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# Environmental effects on growth, reproduction, and life-history traits of loggerhead turtles

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## Abstract

Understanding the relationship between the environmental conditions and life-history traits (such as growth, reproduction, and size at specific life stages) is important for understanding the population dynamics of a species and for constructing adaptable, relevant, and efficient conservation measures. For the endangered loggerhead turtle, characterizing effects of environmental conditions on the life-history traits is complicated by this species' longevity, global distribution, and migratory way of life. Two significant environmental factors – temperature and available food – often account for most of observed intra-population variability in growth and reproduction rates, suggesting that those two factors determine the biological responses of an individual. Adopting this hypothesis, we simulate a range of the two environmental factors to quantify effects of changes in temperature and food availability on an individual's physiology (energy investment into processes such as growth, maturation, and reproduction) and the resulting life-history traits. To represent an individual, we use a previously developed mechanistic dynamic energy budget (DEB) model for loggerhead turtles. DEB models rely on one of the empirically best validated general ecological theories, which captures rules of energy acquisition and utilization. We found that the ultimate size (length and mass) is primarily affected by food availability, whereas growth

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and maturation are primarily affected by temperature whilst also showing positive correlation with available food. Reproduction increases with both food availability and temperature because food availability determines energy investment into egg production, and temperature affects the rate of related processes (such as vitellogenesis). Length at puberty varies between simulated scenarios by only a small proportion, suggesting that inter-individual variability plays a larger role for length at puberty than the environmental factors do.

*Keywords:* Loggerhead turtle, Environmental effects, Life history, Mechanistic model, Conservation, Marine ecology, Climate change

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## 1. Introduction

Inter-individual and between-population differences in growth, maturation, and reproduction of loggerhead turtles (*Caretta caretta*) obstruct design of general conservation measures applicable to all regional management units and/or populations of this species [1]. Like other marine turtles, loggerheads are extremely vulnerable to natural and anthropogenic pressures due to temperature-dependent sex determination (TSD), long period required to reach puberty and reproduce, migratory way of life, and global distribution encompassing terrestrial habitats (beaches), open seas, and coastal waters [2, 3, 4, 5]. In addition to the conditions present on land (e.g., predators, nest infestations, nest overheating or inundation, pressures related to tourism), the abiotic and biotic conditions in the *marine* environment also greatly affect the development (growth and maturation) and survival of individuals, thus determining the success of conservation measures.

Food availability and temperature could be the major determinants of an individual's growth rate and, because faster growth might increase chances of turtle's survival [6], also the major determinants of the individual's survival. Even though the variability in the observed growth rates of loggerhead turtles has been partially attributed to inter-individual variability within [7, 8] or between [9, 10] populations, most often differences in growth rates have been either partially [9, 8, 10] or mostly [11, 12, 13, 14] attributed to the differences in experienced temperature and food abundance. Loggerhead turtles are a migratory species, and both males and females had been observed to follow certain types of temperature and food fronts [15], and/or exhibit fidelity to specific feeding areas [16, 17]. Growth can be up to 30% faster in a neritic

26 habitat ([18] as cited in [19]). As neritic habitats are characterized by food of  
27 higher energy content and higher temperatures [19], the higher growth rate  
28 in a neritic habitat further supports the thesis that food and temperature  
29 are the chief determinants of loggerhead turtle growth.

30       Reproduction is the other individual-based biological process that is ex-  
31 tremely important for resilience and survival of a species [20]. A direct cor-  
32 relation between growth rates and reproduction output has already been  
33 suggested [21, 14], but not quantified. Different habitats, characterized by  
34 food and temperature, have been linked to drastically different adult sizes  
35 and different reproduction patterns, with the environmental factors hypothe-  
36 sized to be the major causes of the variability [22, 2, 23, 19, 24]. The length of  
37 the remigration interval (period between two nesting seasons) has been found  
38 to correlate with the average sea surface temperature (SST) [25], similarly  
39 as the periods between two clutch depositions within a single nesting season  
40 [26, 27, 28]. Large scale environmental fluctuations, such as the North At-  
41 lantic Oscillation and the El Nino Southern Oscillation have also been shown  
42 to account for a large part of nesting variability [29, 30, 31].

43       Climate change, in addition to strongly affecting nesting and breeding  
44 sites (e.g., via changes in sea and sand temperature or in nesting beach areas  
45 susceptible to inundation) and potentially changing the spatial distribution  
46 of loggerhead turtles [3, 5], will also affect temperature and/or food avail-  
47 ability in oceanic and coastal feeding sites of loggerhead turtles [3, 32], thus  
48 affecting growth, reproduction, and other biological processes. Effects that  
49 global climate change might have on loggerhead turtles have received in-  
50 creased attention in the last decade (e.g., [33, 2], see also [3, 5] for a review).  
51 Slow-acting threats such as the climate change are, however, hard to study  
52 on a short time scale for which data is available [34], especially when trying  
53 to understand the balance between beneficial and detrimental effects caused  
54 by the same change. For example, higher SST might be beneficial by trigger-  
55 ing an earlier nesting season with an increase of hatchling survival [28] and  
56 shorter internesting intervals [26], but also detrimental by causing some  
57 populations of loggerhead turtles to decline due to changes in resource avail-  
58 ability [2]; understanding the combined effect is much more complicated than  
59 understanding each effect alone. The omnivorous loggerhead turtles feeding  
60 on various invertebrates are considered more resilient to changes in resource  
61 availability compared to specialized species such as leatherback, hawksbill, or  
62 herbivorous green turtles [2, 3], but a trophic mismatch is possible, especially  
63 for oceanic life stages of loggerhead turtles [3].

64 Furthermore, mechanisms by which changes in food availability and tem-  
65 perature *independently* affect the biological processes are extremely hard  
66 to study empirically for a long lived, large, and widely distributed species  
67 such as the loggerhead turtle. Hence, these mechanisms have only partially  
68 been explored and remain largely unquantified. Mechanistic deterministic  
69 models can generally help, especially with quantifying the consequences of  
70 a wide range of environmental conditions and with predicting the biological  
71 responses of individuals to environmental change [2, 34], but have not been  
72 used to investigate effects of environmental factors on loggerhead turtles.

73 Adopting the hypothesis that food availability and temperature are the  
74 two key environmental factors that determine the physiological processes and  
75 life history traits of loggerhead turtles, we use a previously constructed and  
76 calibrated mechanistic model of the North Atlantic loggerhead turtle [35] to  
77 decipher the effects of the two environmental factors (food availability and  
78 temperature) on biological traits of the loggerhead turtle.

79 In the following sections we first explain how we mapped the environmen-  
80 tal factors to the energy budget and physiological processes (such as growth,  
81 maturation, and reproduction) of the loggerhead turtle. Second, we visualize  
82 the results of our simulations in terms of several key life-history traits: age  
83 and length at puberty, seasonal and cumulative reproduction output of ma-  
84 ture turtles, and ultimate size (length and mass of fully grown adults). We  
85 conclude with the summary of our most important results and implications  
86 thereof, including the implications of climate change.

## 87 2. Methods

88 Physiological processes of loggerhead turtles were simulated using a mech-  
89 anistic model based on Dynamic Energy Budget (DEB) theory [36] - a  
90 metabolic theory successfully applied to almost 700 animals from all major  
91 taxa (see the Add-my-pet collection [37]), and used in over 500 publications  
92 (see [http://www.bio.vu.nl/thb/deb/DEB\\_papers.pdf](http://www.bio.vu.nl/thb/deb/DEB_papers.pdf) for a complete list).  
93 Model setup is explained in Subsection 2.1. The predicted properties were  
94 analyzed in the context of currently experienced environmental conditions,  
95 and compared to the properties reported in literature. In addition to in-  
96 vestigating life history traits, we also analyzed scaling of body mass with  
97 carapace length, and scaling of reproduction output with carapace length for  
98 a reduced set of environments. Schematic presentation of the study setup  
99 can be found in Figure 1. To reduce variability that could be introduced

100 by differences between populations, only one, the North Atlantic population,  
 101 was studied (see also [38]). Environmental conditions were simulated as a  
 102 range of deviations from current food availability (estimated from available  
 103 data [35]) and a range of ecologically realistic average sea surface temper-  
 104 atures (from Hawkes et al. [39]). Exact environmental simulation setup is  
 105 explained in Subsection 2.2.

