of the interseasonal variability, and
 1145 white or black dashes indicate quantiles at 50%. White arrows represent changes in the value

1146 of indices if expected phenological shifts are considered and white dots represent the situation
 1147 where changes in the value of indices are <0.002 . Current indices were calculated based on
 1148 seasons when nests were surveyed (using the “season-specific description” of nesting activity,
 1149 see Methods): $n = 6$ at Dalyan Beach (**DB**), $n = 3$ at Blackbeard Island (**BI**), $n = 5$ at Wassaw
 1150 Island (**WI**), $n = 16$ at Boca Raton (**BR**), $n = 26$ at Praia do Forte (**PF**), $n = 14$ at Rio de
 1151 Janeiro (**RJ**) and $n = 32$ at Bhanga Nek (**BN**). Projected indices (i.e., forecasts for the 2062-
 1152 2100 period) were calculated under two scenarios for future Representative Concentration
 1153 Pathways (RCPs) in greenhouse gas concentration (an optimistic scenario and a pessimistic
 1154 scenario, respectively RCP4.5 and RCP8.5) and based on all future seasons ($n = 38$) using the
 1155 “global description” of nesting activity (see Methods).

1156

1157 **TABLES**

1158 **Table 1. Differences between required and expected phenological shifts (climatic debts)**

Nesting site	Index	RCP4.5	RCP8.5
		(number of days)	(number of days)
Dalyan Beach, Turkey	HSI	$0 - 8.3 = -8.3$	$21 - 20.2 = 0.8$
	SRI	$10 - 8.3 = 1.7$	$26 - 20.2 = 5.8$
Blackbeard Island, Georgia	HSI	$50 - 8.3 = 41.7$	$81 - 20.2 = 60.8$
	SRI	$53 - 8.3 = 44.7$	$67 - 20.2 = 46.8$
Wassaw Island, Georgia	HSI	$52 - 8.3 = 43.7$	$76 - 20.2 = 55.8$
	SRI	$58 - 8.3 = 49.7$	$74 - 20.2 = 53.8$
Boca Raton, Florida	HSI	$54 - 8.3 = 45.7$	$90 - 20.2 = 69.8$
	SRI	*	*
Praia do Forte, Brazil	HSI	$104 - 8.3 = 95.7$	none
	SRI	$79 - 8.3 = 70.7$	none
Rio de Janeiro, Brazil	HSI	$43 - 8.3 = 34.7$	$118 - 20.2 = 97.8$
	SRI	$37 - 8.3 = 28.7$	$112 - 20.2 = 91.8$
Bhanga Nek, South Africa	HSI	$27 - 8.3 = 18.7$	$81 - 20.2 = 60.8$
	SRI	$34 - 8.3 = 25.7$	$77 - 20.2 = 56.8$

1159 **Legend:** This Table shows the shifting of nesting phenology (in minimum number of days
 1160 earlier) required for projected Hatching Success Indices (HSIs in survival proportion: white
 1161 rows) and Sex Ratio Indices (SRIs in male proportion: grey rows) (quantiles at 50%) to

1162 remain within current ranges (i.e., beyond quantiles at 25% of current indices) under two
1163 scenarios of Representative Concentration Pathways (RCPs) of greenhouse gas concentration:
1164 an optimistic scenario (RCP4.5) and a pessimistic scenario (RCP8.5). Climatic scenarios
1165 reflect future temperature changes (2062-2100) as compared to current thermal conditions
1166 (1979-2016). Climatic debts (values in bold) are calculated by subtracting expected
1167 phenological shifts (8.3 and 20.2 days earlier, respectively for RCP4.5 and RCP8.5) from
1168 required ones (i.e., climatic prices: values in italics). Negative values indicate that
1169 phenological shifts can effectively offset future changes, positive values indicate the opposite
1170 situation, and “none” means that no climatic price was found. *Climatic debts were not
1171 calculated because projected SRIs lie within or above the range of current indices.

1172

SUPPLEMENTARY MATERIAL

The climatic debt of loggerhead sea turtle populations in a warming world

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This document contains Supplementary Notes A1-A4, Supplementary Figures A1-A5, and Supplementary Tables A1-A7.

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Supplementary Notes

Note A1. Nest temperatures

We modelled nest temperature based on site-specific relationships with environmental temperature (Table A4). The average daily fluctuations (daily maxima - daily minima) ranged from 0.26°C to 1.09°C and the metabolic heating (temperature at the end of incubation modelled from a linear relationship with incubation time) ranged from 1.56°C to 4.55°C (Table A4). This modelling approach allowed for an accurate prediction of nest temperature (R-squared = 0.74), albeit slightly underestimating actual nest temperature at high temperatures and overestimating actual nest temperature at low temperatures (Figure A1).

Note A2. Thermal reaction norms for embryonic growth rate

We estimated nesting population-specific thermal reaction norms (TRNs) for embryonic growth rates (Figure A2) for the loggerhead sea turtle (*Caretta caretta*). The TRNs for growth rate are found similar within all RMUs except within the Southwest Atlantic RMU (Table A6). Populations nesting in Mediterranean (Turkey, Libya and Cyprus) exhibit a non-monotonic pattern where the growth rate increases with temperature until 32°C and then growth rate slightly decreases up to approximately 35°C (Figure A2a). Populations nesting along the Northwest Atlantic coast (Florida and Georgia) exhibit a monotonic pattern where the growth rate increases steadily with temperature (Figure A2b). Populations nesting along the Southwest Atlantic coast (Brazil) exhibit two contrasted patterns (Figure A2c): the population nesting at Rio de Janeiro exhibit a bell-shaped pattern where the growth rate increases sharply with temperature to reach a maximum at 29.8°C and decreases considerably above this temperature whereas the growth rate for the population nesting at Praia do Forte increases steadily with temperature to reach a maximum at 33°C and decreases above to this temperature (Figure A2c). The Population nesting along the Southwest Indian Ocean (South Africa) exhibits a monotonic pattern where the growth rate increases steadily with temperature but does not reach temperatures as high as in Florida and Georgia (Figure A2d).

Note A3. Thermal tolerance curve of embryos

Thermal tolerance curves of loggerhead embryos are found similar among all RMUs studied here: Mediterranean, Northwest Atlantic, Southwest Atlantic, Southwest Indian and South Pacific (AICc = 289.33, Akaike weight = 0.97). If temperature remains constant throughout incubation, more than 50% of embryos are expected to survive between 24.8°C and 33.1°C and less than 0.1% are expected to survive outside the range from 24.2°C to 35.3°C (Figure A3). To predict the hatching success of a clutch in natural conditions, a correction parameter of 0.32°C must be added to the mean nest temperature (for the whole incubation).

Note A4. Thermal reaction norms for sex ratio

To produce sex ratio estimates, we inferred nesting population-specific TRNs for sex ratio based on previous incubation experiments carried out at constant temperature in laboratory conditions (Figure A4) for the loggerhead sea turtle. The pivotal temperature (P) is 29.23°C

(SE = 0.09) for populations nesting in Mediterranean with a transitional range of temperatures (TRT) ranging from 28.46°C to 29.99°C (Figure A4a). $P = 28.97^{\circ}\text{C}$ (SE = 0.06) for populations nesting along the Northwest Atlantic with a TRT ranging from 27.26°C to 30.69°C (Figure A4b). $P = 29.12^{\circ}\text{C}$ (SE = 0.06) for populations nesting along the Southwest Atlantic with a TRT ranging from 28.31°C to 29.94°C (Figure A4c). $P = 29.24^{\circ}\text{C}$ (SE = 0.08) for populations nesting along the Southwest Indian with a TRT ranging from 28.77°C to 29.71°C (Figure A4d).

Supplementary Figures

Figure A1. Nest temperature fit quality

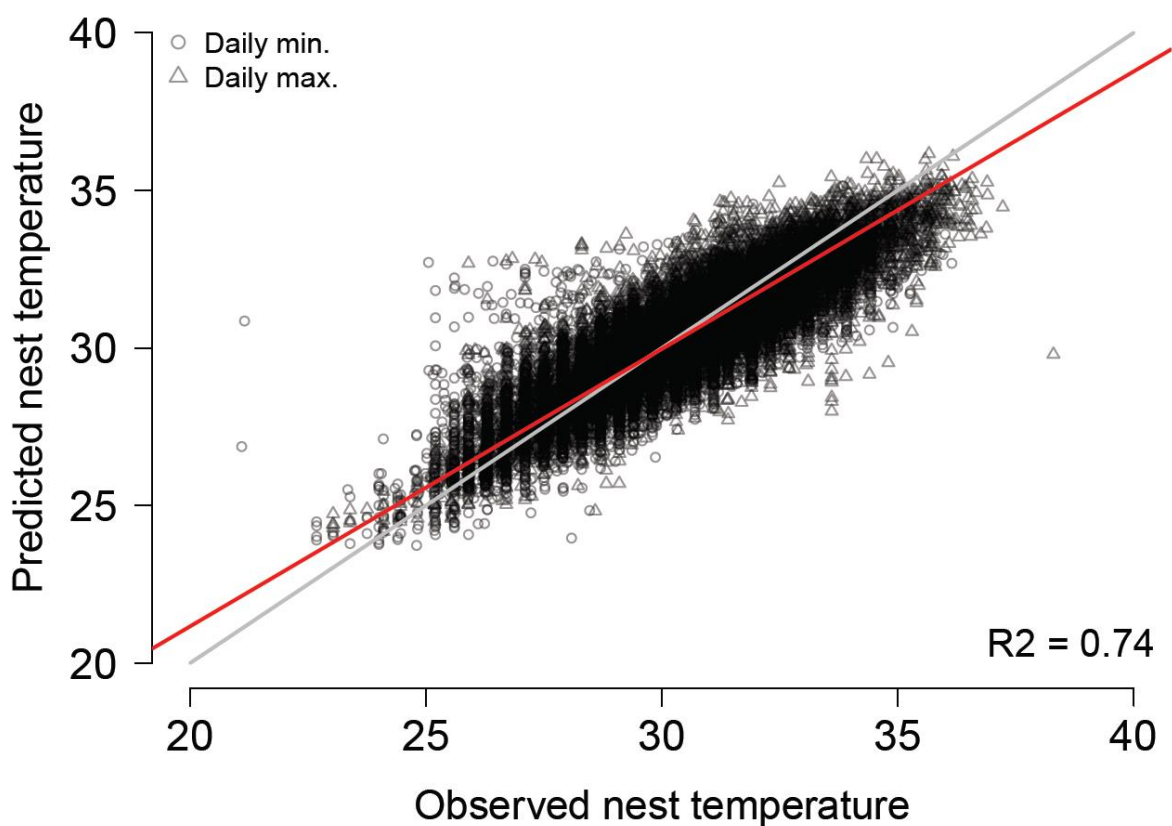


Figure A1. This Figure shows the orthogonal regression between predicted nest temperature and observed nest temperature (red line), data from all seven studied nesting sites pooled together. The grey line represents the line of equality. As a measure of the goodness of fit, we calculated the R-squared coefficient of determination (R^2), which gives a measure of the fraction of variance explained by the model.