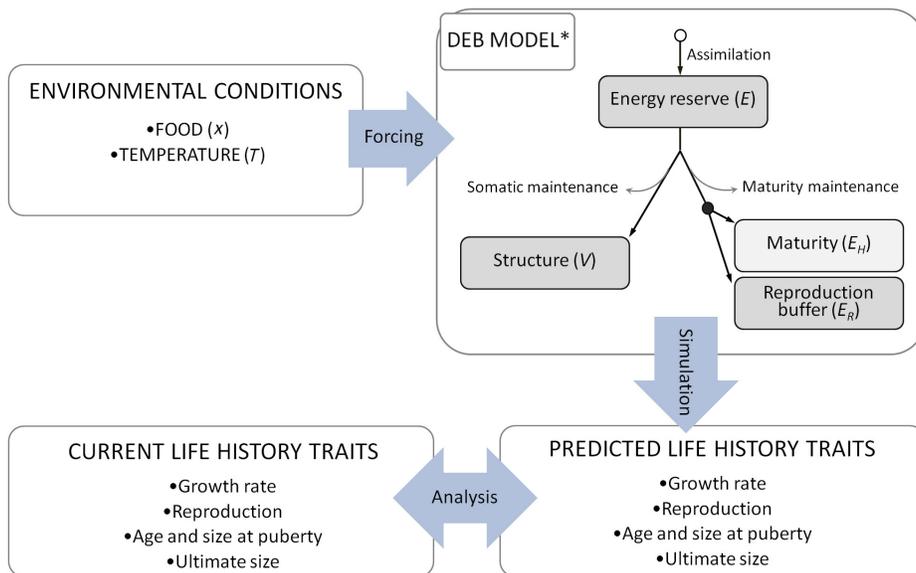


Figure 1: Schematic presentation of the study setup. Main environmental forcing factors are (scaled) food density ( $x$ ) and temperature ( $T$ ) which vary between simulations, but are kept constant throughout each simulation of the turtle’s life-cycle. Simulated and analyzed traits included growth rates, reproduction rates, seasonal and cumulative reproduction output, size (length and mass) and age at puberty, size of fully grown adults, as well as the relationships of length and mass, and length and seasonal reproduction output. \*Scheme of the standard DEB model. The rectangles are the main state variables; circles denote metabolic switches: empty circle – onset of feeding, full circle – onset of reproduction; see subsection 2.1 for a brief overview. Detailed description of the model and its parameterization for the North Atlantic loggerhead turtle can be found in Marn et al. [35]. The main parameters of the model (from Marn et al. [35]) are listed in Table 1.

106 *2.1. Mapping the environmental factors to the energy budget and biology of*  
107 *loggerhead turtles*

108 Biology of loggerhead turtles was studied by following physiological pro-  
109 cesses (such as growth, maturation, and reproduction), and life-history traits  
110 (growth rates, age and size at puberty, size of fully grown adults - ultimate  
111 size, relationships between length and mass, and length and reproduction  
112 output). We predicted the processes and the traits at a given food level and  
113 temperature using a mechanistic model [35] based on a general metabolic  
114 theory (Dynamic Energy Budget - DEB theory, see [40, 41, 42, 43, 44, 45] for  
115 in-depth discussion). Relevant DEB-related terms and concepts are briefly  
116 presented (following the length-energy framework in Kooijman [36]) in the  
117 next four paragraphs. Detailed description of the standard DEB model for  
118 the North Atlantic loggerhead turtle, including the model's parameterization  
119 and validation, can be found in [35].

120 The North Atlantic loggerhead turtle can be described well by the sim-  
121 plest (standard) form of DEB models [35]. The standard DEB model recog-  
122 nizes *three life stages* of an individual - embryo (does not feed or reproduce),  
123 juvenile (feeds but does not reproduce), and adult (feeds and reproduces).  
124 Transitions (birth and puberty, respectively) between life stages occur when  
125 the amount of energy, measured in Joules, cumulatively invested into in-  
126 crease in complexity (maturation), reaches a certain threshold. The variable  
127 tracking the investment is called maturity, and its thresholds - maturity  
128 at birth and maturity at puberty - are expressed in Joules (J). Within the  
129 DEB-framework, an individual (turtle) is defined by *three state variables* that  
130 change with time: In addition to 'maturity' (symbol  $E_H$ , unit J), the stan-  
131 dard DEB model tracks 'structure' (symbol  $V$ , unit  $\text{cm}^3$ ) and 'energy reserve'  
132 (symbol  $E$ , unit J)(Figure 1). When food is abundant, all three state vari-  
133 ables increase with time until puberty, after which maturation ceases and the  
134 energy is directed into reproduction. The energy committed to reproduction  
135 is tracked by an auxiliary state variable, 'reproduction buffer' (symbol  $E_R$ ,  
136 unit J); the energy accumulated in the buffer is utilized for egg production  
137 prior to nesting. To calculate the reproduction output, we assumed that  
138 nesting occurs every two years [46] if there is enough energy stored in the  
139 reproduction buffer to produce at least one egg (210 kJ [47]).

140 Structure, energy reserve (and the reproduction buffer in the adult stage)  
141 contribute to the biomass of a turtle. Structure and energy reserve were con-  
142 verted to length and mass of the individual using standard auxiliary equa-  
143 tions [36, 35]. Age at puberty corresponds to the age at which the 'maturity

144 at puberty' threshold is reached [36], which is earlier than the actual first  
145 reproductive event.

146 *Processes and parameters.* Energy reserve in DEB models serves as a  
147 buffer between the individual and the environment during short-term en-  
148 vironmental fluctuations. Adults and juveniles assimilate energy from the  
149 environment into the reserves, from which energy can be utilized for main-  
150 tenance, growth, maturation, and reproduction even during food shortages.  
151 Energy utilization and allocation among processes will depend on parameter  
152 values (see Lika et al. [48] for an example of parameterization). The main  
153 parameters of the model, estimated for the loggerhead turtle by Marn et al.  
154 [35] are listed in Table 1.

155 DEB theory relies on a  $\kappa$ -rule [36, 49, 50], which guarantees that mat-  
156 uration and growth do not compete. Structure and maturity both require  
157 maintenance (named somatic and maturity maintenance, respectively). So-  
158 matic maintenance has absolute priority: energy investment into growth,  
159 maturation, and reproduction is possible only after maintenance has been  
160 paid. Note that energy reserve and the reproduction buffer do not require  
161 maintenance in DEB models.

162 Assimilation of energy from the environment into the turtle, i.e., the  
163 amount of energy per unit of time that will be transformed into energy reserve  
164 [36] is determined by the assimilation flux,  $\dot{p}_A$ :

$$\dot{p}_A = \{\dot{p}_{Am}\} V^{2/3} \frac{x}{x+1}, \quad (1)$$

165 where  $V$  is structural volume,  $\{\dot{p}_{Am}\}$  is the maximum surface area-specific  
166 assimilation rate, and  $x$  is food density scaled by the (species- and food-type  
167 specific) half-saturation constant,  $K$ . Note that  $V^{2/3}$  represents surface area  
168 of structure. The fraction appearing in Equation 1 is often denoted  $f$  and  
169 called the scaled functional response:

$$f = \frac{x}{x+1}. \quad (2)$$

170 Quantity  $f$  is a saturating function of food density which has a minimal  
171 value of zero when no food is available, and a maximal value of 1 when food  
172 is abundant. The scaled functional response can also be defined as a fraction  
173 of the maximum feeding rate of an individual of the given size [36, 51],  
174 depending not only on the environment but also on the physiology of an  
175 individual. Scaled functional response for North Atlantic loggerhead turtles,

Table 1: Standard DEB model primary and auxiliary parameters for North Atlantic loggerhead turtle population used in simulations. Detailed description of the model pertaining to the North Atlantic loggerhead turtle (including data used for parameter estimation and discussion regarding the validity, implications, and applicability of the model) can be found in Ref. [35]. Rate parameters are listed at the reference temperature  $T_{\text{ref}}=273\text{ K}$ . Notation: square brackets, [ ], indicate parameters normalized to structural volume, and curly brackets, { }, indicate parameters normalized to structural surface area (see [www.bio.vu.nl/thb/research/bib/Kooy2010\\_n.pdf](http://www.bio.vu.nl/thb/research/bib/Kooy2010_n.pdf) for details on notation).

Parameter	Symbol	Value	Unit
Maximum specific assimilation rate	$\{\dot{p}_{Am}\}$	906.1	$\text{J d}^{-1} \text{cm}^{-2}$
Digestion efficiency (of food to reserve)	$\kappa_X$	0.8	-
Energy conductance	$\dot{v}$	0.0708	$\text{cm d}^{-1}$
Allocation fraction to soma	$\kappa$	0.6481	-
Reproduction efficiency	$\kappa_R$	0.95	-
Somatic maintenance	$[\dot{p}_M]$	13.25	$\text{J d}^{-1} \text{cm}^{-3}$
Maturity maintenance rate coefficient	$\dot{k}_J$	0.002	$\text{d}^{-1}$
Specific cost for structure	$[E_G]$	7847	$\text{J cm}^{-3}$
Maturity at birth	$E_H^b$	3.809e+04	J
Maturity at puberty	$E_H^p$	8.73e+007	J
Arrhenius temperature	$T_A$	7000	K
Shape coefficient	$\delta_{\text{SCL}}$	0.3744	-
Specific densities	$d_V, d_E$	0.28	$\text{g cm}^{-3}$

Other primary and auxiliary parameters: Maximum searching rate,  $\{\dot{F}_m\} = 6.51 \text{ d}^{-1} \text{cm}^{-2}$ ; Defaecation efficiency (of food to faeces),  $\kappa_P = 0.1$ ; Reproduction efficiency,  $\kappa_R = 0.95$ ; Maturity maintenance rate coefficient,  $\dot{k}_J = 0.002 \text{ d}^{-1}$ ; Weibull aging acceleration,  $\dot{h}_a = 1.85e - 0101 \text{ d}^{-2}$ ; Gompertz stress coefficient,  $s_G = 0.0001$

176 marked hereafter as  $f_C$ , was estimated as  $f_C = 0.81$  [35]; the corresponding  
177  $x_C$  can then be back-calculated using Equation 2.

178 In subsequent analyses,  $K$  and  $\{\dot{p}_{Am}\}$  were assumed constant through-  
179 out the turtle life cycle, meaning that only changes in food *quantity* were  
180 taken into account, while food quality was assumed to be constant. This  
181 was a simplification. The effects of food quality could be accounted for by  
182 modifying  $\{\dot{p}_{Am}\}$  by a dimensionless food quality parameter (see Section 2  
183 in [52]); food of better quality would result in a higher assimilation flow (see  
184 Equation 1). The effect on the assimilation would, however, be difficult to  
185 differentiate from the effect of changes in food density (Equation 1) because  
186 both effects act to reduce assimilation flux, i.e., reduce  $f$ . In other words,

187 predictions for an environment with lower food *quality* would be qualitatively  
188 indistinguishable to predictions for an environment with lower food *quantity*  
189 presented herein.

190 The other environmental factor that will strongly influence the energy  
191 budget and biology of ectothermic organisms such as sea turtles is temper-  
192 ature. DEB theory argues that changes in temperature equally affect all  
193 metabolic rates (see Section 1.2 in Kooijman [36]). Because the body tem-  
194 perature of juvenile, sub-adult and moderately active adult chelonid turtles  
195 corresponds to the surrounding water temperature [53] (as would be expected  
196 for an ectotherm), we used the sea surface temperature as a proxy for body  
197 temperature. The average temperature experienced by the loggerhead tur-  
198 tles was set to 21.8° C [33, 54] ( $T_C=294.95$  K). All rates and parameters of  
199 DEB models are generally expressed at a reference temperature of 20° C  
200 ( $T_{\text{ref}} = 293.15$  K) [36]; for consistency, we adhere to the principle. Correc-  
201 tion for the effect of temperature is done using the Arrhenius equation (from  
202 Equation 1.2 in [36]):

$$C(T) = \exp\left(\frac{T_A}{T_{\text{ref}}} - \frac{T_A}{T}\right), \quad (3)$$

203 where  $C(T)$  is the correction factor for a certain temperature  $T$ , and  $T_A$  is  
204 the Arrhenius temperature equal to 7000 K for loggerhead turtles [35]. For  
205 example, the assimilation flux (Equation 1) at temperature  $T$  is:  $\dot{p}_A(T) =$   
206  $\dot{p}_A(T_{\text{ref}}) * C(T)$ .

## 207 2.2. Simulating the environment

208 Simulations were performed over a 31x31 grid of different environmental  
209 conditions using 15 equidistant values higher and 15 equidistant values lower  
210 than the current values for scaled food density ( $x_C$ ) and temperature ( $T_C$ ).  
211 In total, 961 environments were thus simulated as possible combinations of  
212 food density and temperature. During each simulation, which lasted a turtle's  
213 lifetime of 65 years, the environment was assumed to be constant.

214 Values for *scaled food density* ( $x$ ) ranged from a decrease of 75% to an  
215 increase of 200% relative to the current scaled food density ( $0.25x_C$  to  $3x_C$ ).  
216 Equation 2 was employed to turn each simulated food density into the scaled  
217 functional response ( $f$ ) (Figure 2.2, left panel), which was then used as a  
218 proxy for *food availability*. Explored scaled food densities ranged from those  
219 resulting in a very high scaled functional response ( $f > 0.9$ ) to those identified

220 in the preliminary analysis as unable to sustain reproduction ( $f \leq 0.6$ ).  
221 We assumed that values outside this range are rarely (if ever) present in  
222 nature: scaled functional responses close to the maximum are reached only  
223 at extremely high food densities (for example,  $f = 0.999$  for loggerhead  
224 turtles is reached at a scaled food density 22 times higher than the currently  
225 estimated density,  $x_C$ ), and values lower than the simulated ones would imply  
226 extinction due to lack of reproduction.

227 Values for *temperature* ranged from 287.15 K to 303.15 K (14° C to 30° C  
228 [39, 54]). Metabolic rates were corrected for each simulated temperature  
229 using Equation 3 (Figure 2.2, right panel). The loggerhead turtles in the  
230 North Atlantic rarely experience sea temperatures outside this range, even  
231 during winter [39], with adults being more efficient than juveniles in keeping  
232 their body temperature close to optimal values [55, 54].

233 In addition, a subset of 30 environments was set up to disentangle the roles  
234 of food availability and temperature, and to present results in a more straight-  
235 forward manner. To emphasize the role of food availability, 15 environments  
236 were set up with equidistant scaled food densities (15 values for scaled food  
237 density ranging from  $0.25x_C$  to  $3x_C$ ), but with a single temperature ( $T = T_C$ ).  
238 Similarly, to emphasize the role of temperature, 15 environments were set up  
239 with equidistant temperatures (15 values ranging from 287.15 K to 303.15 K),  
240 but with a single food density ( $x = x_C$ ).

241 Each environment was simulated for a duration of 65 years, correspond-  
242 ing to the age of the oldest recorded loggerhead turtle [56]. Simulations  
243 presented here therefore implicitly assume that loggerhead turtles keep their  
244 food intake and body temperature relatively stable through out their life.  
245 This simplification is justified in the sense that the turtles (i) modulate food  
246 intake by adapting searching activities to satisfy their energy needs and (ii)  
247 stabilize experienced temperature by following thermoclines [54]. Habitat  
248 shifts during a life-time (such as those from a pelagic to a neritic environ-  
249 ment [57]) are therefore not explicitly modeled. Although beyond the scope  
250 of this study, the model in principle allows exploring changes in the average  
251 conditions at some point in the life cycle. All simulations were performed in  
252 Matlab R2011b. Modified "EVHR" scripts by L. Pecquerie<sup>1</sup> were used with  
253 permission.

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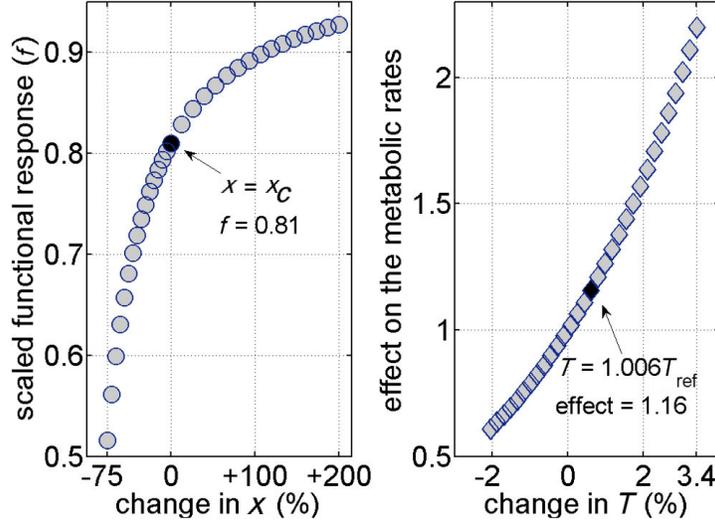


Figure 2: Simulated environmental factors: scaled food density ( $x$ , left panel) and temperature ( $T$ , right panel) on the x-axes, plotted with the corresponding scaled functional response ( $f$ , Equation 2) and the effect on metabolic rates (Equation 3) on the y-axes (see Subsection 2.1 for details). Scaled food density is expressed here as a decrease ( $\leq -75\%$ ) or an increase ( $\geq +200\%$ ) of the *current* scaled food density ( $x_C$ ). Temperature is expressed here as a decrease ( $\leq -2\%$ ) or an increase ( $\geq +3.4\%$ ) of the *reference* temperature ( $T_{\text{ref}} = 293.15 \text{ K} = 20^\circ \text{C}$ ) – the temperature at which all DEB rate parameters are generally given [36]. The left panel of the figure illustrates why a relatively large decrease in (scaled) food density will have a much stronger effect than an equally large increase in (scaled) food density ( $f$  is a saturating function of  $x$ ). Biological processes and rates (such as maintenance, assimilation, and growth) are, in contrast, exponential functions of temperature: for example, a 2% decrease in temperature will have a somewhat weaker effect (40% slower rate relative to the rate at  $T_{\text{ref}}$ ) than an analogous increase (resulting in a 60% faster rate relative to the rate at  $T_{\text{ref}}$ ). Conditions used as current for the North Atlantic populations ( $x_C$  and  $T_C$ ) are marked with full symbols.

## 254 **3. Results**

### 255 *3.1. Selected life-history traits*

256 The patterns that emerge while predicting the selected life-history traits  
257 (age and length at puberty, length and mass of fully grown adults, and sea-  
258 sonal and cumulative reproduction output of fully grown adults) in the simu-  
259 lated 31x31 environmental grid of food density and temperature reveal which  
260 of the two environmental characteristics (food availability or temperature)  
261 has the predominant effect on a specific life-history trait (Figure 3). For ex-  
262 ample, values for a trait predominantly affected by food availability (plotted  
263 on the x-axis) will vary from left to right, but remain constant from top to  
264 bottom. Analogously, if trait values vary from top to bottom, but not from  
265 left to right, temperature (plotted on the y-axis) has the predominant effect  
266 on the trait. A diagonal pattern suggests that the trait is simultaneously  
267 affected by both environmental conditions.

268 Food availability strongly affects length of a fully grown adult (ultimate  
269 length), which varied between 61 and 110 cm straight carapace length (SCL)  
270 for the set of simulated environments (Figure 3.A, and Figure 4.A). Tempera-  
271 ture, by contrast, does not affect the ultimate length an individual can reach  
272 ([42, 36, 45], see also Figure 4.A, and Figure 5, top left panel). However,  
273 because growth is slower at lower temperature (Figure 5, top left panel), an  
274 individual might die before reaching its ultimate length. This is mirrored  
275 in our results: the duration of simulations corresponds to the maximum life  
276 span, so the realized ultimate length is smaller at lower temperatures.