Figure A2. Thermal reaction norms for embryonic growth rate

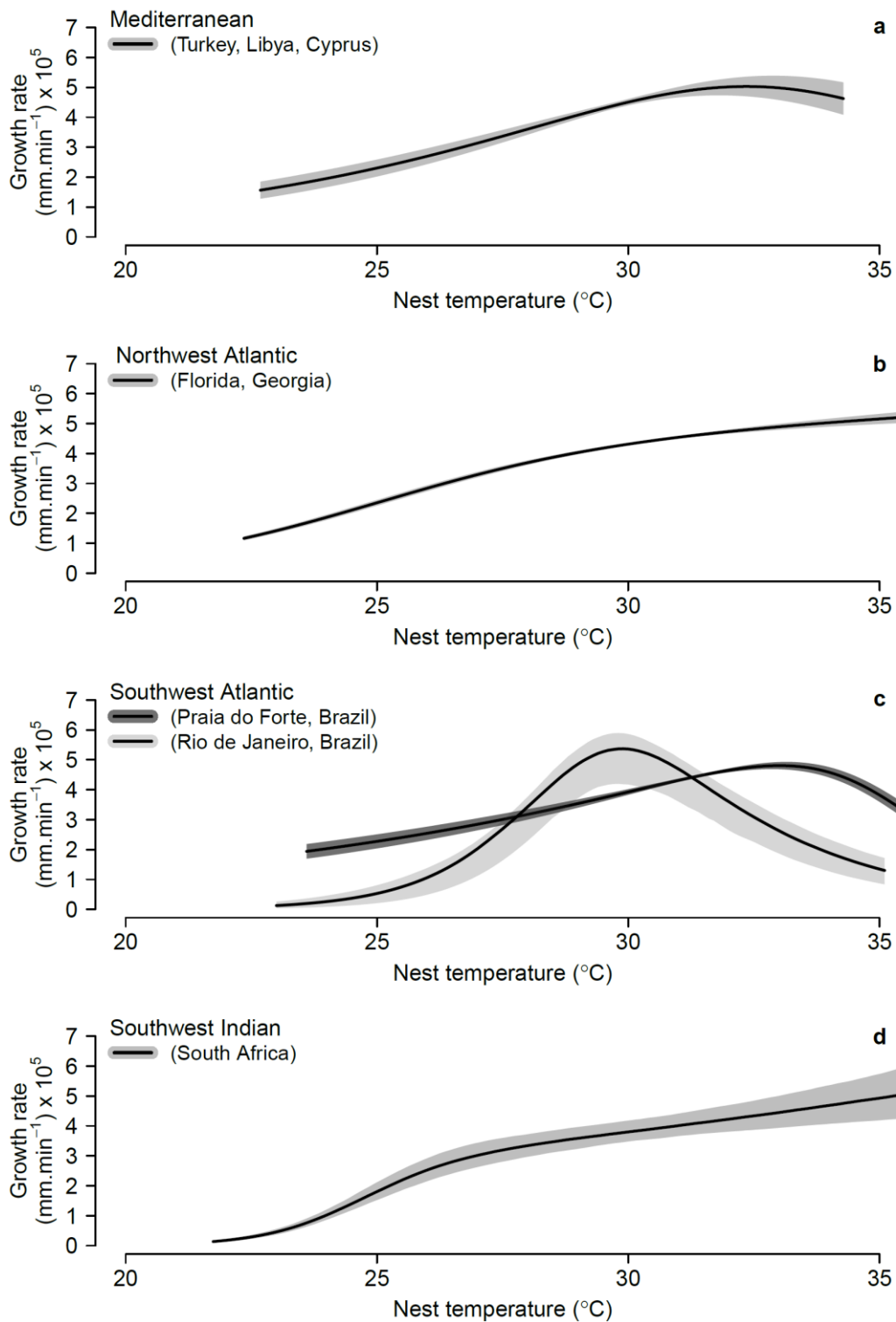


Figure A2. Expected embryonic growth rate (black curves) is shown along the range of temperatures recorded within nests at nesting sites in Mediterranean (a), Northwest Atlantic (b), Southwest Atlantic (c) and Southwest Indian (d) Regional Management Units (see Table A1). Grey areas show the confidence interval at 95%.