277 Length at puberty generally exhibits limited variation with food avail-  
278 ability: predicted values range from 76.6 cm SCL to 77.2 cm SCL, and are  
279 not affected by temperature (Tables C.4 and C.3 in Appendix C). A simi-  
280 lar effect of food availability (but not temperature) on mass at puberty is  
281 observed, with a relatively narrow range of predicted values (Tables C.4 and  
282 C.3 in Appendix C).

283 A predominant effect of food availability, but also a relatively strong ef-  
284 fect of temperature, are predicted for mass of fully grown adults (ultimate  
285 mass) (Figure 3.B, Figure 4.C and D). Predictions for ultimate body mass in  
286 the environments differing in food availability have a wider range than those  
287 for the environments differing in temperature (compare Table C.3, column 7  
288 and Table C.4, column 4 in Appendix C). This was expected because food  
289 availability affects the maximal reachable ultimate length (and body mass  
290 scales approximately with length cubed [58]), whereas the temperature gen-

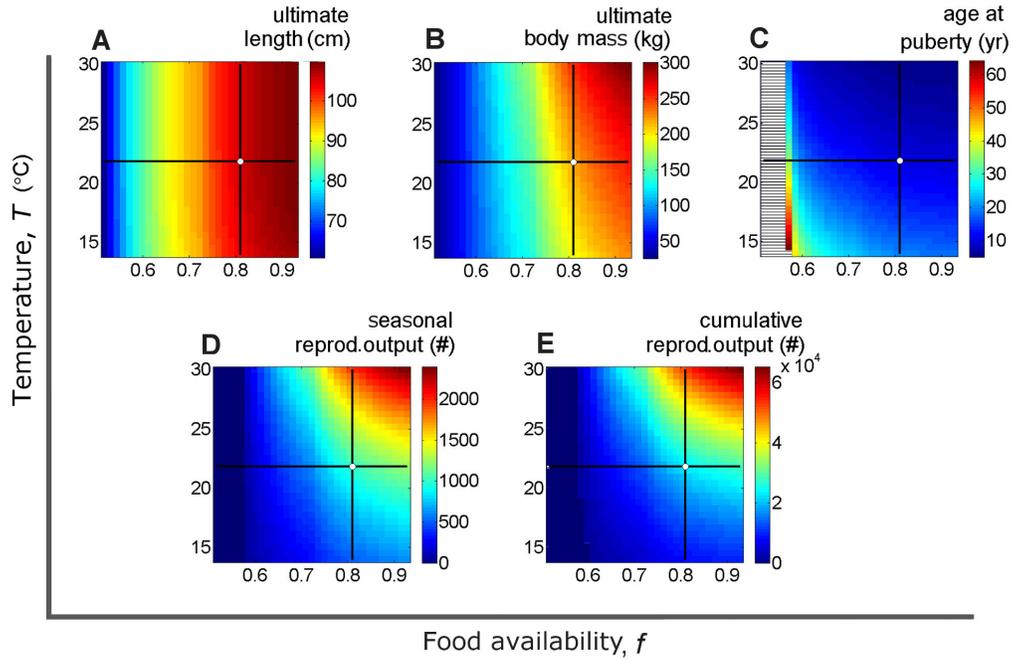


Figure 3: The effects of the environment on the selected life history traits of North Atlantic loggerhead turtles. Food availability (scaled functional response,  $f$ ) is on the x-axis and temperature ( $T$ , denoted in degrees Celsius) is on the y-axis. Values of the traits are represented by colors; see color map on the right of each panel for corresponding absolute values. Panels: [A,B,D,E] traits of fully grown adults: A. length (cm SCL); B. body mass (kg); D. seasonal reproductive output (number of eggs in a nesting season, #); E. cumulative reproductive output (number of eggs in a lifetime, #). Panel C: age at puberty (year). At low food availability ( $f < 0.6$ ), puberty cannot be reached, hence a part of panel C contains no data (marked with horizontal bars). The corresponding parts in panels D and E have values of zero indicating no reproduction. Two thick lines in the panels denote the subsets of the environments: at the horizontal lines ( $T = T_C = 21.8^\circ\text{C}$ ) environments differ in food availability, and at vertical lines ( $f = f_C = 0.81$ ) environments differ in temperature. The white circle at the lines' intersection marks the environmental conditions currently experienced by the North Atlantic loggerhead turtles [39, 54, 35]. (Simulation setup explained in Section 2.2)

291 erally does not affect the ultimate length (but can slow down growth, see  
292 above). To explain why temperature, somewhat counter-intuitively, has a  
293 relatively large affect on ultimate body mass, predictions for the body mass  
294 need to be analyzed in the context of predictions for the reproduction output  
295 which *are* affected by temperature. Namely, mass of the reproduction buffer  
296 was included when calculating the ultimate body mass: the model predicts  
297 that mass of the reproduction buffer is between 8% and 25% of the ultimate  
298 body mass at different environmental temperatures (under the assumption of  
299 biannual reproduction). The proportion of ultimate body mass attributable  
300 to a reproduction buffer is between 2% and 17% in environments differing  
301 in food availability. A favorable environment (high food availability, high  
302 temperature) therefore affects ultimate body mass via two mechanisms: (i)  
303 by allowing individuals to grow to a larger size, and (ii) by providing more  
304 energy for reproduction, which results also in larger mass of the reproduction  
305 buffer.

306 Both simulated environmental factors strongly affect age at puberty, and  
307 (seasonal and cumulative) reproduction output of fully grown adults (Fig-  
308 ure 3.C, D, and E, see also 4.E to H). Predictions for age at puberty range  
309 from 5.5 years to >60 years (Figure 3.C). For environments characterized  
310 with food availabilities  $f \leq 0.6$ , the model predicted that puberty cannot be  
311 reached, resulting also in no reproduction. In a subset of environments dif-  
312 fering only in food availability (with temperature 21.8° C) the predictions for  
313 age at puberty range from 9.72 years to 28.71 years (mean value of 13.35 yr)  
314 (Table C.3, column 3 in Appendix C), and in a subset of environments differ-  
315 ing only in temperature (with  $f = 0.81$ ) the predictions range from 6.49 years  
316 to 23.52 years (mean value of 13.31 yr) (Table C.4, column 2 in Appendix C).  
317 In the range between 18° C and 26° C, a temperature difference of 1° C results  
318 in approximately a 1-year difference in age at puberty. Outside of this range,  
319 age at puberty changes at an approximate rate of 0.5 years for every degree  
320 centigrade between 26° C and 30° C and 2 years for every degree centigrade  
321 between 14° C and 18° C, suggesting a strong negative effect of temperatures  
322 lower than 18° C on maturation.

323 Seasonal and cumulative reproduction output both have a range of an  
324 order of magnitude in a subset of environments that differ in temperature,  
325 and of two orders of magnitude in a subset of environments that differ in  
326 food availability (last two columns in Tables C.3 and Table C.4 in Appendix  
327 C, respectively, see also Figure 4.G and H). The reproduction buffer can be  
328 a substantial part of adult sea turtle's body mass [21], but it is unlikely that

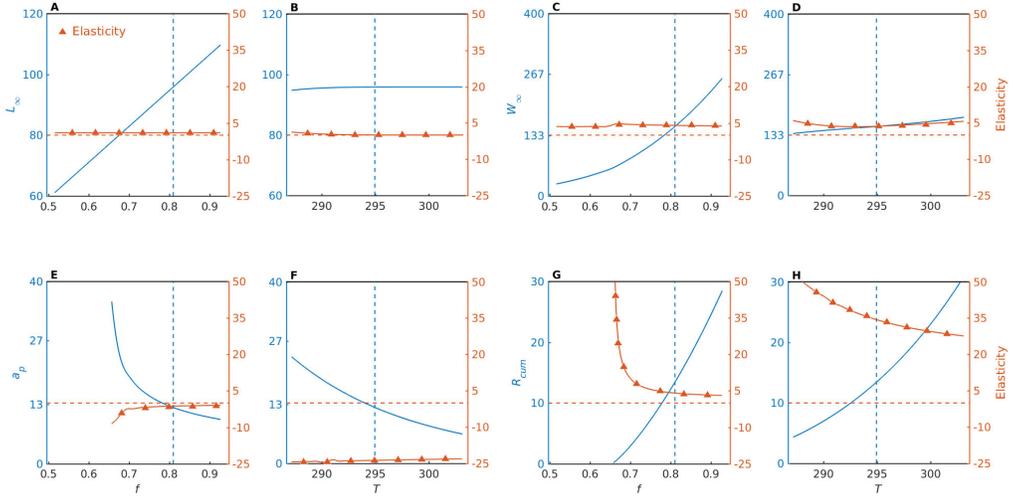


Figure 4: Elasticity analysis, showing the relative change of a life history trait (on the left y-axis), if the forcing variable (on the x-axis) changes by 1%. The horizontal dashed line marks elasticity equal to zero, which means that the life-history trait is independent of the forcing variable. If elasticity is a non-zero constant, then the life-history traits depends on the forcing variable, but the relationship is linear. Larger elasticity implies larger sensitivity of the life-history trait to  $f$  or  $T$  (on the x-axis). The elasticity of the reproductive output has the most non-linear relationship, especially in the range of  $f$  and  $T$  values where puberty is barely reachable.