Figure A3. Thermal tolerance curve of embryos

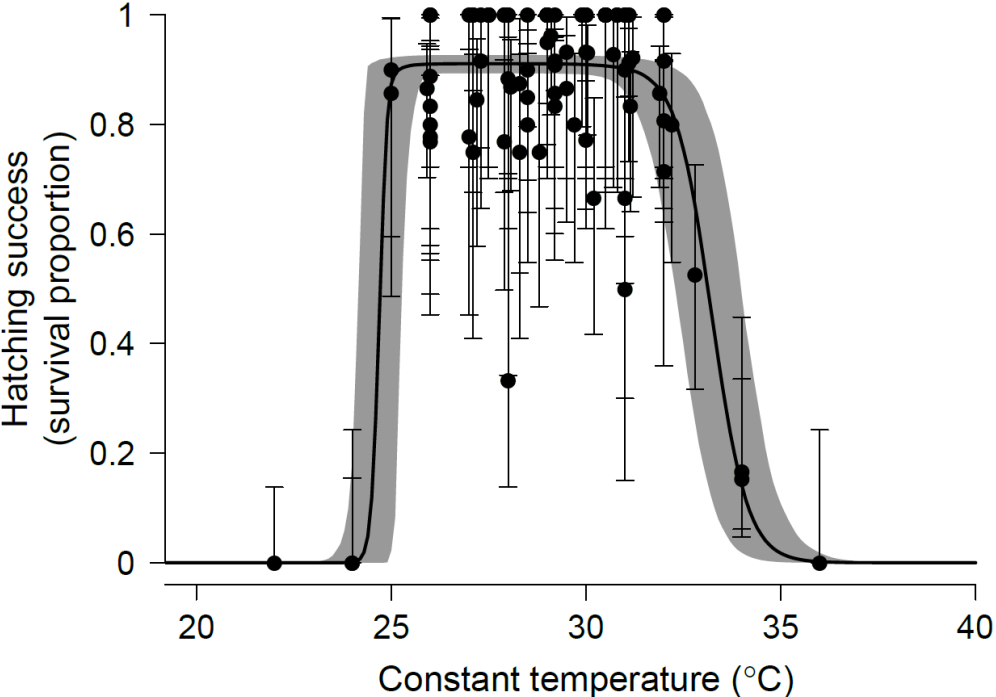


Figure A3. Expected hatching success (black curve) based on constant temperature experiments previously carried out in laboratory conditions (see Table A7). Grey area shows the confidence interval at 95%. Observed hatching success at several constant incubation temperatures is shown (black points are the average hatching success and error bars show the confidence interval of observations).