329 it would reach the 43kg predicted for warm environments with high food  
 330 availability. Rather than accumulating such a large reproductive buffer, the  
 331 turtle is more likely to reproduce annually if conditions are so favorable.

### 332 3.2. Growth and reproduction rates

333 Predicted growth curves in Figure 5 (top two panels) show faster growth  
 334 at higher food availability and temperature with one notable difference: in-  
 335 creased food availability positively affects the size of fully grown adults (Fig-  
 336 ure 5, top left panel), whereas the temperature does not. At lower tem-  
 337 peratures, however, it takes more time to become a fully grown individual  
 338 (Figure 5, top right panel).

339 Predicted reproductive output increases with both food availability and  
 340 temperature (Figure 5, bottom two panels, see also Figure 4.G and H), with  
 341 the range of the predicted values larger in the subset of environments differ-  
 342 ing in food availability (Figure 5, bottom left panel). Interestingly, the model

343 predicts a very similar seasonal reproduction output for lower temperature  
344 and higher food availability as it does for higher temperature and lower food  
345 availability, highlighting a synergistic effect of the two environmental fac-  
346 tors on reproduction. For example, a fully grown adult turtle has an almost  
347 identical reproduction output in an environment characterized by tempera-  
348 ture of 21.8°C and food availability  $f \approx 0.87$ , as it does in an environment  
349 with temperature of 30°C and food availability  $f = 0.81$ . Similarly, a fully  
350 grown adult turtle experiencing a temperature of 21.8°C and food availabil-  
351 ity  $f \approx 0.7$ , has an almost identical reproduction output as if experiencing a  
352 temperature of 14°C and food availability  $f = 0.81$ .

### 353 *3.3. Scaling of body mass and seasonal (biannual) reproduction output with* 354 *carapace length*

355 The relationship between straight carapace length (SCL) and body mass  
356 does not markedly differ between the simulated environments (Figure 6, top  
357 two panels), but subtle differences are present. Because food availability  
358 has a strong effect on the maximal reachable length (Subsections 3.1 and  
359 3.2), the length-mass curve is extended in environments with higher food  
360 availability (Figure 6, top left panel). The temperature does not have such  
361 an effect on the ultimate body size (Subsections 3.1 and 3.2), so the length-  
362 mass relationship stays the same in all environments (Figure 6, top right  
363 panel). The scatter of the predicted body mass values is somewhat larger in  
364 the range of SCL values  $\geq 77$  cm SCL (corresponding to length at puberty,  
365 Subsection 3.1). The scatter can be explained by fluctuations (in mass) of  
366 the reproduction buffer (Figure 5, bottom two panels).

367 The seasonal biannual reproduction output and carapace length scale lin-  
368 early in all simulated environments, but with markedly different patterns  
369 depending on whether food availability or temperature differ between the  
370 simulations (Figure 6, bottom two panels). When environments differ in food  
371 availability, the seasonal reproduction is seemingly completely positively re-  
372 lated to the carapace length (Figure 6 bottom left panel), suggesting that in-  
373 dividuals of the same length will have the same seasonal reproduction output  
374 regardless of the experienced food availability. By contrast, when environ-  
375 ments differ in temperature, individuals of a given carapace length produce  
376 more eggs in environments with higher temperatures (Figure 6, bottom right  
377 panel). This implies that, when food is abundant, the available time (dura-  
378 tion of the nesting season, duration of the inter-nesting period, etc.) becomes  
379 the limiting factor.

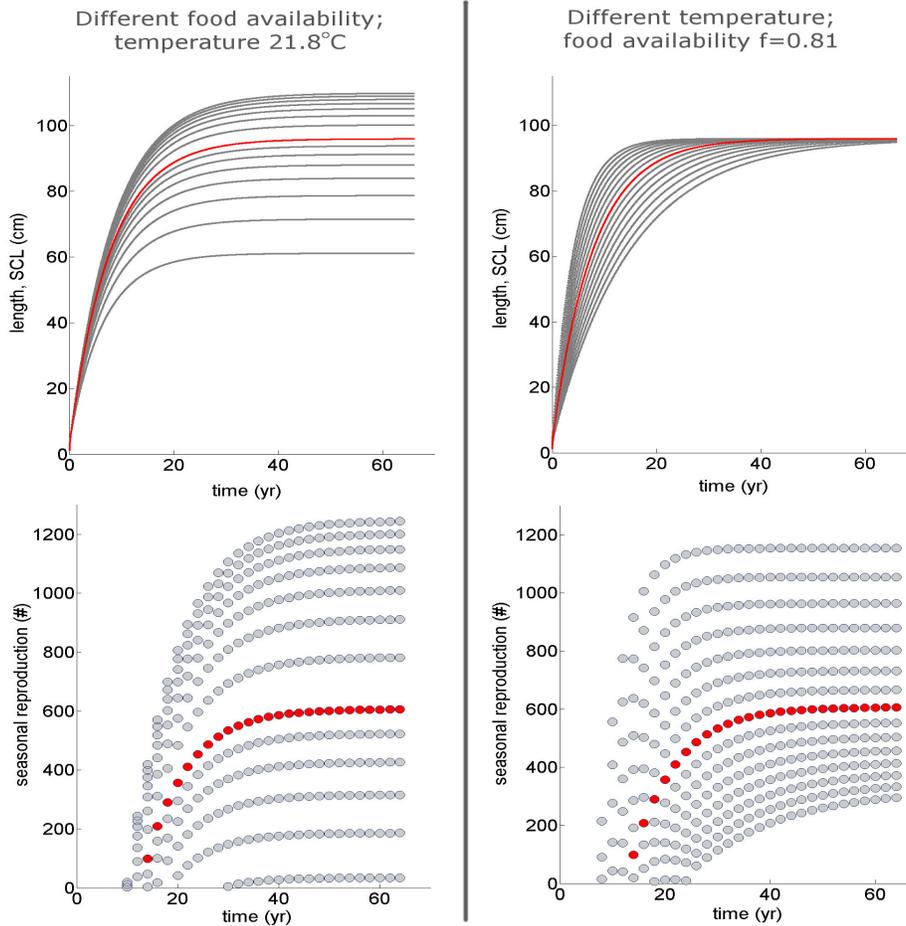


Figure 5: Growth curves (top two panels) and biannual reproduction curves (bottom two panels) predicted for a subset of environments differing in food availability or temperature. Left panels: Food availability ranging from  $0.516 \leq f \leq 0.927$  at  $T = T_C = 294.95$  K ( $21.8^\circ\text{C}$ ). Right panels: temperature ranging from  $287.15$  K ( $14^\circ\text{C}$ ) to  $303.15$  K ( $30^\circ\text{C}$ ), with  $f = f_C = 0.81$ . Growth and reproduction at  $f_C$  and  $T_C$  are denoted in red. At lower food availability, loggerhead turtles reach a smaller size, which results in lower reproduction. At lower temperatures, loggerhead turtles grow slower and start reproducing later, but the ultimate length and length at puberty are not affected.

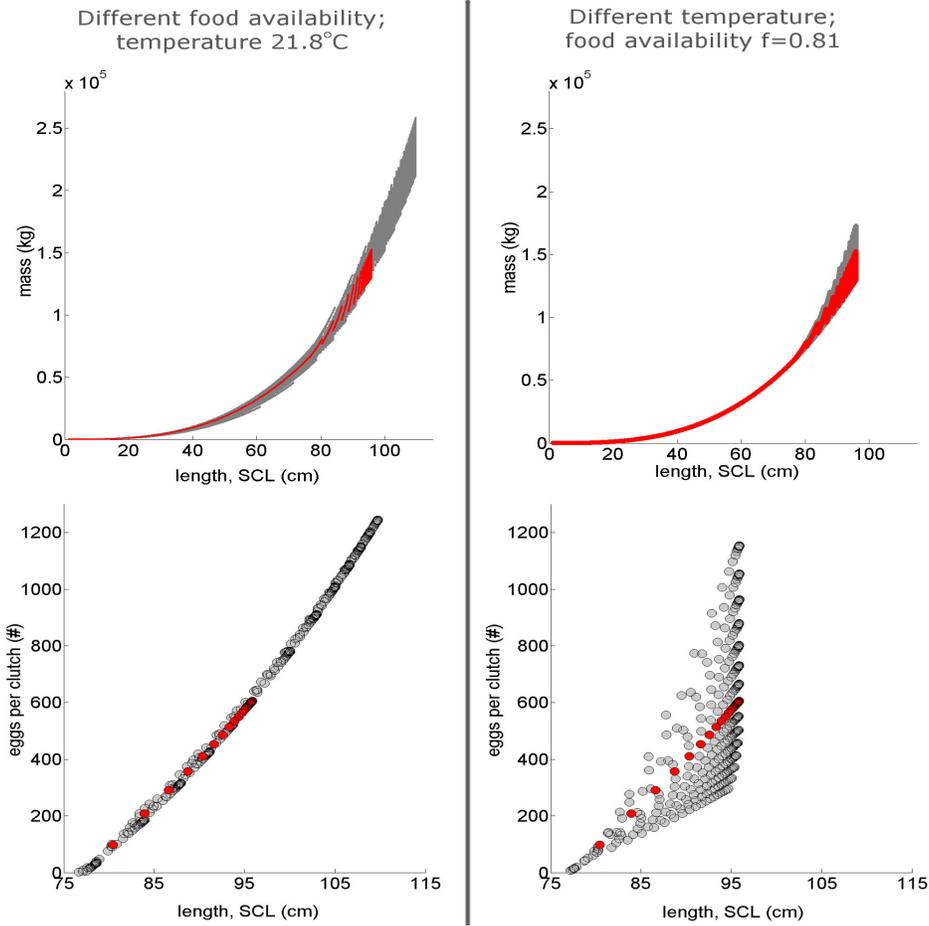


Figure 6: The relationship between carapace length and body mass (top two panels), and carapace length and seasonal (biannual) reproduction output (bottom two panels) as predicted for a subset of environments differing in food availability or temperature. Left panels: Food availability ranging from  $0.516 \leq f \leq 0.927$  at  $T = T_C = 294.95$  K ( $21.8^\circ\text{C}$ ). Right panels: temperature ranging from  $287.15$  K ( $14^\circ\text{C}$ ) to  $303.15$  K ( $30^\circ\text{C}$ ), with  $f = f_C = 0.81$ . The length-mass and length-reproduction relationships at  $f_C$  and  $T_C$  are denoted with red color. In warmer environments with more available food, turtles grow to larger sizes, and hence have larger reproduction outputs. Reproduction output of turtles with a specific carapace length is strongly affected by the simulated temperature: the reproductive output is larger at a higher temperature.

## 380 4. Discussion

381 Processes (growth, maturation, and reproduction), as well as life history  
382 traits (ultimate size, age and size at puberty, and the reproduction output),  
383 are affected by both the environment (temperature and food availability),  
384 and the individual characteristics (physiology of a loggerhead turtle). The  
385 DEB model helps disentangle the effects of the two causes of variability by  
386 conceptually separating the effects of physiology (represented by DEB model  
387 parameter values) from the effects of the environment (food availability and  
388 temperature). By fixing the physiology, and only varying environmental  
389 conditions, our results demonstrate the extent to which two environmental  
390 factors (food availability and temperature) can affect the processes and the  
391 life history traits. Below, we put the results into the context of existing  
392 knowledge and data.

### 393 4.1. *The non-linear relationship between the two studied environmental fac-* 394 *tors and the physiology of loggerhead turtles*

395 Defining the relationships between environmental factors and the result-  
396 ing life-history traits (Subsection 2.1) was the baseline for predicting the ef-  
397 fects of the environmental conditions on the observable biological quantities.  
398 Ranges of the simulated temperature and food availability, albeit somewhat  
399 arbitrarily chosen, are realistic: the simulated temperature range has been  
400 reported for North Atlantic loggerhead turtles [39], and the simulated food  
401 density ranges from values at which reproduction is impossible (implying ex-  
402 tinction), and values giving functional response very close to the maximal.  
403 The non-linear relationships for the dependence of the scaled functional re-  
404 sponse on (scaled) environmental food density (a proxy for food availability,  
405 Equation 2), and of the metabolic rates on temperatures (Equation 3) were  
406 taken from the thoroughly tested DEB theory [36, 45].

407 The current food availability was estimated to be relatively high ( $f_C =$   
408 0.81 [35]), and, because food availability is a saturating function of scaled  
409 food density (Equation 2, Figure 2.2, left panel), *reducing* scaled food density  
410 has a much stronger effect on the predicted traits than *increasing* it by the  
411 same relative amount. If food availability is low to begin with, even a small  
412 further reduction of food density results in a large decrease in the scaled  
413 functional response (Figure 2.2), and a strong negative effect on the bio-  
414 logical traits. The consequences of reduced food availability in areas where  
415 food availability is relatively low (e.g., in the Mediterranean Sea and oceanic

416 habitats [59, 19]) may, therefore, be more dramatic than in areas with high  
417 food availability.

418 The exponential relationship between temperature and physiological rates  
419 (Equation 3) results in a relatively large effect of a small temperature change  
420 on metabolic rates: for the range of simulated temperatures, the rates were  
421 suggested to be as much as 40% smaller and up to 120% greater than the rates  
422 at the reference temperature of 293.15 K=20 °C (Figure 2.2, right panel).  
423 Although the change may seem drastic, it is still realistic. If we assume  
424 loggerhead turtles experience a temperature of around 20° C in the oceanic  
425 habitat [19], and then move to a neritic habitat characterized by 24° C [19],  
426 the model predicts an increase in metabolic rates by almost 40%. This pre-  
427 diction is consistent with the noted "up to 30% faster growth" in a neritic  
428 habitat reported by Snover [18] (as cited in Ref. [19]).

#### 429 *4.2. How do the predicted growth and reproduction curves compare to data?*

430 Growth rates generally differ between life stages and between populations  
431 (genetic stocks) of loggerhead turtles [9, 10, 14]. However, *similar* growth  
432 rates were also reported between individuals belonging to different popula-  
433 tions and/or life stages [11, 13, 14] suggesting a strong influence of extrinsic  
434 (e.g., environmental) factors. Growth estimates derived from capture-mark-  
435 recapture data (e.g., [9, 11, 60]), growth marks on the bones (e.g., [61, 8, 62]),  
436 or length frequency analyses (e.g., [12, 63]) should therefore be interpreted in  
437 the context of the environmental data, with possibly special emphasis on the  
438 conditions present during the initial part of the development [64, 65, 7]. The  
439 intertwining effect of food availability and temperature on growth curves (and  
440 thus growth rates) of identical individuals reproduced by the model (Figure 5,  
441 top two panels) highlights why a direct comparison of growth data could be  
442 misleading.

443 Different environmental conditions may result in practically indistinguish-  
444 able growth rates. For example, in warmer environments with low food avail-  
445 ability growth rates of sea turtles might decrease between 50 cm and 60 cm  
446 straight carapace length (SCL) (this study) because individuals approach ul-  
447 timate size [66, 9, 14]. In an environment with high food availability but  
448 low temperature, our results show that growth rates might decrease around  
449 the said size range due to a decrease in temperature. The inter-dependency  
450 of growth and environmental conditions can be reconstructed with the help  
451 of a DEB model [67, 51] by combining, e.g., the environmental data, our  
452 mechanistic model for loggerhead turtles, and skeletochronology.

453 The model can be (partially) validated by calculating the growth rates  
454 plotted in Figure 5, and comparing them with literature. For example, the  
455 model predicts that growth from 25 cm to 75 cm SCL requires between 7  
456 and 19 years (when food availability is varied at temperature of 21.8° C),  
457 and between 5 and 18 years (when temperature is varied at  $f =$   
458 0.81). The low ends of the predicted ranges correspond to environments  
459 characterized by warm temperatures and high food availability; an example  
460 of such an environment could be the Southern Bahamas, where extremely  
461 fast growth was observed. Two loggerhead turtles needed just 3 to 4 years  
462 to grow from 25 cm to 75 cm SCL [11].

463 The average prediction in simulated environmental subsets is around 10  
464 years to grow from 25 cm to 75 cm SCL. This is consistent with the observed  
465 time needed for the Florida population, Frazer and Ehrhart [68] (in Ref. [11]),  
466 for which estimates indicate 10 (von Bertalanffy model) to 16 years (logistic  
467 model) are needed to achieve the same growth. Available information for a  
468 different size span (growth from 50 cm to 75 cm SCL) is also in agreement  
469 with our results: Mendonça [9] calculated that Florida loggerheads need 5  
470 years to grow from 50 cm to 75 cm SCL, whereas the average time predicted  
471 by the model for the simulated subset of the environments is around 6.5 years  
472 (between 3 and 12 years for varying food, and between 4 and 14 for varying  
473 temperature). A more elaborate report on the predicted growth rates (in cm  
474  $\text{yr}^{-1}$ ) in the context of literature values can be found in Appendix A.

475 A direct comparison of the *reproduction output* predicted by the model  
476 and the values reported in literature is complicated by the many uncertain-  
477 ties that plague *in situ* observations of the total seasonal reproduction output  
478 (and thus also the cumulative reproductive output) of an individual female  
479 [47, 46, 69]. Examples where annual reproduction output *is* reported or  
480 calculated are rare, but available information corroborates our results: we  
481 predict that mass of the reproduction buffer (when reproduction is biannual)  
482 is between 2% and 25% of the ultimate mass, which is consistent with ap-  
483 proximately 10% of the total body mass reported for annual clutch mass of  
484 marine, freshwater, and terrestrial turtles [21].

485 Seasonal and cumulative reproduction output of individuals in our study  
486 was positively affected by both food availability and temperature. The range  
487 of predictions was larger when environments differed in food availability than  
488 in temperature (Subsections 3.1 and 3.2). The results therefore imply that  
489 sea turtles in warmer and energy richer neritic environments [19] will have a  
490 larger reproduction output than those in an oceanic environment, but also

491 that the simulated range of food availability has a stronger influence on the  
492 reproduction output than the simulated range of temperature. The reproduc-  
493 tion output has indeed been linked to the type of habitat (oceanic vs neritic)  
494 [23], with the dichotomy between smaller adult females having a smaller  
495 reproduction output and larger adult females having a larger reproduction  
496 output explained primarily by energy available for reproduction [23].

497 While the link between food (energy) availability and reproduction output  
498 is straightforward, the link between temperature and reproduction reported  
499 in the literature is somewhat ambiguous: Chaloupka et al. [2] hypothesized  
500 that loggerhead turtles with a higher reproduction output experienced en-  
501 vironments with a higher food abundance and *lower* temperature than the  
502 loggerheads with a lower reproduction output, suggesting that the effect of  
503 temperature on reproduction output, if present at all, is minor. Further-  
504 more, no correlation was found between temperature at the *breeding* sites  
505 and reproductive output (number of clutches per nesting season) [28], but  
506 the correlation *was* found between reproductive output and temperature at  
507 *feeding* sites [70]. Loggerhead turtles spend just a fraction of their time  
508 at breeding sites where they do not feed. During this period the processes  
509 related to egg production (such as vitellogenesis) take place [71, 72].