Figure A4. Thermal reaction norms for sex ratio

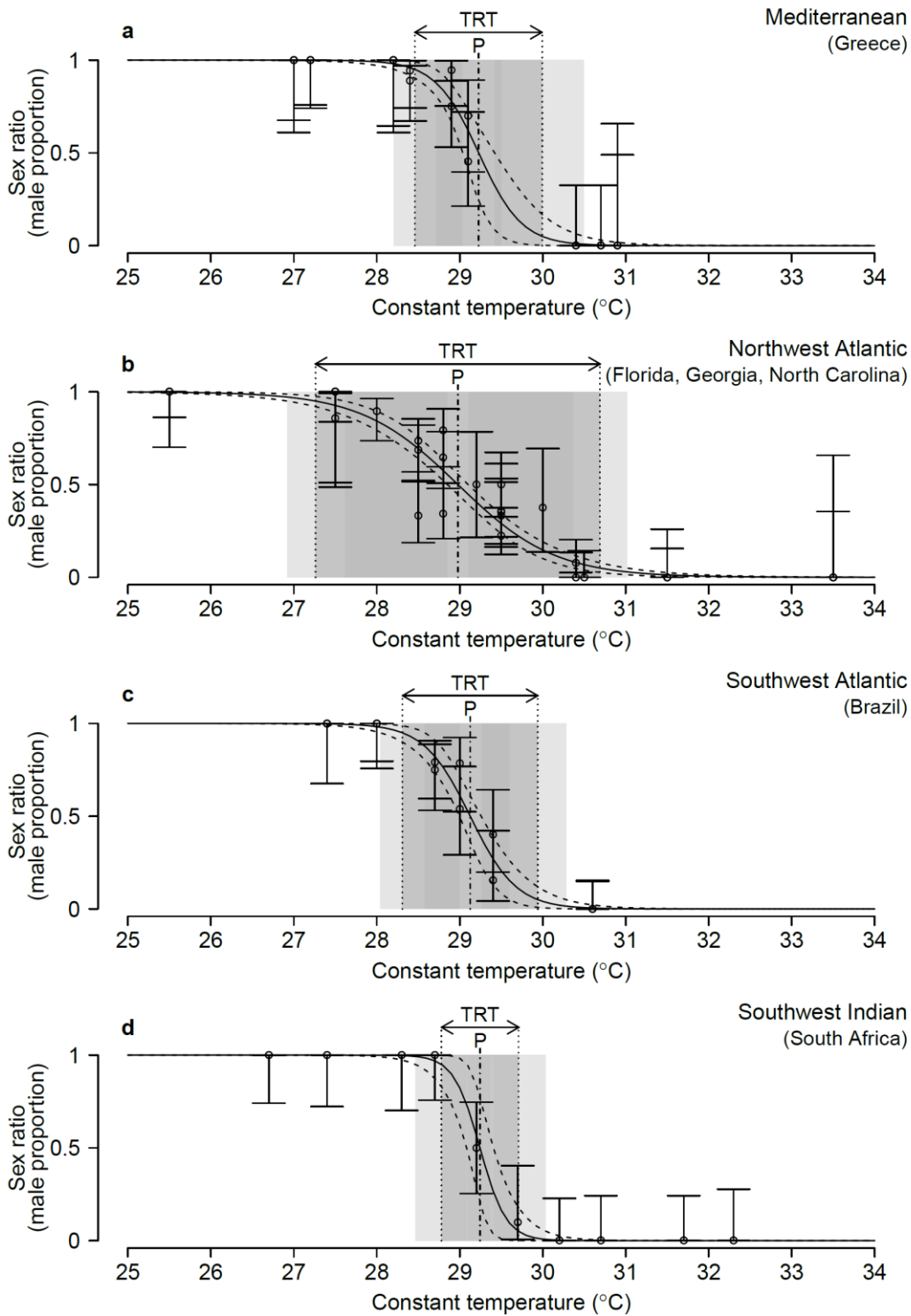


Figure A4. Expected sex ratio (black curves) based on constant temperature experiments previously carried out in laboratory conditions for populations nesting in Mediterranean (a) [1], Northwest Atlantic (b) [2-4], Southwest Atlantic (c) [5] and Southwest Indian (d) [6] Regional Management Units (see Methods, section “Estimating sex ratio”). Black dashed curves represent the confidence interval at 95%. Observed sex ratio at several constant incubation temperatures is shown (black points are the average sex ratio and error bars show the confidence interval of observations). Dark grey areas between the vertical dotted lines indicate the transitional range of temperatures (TRT). The vertical dash-dotted line within the TRT indicates the Pivotal temperature (P). Shades of grey indicate the overlapping confidence intervals of TRT and P.