510 The apparent conflict can, however, easily be resolved by following the  
511 reasoning used for the model construction. The assumption made in our  
512 model was that the energy is assimilated from the environment and invested  
513 into the reproduction buffer continuously throughout the year [36], i.e., we  
514 do not differentiate between fractions of time at feeding and breeding sites.  
515 Higher energy investment into the reproduction buffer (and thus production  
516 of more eggs) predicted by the model can be a result of two distinct fac-  
517 tors: (i) higher food abundance in the environment (more energy available  
518 for assimilation), and (ii) warmer environment (faster assimilation of energy  
519 and production of eggs). Areas of higher temperature could be combined  
520 with higher food quality [19, 14], but do not need to in order to correlate  
521 with a higher reproduction output (more eggs per turtle)—such areas could  
522 affect metabolic rates just via temperature (Equation 3, Table C.4). Either  
523 scenario would result in more energy being continuously invested into the re-  
524 production buffer, thus increasing the reproductive output. In the context of  
525 continuous investment into reproduction, the predicted positive correlation  
526 of temperature and the reproduction output complies with the “capital breed-  
527 ers” hypothesis, where temperature at breeding sites may affect the timing  
528 of breeding events, but not the total energy committed to breeding [33].

529 Furthermore, our results imply that increasing either temperature or food  
530 availability, in addition to increasing the reproduction output, increases the  
531 growth rate and decreases age at puberty, i.e., increases the maturation rate  
532 (Figures 3-6). This link has already been hypothesized by Iverson [21], who  
533 noted that maturation rates and annual reproduction output could be di-  
534 rectly linked to growth rates, i.e., the rate of energy acquisition.

535 Predictions for maturation rates, i.e., the time required to reach puberty  
536 varied greatly between simulated environments: predicted values were be-  
537 tween 10 years and 15 years for most of the simulated range, but also values  
538 as small as 5.5 years were predicted for environments with high food availabil-  
539 ity and high temperature, and values larger than 40 years were predicted for  
540 environments with low food availability and low temperature (Figures 3.C).  
541 Mendonça [9] estimated that loggerhead turtles needed between 10-15 years  
542 to reach puberty, but also noted that loggerhead turtles reared in captivity  
543 need 6-8 years, and loggerhead turtles in the Pacific 25-30 years to reach  
544 puberty (References in [9]). Wild loggerhead turtles in the North Atlantic  
545 might need as long as 19 years to >35 years to mature [18, 8, 73]. It is rea-  
546 sonable to assume that captive-reared loggerhead turtles experience a higher  
547 average temperature and/or fewer exposures to low temperatures, as well  
548 as a higher food availability compared to those in the wild, making model  
549 predictions in excellent agreement with observed data.

#### 550 *4.3. Scaling of body mass and seasonal (biannual) reproduction output with* 551 *carapace length*

552 The analyzed relationship of carapace length and body mass exhibited less  
553 variation across the simulated environments compared to the relationship  
554 of carapace length and seasonal reproduction output (Figure 6). Limited  
555 variation in scaling of body mass with carapace length is in agreement with  
556 the empirical finding that a single curve explains the whole size range, with  
557 a high measure of goodness of fit even when data from more populations are  
558 pooled into analysis ( $R^2 = 0.97$ , [58]).

559 Scaling of seasonal reproduction output with carapace length should be  
560 interpreted with the assumption about biannual nesting in mind (Section 2,  
561 see also Subsection 4.4), but is nonetheless informative when analyzing the  
562 commonly reported relationship of carapace length and clutch size (e.g., in  
563 [47, 46, 74]). For example, our results imply that individuals of the same size  
564 will have a similar seasonal reproduction output regardless of the experienced

565 food availability (Figure 6, bottom left panel), suggesting a positive corre-  
566 lation between carapace length and clutch size. However, the reproduction  
567 output of an individual of a certain length strongly varies with temperature  
568 (Figure 6, bottom right panel), suggesting that the positive correlation be-  
569 tween carapace length and clutch size should have a large scatter. Since  
570 loggerhead turtles experience variable environmental factors, we expect to  
571 observe a positive correlation between carapace length and clutch size, with  
572 a large scatter or low goodness of fit measure; indeed, this is true ( $R^2 = 0.30$   
573 [47],  $R^2 = 0.29$  [74], see also Figure 1 in [46]).

574 Patterns in the scaling relationships also suggest two distinct mechanisms  
575 through which a warmer environment with more available food can result in  
576 a higher reproduction output: (i) higher food availability enables individuals  
577 to grow to a larger size, and larger size has a strong correlation to the sea-  
578 sonal and cumulative reproductive output; (ii) warmer temperature affects all  
579 metabolic rates (including food assimilation, energy mobilization, and chem-  
580 ical transformations [36]), many of which are involved in production of eggs  
581 [71, 75]. This is consistent with the empirical finding that a higher temper-  
582 ature at *breeding* sites correlates with the shorter period between two clutch  
583 depositions within a single nesting season [26, 27, 28], probably by increasing  
584 the rate of processes related to vitellogenesis [71]. Hence, two individuals ex-  
585 perience the same food availability, but exposed to different temperatures  
586 during the year, will have a different reproductive output: the individual  
587 that experienced higher temperature will have a higher reproductive output  
588 due to both having accumulated more energy for reproduction, and a faster  
589 vitellogenesis. This result implies that, at high energy accumulation rates  
590 (feeding in warm environments with abundant food), temperature at breed-  
591 ing sites may become the limiting factor in reproduction: higher temperature  
592 will result in a shorter period between two nest depositions within a nesting  
593 season, whereas lower temperature will require a longer nesting season.

#### 594 4.4. Model considerations

595 We assumed a constant environment (characterized by constant food  
596 availability and temperature) for our simulations. Loggerhead turtles cer-  
597 tainly do not experience the same environmental conditions during their en-  
598 tire life cycle, but the annual averages should not differ too much between the  
599 years. In the context of the simulation, the seasonal variation should mostly  
600 cancel out (months at higher-than-average temperature roughly canceling

601 out months at lower-than-average temperature). The model in principle al-  
602 lows exploring fluctuations in the conditions, but the previous explorations  
603 of DEB models show that results for life history traits such as length and  
604 mass of fully grown adults would show the same patterns, and the growth  
605 and reproduction curves would include more fluctuations but would show the  
606 same general trend [36]. Including changes in the average conditions at some  
607 point in the life cycle, e.g., to mirror the ontogenetic habitat shift [57] could  
608 make an informative extension of the standard model.

609 We assumed biannual reproduction and did not transform the predicted  
610 seasonal reproduction output into number of clutches (nests). In the field,  
611 most often a clutch size is used as a measure of the reproduction output of  
612 females [46, 74], or nest counts in a nesting season are used for assessing the  
613 reproduction (nesting) activity of a specific population (e.g., [31]). Trans-  
614 forming the seasonal biannual reproductive output (predicted by the model)  
615 to the number of nests per nesting season or number of eggs per clutch is com-  
616 plicated by the trade-off between the number of clutches (nests) per season,  
617 eggs per clutch, internesting intervals, and remigration intervals [47, 21, 46].  
618 Generally, loggerhead turtles that are not first-time nesters have a modal  
619 value of 4-5 nests per nesting season [46, 76, 69], and nests with fewer than  
620 50 eggs or more than 200 eggs are rarely observed in nature [47, 77, 78], so  
621 a seasonal reproduction output of around 100 eggs (for first time nesters)  
622 up to around 1000 eggs would be realistic. By forcing the reproduction to  
623 occur every two years if there is enough energy in the reproduction buffer  
624 even for a single egg, and not limiting the number of eggs per season (see  
625 Section 2), unrealistically small and large seasonal reproduction outputs were  
626 predicted (Figure 3.D; Tables C.3 and C.4 in Appendix C). It is more likely  
627 that those loggerhead turtles with more energy available will have shorter  
628 remigration intervals (i.e., reproduce every year), whereas those with less  
629 energy available will have longer remigration intervals (i.e., reproduce three  
630 or more years apart) [23]. The reproduction output could be constrained by  
631 a minimal and a maximal seasonal outputs, and the remigration intervals  
632 allowed to correlate with temperature [25]. It is likely that remigration in-  
633 tervals with a modal value of 2-3 years, yet ranging from 1 to 7 years [74]  
634 could be reproduced in such a way, and more realistic seasonal reproduction  
635 output values could be obtained. Nevertheless, we decided to implement a  
636 remigration interval of 2 years [46]. Even though this simplification occa-  
637 sionally resulted in predictions for a seasonal reproduction output smaller  
638 or larger than observed, the predictions for cumulative reproduction output

639 were not affected. In addition, by omitting an additional layer of complexity,  
640 the interpretation of results was kept more straightforward, and comparisons  
641 between model predictions and data are still possible and informative.