Figure A5. Required and expected phenological shifts

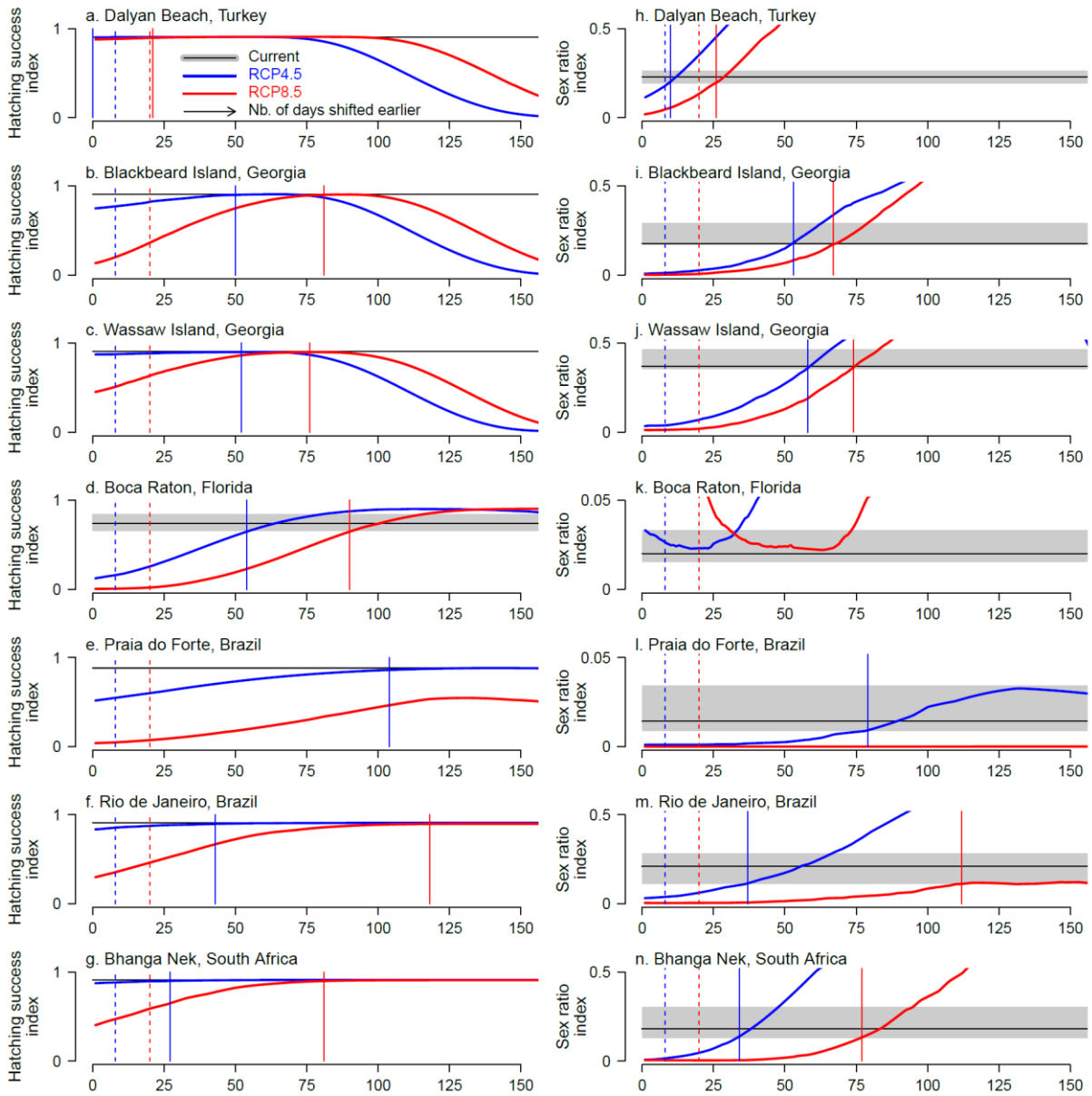


Figure A5. Changes in projected hatching success and sex ratio indices (quantiles at 50%) if nesting seasons were shifted earlier from 1 to 365 days (here shown until 150 days only) according to two scenarios of Representative Concentration Pathways (RCPs) of greenhouse gas concentration: an optimistic scenario (RCP4.5: blue curves) and a pessimistic scenario (RCP8.5: red curves). Horizontal black lines (quantiles at 50%) and grey areas (quantiles at 25% and 75%) represent current ranges of hatching success or sex ratio indices. Vertical colored solid lines indicate the number of days required for projected indices to reach the lower limit (quantiles at 25%) of current indices. Vertical colored dashed lines indicate the number of days shifted earlier resulting from expected temperature-induced phenological shifts (8.2 and 20.2 days earlier, respectively for RCP4.5 and RCP8.5). Projections are shown for populations nesting at Dalyan Beach, Turkey (respectively, **a** and **h**), at Blackbeard Island, Georgia (respectively, **b** and **i**), at Wassaw Island, Georgia (respectively, **c** and **j**), at Boca Raton, Florida (respectively, **d** and **k**), at Praia do Forte, Brazil (respectively, **e** and **l**), at Rio de Janeiro, Brazil (respectively, **f** and **m**) and at Bhanga Nek, South Africa (respectively, **g** and **n**). Note that the y-axis scale was adjusted (from 0 to 0.05 instead of 0 to 0.5) for the sex ratio index at Boca Raton and Praia do Forte (respectively, **k** and **l**) to allow for proper visualization of current ranges.

Supplementary Tables

Table A1. Information about nest temperature data from several nesting sites among four Regional Management Units (RMUs)

RMU	Country	Location	Latitude	Longitude	Seasons	Datalogger type	Nb. of nests	Source	
Mediterranean	Turkey	Dalyan Beach	36°47' N	28°37' E	2010	Tinytalk-Temp (resolution 0.37°C, Orion Components Ltd., UK)	21	[8-11]	
		Fethiye Beach*	36°39' N	29° 6' E	2000	Tinytalk-Temp (resolution 0.37°C, Orion Components Ltd., UK)	2	[12]	
	Cyprus	Alagadi*	35°33' N	33°47' E	1999	Tinytalk-Temp (resolution 0.37°C, Orion Components Ltd., UK)	2	[13]	
	Libya	Gulf of Sirte	31°12' N	16°35' E	2009	LogTag HAXO-8 (resolution 0.1°C, LSTechnology, UK)	14	[11]	
Northwest Atlantic	Georgia	Blackbeard Island	31°28' N	81°12' W	2003	2K HOBO temperature data loggers (Onset Computer Corp)	39	[14]	
		Wassaw Island	31°53' N	80°58' W	2004	2K HOBO temperature data loggers (Onset Computer Corp)	27	[14]	
	Florida	Boca Raton		26°21' N	80° 4' W	2002-2004	Hobo H8 temperature data loggers (Onset Computer Corp)	16	This study
						2010-2016	Hobo U22-001 temperature data loggers (Onset Computer Corp)	39	This study
		Juno Beach	26°52' N	80° 3' W	2002	Hobo H8 temperature data loggers (Onset Computer Corp)	5	This study	
		Hutchinson Island	27°21' N	80°14' W	2002, 2004	Hobo H8 temperature data loggers (Onset Computer Corp)	9	This study	
		Melbourne	28° 04' N	80°33' W	2002, 2003	Hobo H8 temperature data loggers (Onset Computer Corp)	9	This study	
		Sarasota	27°15' N	82°32' W	2002	Hobo H8 temperature data loggers (Onset Computer Corp)	12	This study	
		Sanibel	26°25' N	82°05' W	2002, 2010	Hobo H8 temperature data loggers (Onset Computer Corp)	7	This study	
2011	Hobo U22-001 temperature data loggers (Onset Computer Corp)	5	This study						
Southwest Atlantic	Brazil	Praia do Forte	12°30' S	37°58' W	2014-2015	VEMCO Minilog-II-T (resolution = 0.01 °C, AMIRIX System Inc., CA)	16	[15]	
						Thermochron iButton DS1922L-F5 (resolution = 0.0625 °C, Maxim Integrated Products Inc., USA)	22	[15]	
	Rio de Janeiro	21°39' S	41° 1' W	2015-2016	Thermochron iButton DS1922L-F5 (resolution = 0.0625 °C, Maxim Integrated Products Inc., USA)	17	This study		
Southwest Indian	South Africa	Bhanga Nek	26°59' S	32°52' E	2008-2011	Fairbridge Technologies iButton DS1922L-F5 (resolution = 0.5 °C, Maxim Integrated Products)	39	This study	

*Temperature data were extracted from figures in the original publications using the software WebPlotDigitizer version 4.1 (<https://automeris.io/WebPlotDigitizer/>).

Table A2. Information about nesting surveys at seven nesting sites among four RMUs

RMU	Country	Location	Seasons	Monitoring period	Daily patrols	Staff
Mediterranean	Turkey	Dalyan Beach	2010-2015 (N=6)	15-April to 30-September	Yes	DEKAMER
Northwest Atlantic	Georgia	Blackbeard Island	2001-2003 (N=3)	5-May to 1-September	Yes	US Fish and Wildlife Service
					Yes	Georgia Southern University
	Wassaw Island	2000-2004 (N=5)	5-May to 1-September	Yes	Caretta Research Project	
				Yes	US Fish and Wildlife Service	
			Yes	Georgia Southern University		
	Florida	Boca Raton	2001-2016 (N=16)	1-May to 1-October	Yes	Gumbo Limbo Nature Center
Southwest Atlantic	Brazil	Praia do Forte	1989-2014 (N=26)	1-September to 31-March*	Yes	TAMAR
		Rio de Janeiro	2001-2014 (N=14)	1-September to 31-March*	Yes	TAMAR
Southwest Indian	South Africa	Bhanga Nek	1980-2011 (N=32)	15-October to 15-March	Yes	EZEMVELO

*Monitoring patrols were conducted daily from the 1st of September to the 31st of March between 1989 and 2000 and from the 1st of September to the 30th of April after 2000. Nests that were encountered outside these monitoring periods were also included in the dataset.

Table A3. Future changes in environmental temperature

Area	RCP4.5	RCP8.5
South-Europe-Mediterranean	+2.12	+3.93
Eastern-North-America	+2.41	+4.51
North-East-Brazil	+1.77	+3.57
Southern-Africa	+1.96	+3.91
World-Sea	+1.19	+2.89

This Table summarizes region-specific projected near-surface temperature anomalies (in °C) that were retrieved from KNMI (Koninklijk Nederlands Meteorologisch Instituut) Climate Explorer website (https://climexp.knmi.nl/plot_atlas_form.py). Temperature increases are indicated for each scenario of future Representative Concentration Pathway (RCP) in greenhouse gas concentration [7] that was used in this study (see Methods, section “Reconstructing nest temperatures”). White rows indicate temperature anomalies we added to air temperature data and the grey row indicates temperature anomalies we added to sea surface temperature data. Changes in ocean temperature (grey row) were also used to project future temperature-induced phenological shifts.

Table A4. Parameters used to reconstruct nest temperature at seven nesting sites among four RMUs

RMU	Country	Location	Lag.AIR	Lag.SST	Intercept	Coef.AIR	Coef.SST	Coef.MH	AmpT	Ti.Min	Ti.Max	Dist_AIR	Dist_SST
Mediterranean	Turkey	Dalyan Beach	1	1	22.5	0.059	0.103	4.55	0.36	547	1380	4.5	18.3
Northwest Atlantic	Georgia	Blackbeard Island	1	0	4.3	0.209	0.683	2.86	1.09	663	1390	16.7	5.1
		Wassaw Island	1	1	18.3	0.270	0.094	2.39	0.98	647	1380	14.7	2.8
	Florida	Boca Raton	1	0	-3.4	0.331	0.870	1.56	0.84	829	1	6.1	6.6
Southwest Atlantic	Brazil	Praia do Forte	1	0	10.9	0.191	0.516	2.14	0.61	809	3	15.5	4.5
		Rio de Janeiro	1	2	19	0.287	0.078	2.95	1.02	609	1400	19	11.1
Southwest Indian	South Africa	Bhanga Nek	1	1	19.5	0.168	0.168	3.08	0.84	637	1410	11	1.2

Daily mean nest temperature is related with air temperature (AT) dAT days before (Lag.AIR), with sea surface temperature (SST) $dSST$ days before (Lag.SST) and with a linear relationship with the time of incubation that describes temperature changes due to metabolic heating (MH). Estimated coefficients of the generalized linear mixed model (GLMM) are indicated (Intercept = μ , Coef.SST = α , Coef.AIR = β , and Coef.MH = γ). The average daily amplitude of temperature (daily maximum – daily minimum for all days and for all nests) is indicated (AmpT) in °C. The average time during the day when the minimum and the maximum temperatures occur (Ti.Min and Ti.Max, respectively) are indicated in number of minutes after midnight. The distances between the location of nesting beaches and the spatial coordinates of the center of the closest cells (0.125° spatial resolution) within which AT and SST were extracted (respectively, Dist_AIR and Dist_SST) are indicated in km.

Table A5. Straight Carapace Length (SCL) of hatchlings from several nesting sites among four RMUs

RMU	Country	Location	Seasons	Nb. of nests	Mean SCL (SD) in mm	Source	
Mediterranean	Turkey	Dalyan Beach	2010	21	39.33 (1.92)	[8]	
		Fethiye Beach*					
	Cyprus	Alagadi*	2010	21	39.33 (1.92)	[8]	
		Libya					Gulf of Sirte*
Northwest Atlantic	Georgia	Blackbeard Island	2001-2003	970	44.13 (1.64)	This study	
		Wassaw Island	2000, 2002-2004	949	44.80 (1.79)	This study	
	Florida	Boca Raton	2002-2003, 2010-2016	994	43.49 (1.65)	This study	
		Juno Beach	2002	110	45.05 (1.58)	This study	
		Hutchinson Island	2002, 2004	170	44.90 (1.82)	This study	
	Melbourne	Sarasota**	Sarasota**	2002-2003	186	42.35 (1.87)	This study

		Sanibel	2010-2011	145	40.50 (1.75)	This study
Southwest Atlantic	Brazil	Praia do Forte			40.97 (0.96)	[15]
		Rio de Janeiro	2015-2016	210	42.06 (1.84)	This study
Southwest Indian	South Africa	Bhanga Nek	2011	132	43.24 (1.99)	This study

*No hatchling was measured at Fethiye, Turkey, in the Gulf of Sirte, Libya, and at Alagadi, Cyprus, so we used data from the closest population in Dalyan Beach, Turkey.

**No hatchling was measured at Sarasota, Florida, so we used data from the closest population in Sanibel, Florida.

Table A6. Model selection procedure to test for nesting population-specific thermal reaction norms for embryonic growth rate

RMU	Locations	Hypothesis	AICc	DeltaAICc	Akaike weight
Mediterranean	Dal vs. Fet	Independent	104.37	15.96	< 0.001
		Similar	88.41	0	> 0.99
	Dal_Fet vs. Ala	Independent	109.47	13.67	0.001
		Similar	95.80	0	> 0.99
	Dal_Fet_Ala vs. Sir	Independent	145.06	12.73	0.001
		Similar	132.32	0	> 0.99
Northwest Atlantic	HI_JB_BR vs. Mel	Independent	349.50	8.03	0.02
		Similar	341.47	0	0.98
	HI_JB_BR_Mel vs. Sar_San	Independent	450.96	6.39	0.04
		Similar	444.57	0	0.96
	HI_JB_BR_Mel_Sar_San vs. BI_WI	Independent	666.47	6.47	0.04
		Similar	659.99	0	0.96
Southwest Atlantic	Pra vs. Rio	Independent	284.93	0	> 0.99
		Similar	373.66	88.73	< 0.001
Southwest Indian	BN	-	-	-	-

Abbreviations: Dalyan Beach (Dal), Fethiye (Fet), Alagadi (Ala), Sirte (Sir), Hutchinson Island (HI), Juno Beach (JB), Boca Raton (BR), Melbourne (Mel), Sarasota (Sar), Sanibel (San), Blackbeard Island (BI), Wassaw Island (WI), Praia do Forte (Pra), Rio de Janeiro (Rio), Bhanga Nek (BN). Locations of which temperature data were grouped together are linked by underscore marks (_). Models are selected using Akaike Information Criterion corrected for finite sample size (AICc) and Akaike weights [16]. For each test, the hypothesis of the selected model is indicated in bold.

Table A7. Hatching success data from constant temperature experiments for the loggerhead sea turtle

RMU	Country	Location	Temperature	Total nb. of eggs	Hatched	Unhatched	Undeveloped	Source
Mediterranean	Greece	Kyparissia Bay	27.1	8	8	0	NA	[1]
			27.1	8	6	2	NA	
			27.3	12	11	1	NA	
			27.3	12	12	0	NA	
			28.3	8	7	1	NA	
			28.3	8	6	2	NA	
			28.5	20	18	2	NA	
			28.5	20	17	3	NA	
			29	20	20	0	NA	
			29	20	19	1	NA	
			29.2	12	11	1	NA	
			29.2	12	10	2	NA	
			30.5	8	8	0	NA	
			30.5	8	8	0	NA	
			30.8	8	8	0	NA	
			30.8	8	8	0	NA	
			31	4	2	2	NA	
31	4	4	0	NA				
Northwest Atlantic	USA, Georgia	Little Cumberland Island	22	24	0	24	NA	[2, 3]
			24	12	0	12	NA	
			26	12	10	2	NA	
			28	12	4	8	NA	
			30	15	14	1	NA	
			32	12	11	1	NA	
			34	12	2	10	NA	
			36	12	0	12	NA	
			24	21	0	21	NA	
			26	26	20	6	NA	

			28	26	23	3	NA	
			30	35	27	8	NA	
			32	26	21	5	NA	
			34	26	4	22	NA	
Southwest Atlantic	Brazil	Praia do Forte	27.9	8	8	0	NA	[5]
			27.9	8	8	0	NA	
			28.5	15	12	3	NA	
			28.5	16	15	0	NA	
			29.2	24	24	0	NA	
			29.2	22	20	2	NA	
			29.5	15	13	2	NA	
			29.5	15	14	1	NA	
			29.9	15	15	0	NA	
			29.9	15	15	0	NA	
			31.1	22	22	0	NA	
			31.1	23	21	2	NA	
Southwest Indian	South Africa	Bhanga Nek	27.2	13	11	2	NA	[6]
			27.9	14	10	3	NA	
			28.8	12	9	3	NA	
			29.2	14	12	2	NA	
			29.7	15	12	3	NA	
			30.2	15	10	5	NA	
			30.7	14	13	1	NA	
			31.2	13	12	1	NA	
			32.2	15	12	3	NA	
			32.8	19	10	9	NA	
South Pacific	Australia	Heron Island	25	10	6	1	3	[17, 18]
			26	10	8	2	0	
			26	10	8	1	1	
			27	10	7	2	1	
			27.5	10	10	0	0	

	28	10	2	0	8	
	29	10	10	0	0	
	29	10	10	0	0	
	30	10	10	0	0	
	30	10	9	0	1	
	30.5	10	10	0	0	
	31	10	4	2	4	
	31	10	9	1	0	
	32	10	5	2	3	
Mon Repos	25.92	30	26	4	NA	[17, 19]
	27.1	24	24	0	NA	
	28.07	23	20	3	NA	
	29.1	27	26	1	NA	
	30.04	29	27	2	NA	
	31.14	24	20	4	NA	
	31.89	28	24	4	NA	
	25	10	9	1	0	
	26	10	10	0	0	
	26	10	7	2	1	
	26	6	6	0	0	
	27	10	10	0	0	
	27.5	10	9	0	1	
	27.5	10	10	0	0	
	28	10	9	0	1	
	29	10	9	0	1	
	29	10	10	0	0	
	29	10	9	0	1	
	30	10	7	0	3	
	30.5	6	6	0	1	
	30.5	10	9	0	1	
	31	10	9	0	1	

32	10	9	0	1
32	10	10	0	0

This Table summarizes hatching success data used to infer the thermal tolerance curve of embryos. These data come from several constant temperature experiments previously carried out in laboratory conditions using loggerhead eggs from five Regional Management Units (RMUs).

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