642 Climate change is most likely to affect loggerhead turtle populations  
643 through changes of environmental conditions on breeding and nesting sites  
644 [33, 3, 5], so the research has been focused on distribution, temperature-  
645 dependent sex determination, and/or nesting activity (e.g., [2, 3, 5]). How-  
646 ever, conservation efforts require quantification of processes over the whole  
647 life cycle—most of which is in the marine environment, and poorly under-  
648 stood. This study, by focusing on environmental conditions in the marine  
649 environment, therefore provides important missing information and method-  
650 ology for studying specific effects of climate change on loggerhead turtles.  
651 For example (see Appendix B), should the ongoing climate change act on  
652 the loggerhead turtles at sea just by increasing the sea temperature, our re-  
653 sults suggest that the loggerhead turtles will grow and reproduce faster, but  
654 there will be no discernible effect on the size distribution of loggerhead tur-  
655 tles within a population. If, however, such a temperature increase is coupled  
656 with a decrease in food availability, loggerhead turtles will grow at a rate  
657 as if the environment has not changed, but will grow to a smaller size. The  
658 possible increase in temperature can, therefore, mask a moderate decrease in  
659 food availability if growth rates are directly measured in the field, but the  
660 decrease in food availability will result in a different size distribution within  
661 a population due to a larger proportion of smaller individuals.

## 662 5. Conclusion

663 Mechanisms by which environmental factors (food availability and tem-  
664 perature) affect physiological processes are crucial for studying correlations  
665 between environmental trends or oscillations and growth rates, reproduction  
666 output, or other life history traits of sea turtles (e.g., [26, 29, 31]), as well  
667 as for using the conclusions from those studies for conservation activities.  
668 We investigated environmental effects on biology (processes and life history  
669 traits) of North Atlantic loggerhead turtles using a mechanistic model [35]  
670 based on Dynamic Energy Budget (DEB) theory [36]. Our study relies on  
671 the model developed by Marn et al. [35], which successfully reproduced the  
672 full life cycle and general ecological properties of North Atlantic loggerhead  
673 turtles. Marn et al. [35], however, focused on the energy budget of the log-  
674 gerhead turtles and the implied physiological properties such as the ability to

675 cope with periods of starvation, giving a secondary role to the environment.

676 Here, we focus on the environment characterized by average temperature  
677 and food availability experienced by North Atlantic loggerhead turtles, and  
678 the way it shapes growth rates, reproduction rates, scaling relationships, and  
679 other life-history traits of loggerhead turtles. The mechanistic model made  
680 it possible to independently study effects of the two environmental factors  
681 on the selected biological traits. By modifying only the environment, we try  
682 to generate the observed variability in the selected biological properties of  
683 North Atlantic loggerhead turtles.

684 The DEB framework allowed us to map food density and temperature  
685 in the environment onto the energy budget of a loggerhead turtle (Subsec-  
686 tion 2.1) in a thermodynamically consistent and an empirically validated  
687 manner [45]. Relationships that play a critical role in the present analy-  
688 ses are (i) the saturating dependence of the scaled functional response (food  
689 availability, or food intake) of loggerhead turtles on food density and (ii) the  
690 exponential dependence of physiological rates on temperature.

691 Even though our predictions are based on the assumption that all have the  
692 same DEB parameters and only differ in state variables, the predictions suc-  
693 cessfully reproduced many patterns observed in nature (Subsections 4.2 and  
694 4.3). For example, we predict that the scaling of body mass with carapace  
695 length will have limited scatter, while the reproductive output will exhibit a  
696 large degree of scatter, a pattern observed in nature [47, 46, 58, 74]. If, how-  
697 ever, inter-individual variability were markedly higher in real life, we would  
698 expect a high degree of scatter in body mass vs. length as well. Therefore, the  
699 assumption that individuals are almost identical, but experiencing different  
700 environments, is more consistent with the observations than the assump-  
701 tion that differences between individuals are the chief drivers of differences  
702 between individual performance (growth, reproduction, etc).

703 Satisfactory agreement between simulations and available data over a  
704 range of food availabilities and/or temperatures also corroborated the hy-  
705 pothesis that two environmental factors—food availability and temperature  
706 – are the major cause of variability in biological properties of loggerhead tur-  
707 tles within a population (Subsections 4.2 and 4.3). This conclusion may not  
708 apply when individuals of different populations (or life stages) are compared,  
709 yet the results of this study can serve as a good starting point for such com-  
710 parisons (e.g., between individuals belonging to the North Atlantic and the  
711 Mediterranean populations, inhabiting markedly different habitats [59, 10]).

712 The size of fully grown adults was strongly affected by food availability

713 (loggerhead turtles reached smaller sizes at lower food availabilities), whereas  
714 length at puberty was relatively stable within a population. Age at puberty,  
715 and (seasonal and cumulative) reproduction output were positively affected  
716 by both food availability and temperature, with an apparently stronger effect  
717 of food availability than temperature. The results suggest that, should food  
718 density or temperature decrease, loggerhead turtles would need more time to  
719 reach puberty and produce fewer eggs. Temperature had a marginal effect on  
720 the ultimate body mass, influencing the size (and mass) of the reproduction  
721 buffer: reproduction output of a turtle with a specific carapace length was  
722 higher at a higher temperature.

723 Growth and reproduction curves predicted for simulated environments  
724 suggested faster growth and maturation in warmer environments with higher  
725 food availability (such as neritic habitats). Even though faster growth was  
726 predicted at a higher temperature, unless more food was available, the ultimate  
727 size was the same as when temperature was lower. Higher food availability  
728 and higher temperature resulted in a lower age at puberty, and a  
729 higher reproduction output (seasonal and cumulative) of individuals. The  
730 predictions for the reproduction output differed by two orders of magnitude  
731 over the simulated range of food densities, and one order of magnitude over  
732 the range of simulated temperatures, suggesting a strong effect of both food  
733 availability and temperature on the reproduction output. On a population  
734 level, environments with higher food availability might be correlated with  
735 a higher reproduction output because individuals can grow to a larger size,  
736 and because more energy can be (continuously) invested into reproduction.  
737 Warmer environments, by contrast, might result in a higher reproduction  
738 output because of the positive effect of higher temperature on physiological  
739 rates (earlier onset of reproduction, shorter remigration and inter-nesting  
740 intervals, etc). Reduction in food availability adversely impacted all life history  
741 traits in the simulations, and food level reductions below 50% of the current  
742 (scaled) food density made reproduction impossible.

743 The model provides a mechanistic context that can help interpret scaling  
744 of body mass and reproduction output with carapace length. Studies relying  
745 on such scaling (e.g., [46, 58]) typically do not consider environmental conditions.  
746 This practice may be appropriate when the environment is fluctuating  
747 randomly and numbers are large (creating a random error in scaling). However,  
748 if the environmental change has a trend (e.g., due to climate change),  
749 indiscriminately using scaling could result in misleading conclusions; for example,  
750 should a population inhabit an area with stable temperature but

751 declining food availability, the short term effects would be hard to detect  
752 because loggerhead turtles of a specific carapace length would still produce  
753 a corresponding number of eggs expected for that size (Figure 6, bottom  
754 left panel). Long-term effects might become visible decades later, as the  
755 size structure shifts towards smaller adults. Similarly, should temperature  
756 increase or decrease without a change in food availability, short term effects  
757 would show up as an increase or decrease in the reproduction output (num-  
758 ber of eggs per nesting season, Figure 6, bottom right panel), even though  
759 the productivity of an area might not have been affected.

760 Our approach and results present a strong basis for future research. In  
761 addition to the scenarios of several constant temperatures and food densities  
762 tested in this study, temporary changes in temperature and/or food avail-  
763 ability could be simulated. Loggerhead turtles are physiologically capable of  
764 withstanding prolonged periods of starvation [35], and compensatory growth  
765 has been observed [79] in sea turtles experiencing an increased food level  
766 after a period of decreased food availability. The consequences of the compen-  
767 sation on the energy budget later in life are unknown [65], and could be  
768 studied using the DEB model presented here (e.g., see [80]). Our model is (in  
769 principle) also capable of taking into account the effects of changes in food  
770 quality and gut residence time, should specific feeding and digestion data  
771 become available to justify the added complexity of the model. Frequency  
772 and length of the migrations can also be integrated into the model by modi-  
773 fying the energy budget in response to the distance traveled as suggested in  
774 [23, 36]. The added realism of the actually experienced environment might  
775 give a more realistic size and maturation predictions, and also account for  
776 some of the observed intra-population variability in the growth rates, size  
777 and age at sexual maturity. The added complexity, however, would ideally  
778 rely on significantly richer data sets than currently available.

779 Effects of long-term changes in environmental factors, such as those re-  
780 sulting from climate change, could also be investigated using the model,  
781 which could be driven by climate change scenarios to assess the possible con-  
782 sequences (see Appendix B for an illustrative example). For example, an  
783 increase in sea surface temperature may be considered positive because it  
784 increases growth rate and reproduction output, but positive effects on the  
785 population depend on food availability: large decreases in food availability  
786 may negate any positive effects of a temperature increase. Similarly, reduc-  
787 tion in food availability may be compensated by increase in temperature,  
788 but only up to a point. Environmental change could also have a synergistic

789 effect: increase in both food availability and temperature would considerably  
790 increase both the growth rate and reproduction.

791 Quantifying the effects on the population level requires a population dy-  
792 namics model. The developed DEB model can be directly nested into a  
793 population dynamics model using, for example, physiologically structured  
794 approach of De Roos and Persson [81], or individual-based approach of Mar-  
795 tin et al. [82]. Subsequently, the coupled models could be employed to help  
796 the conservation efforts by, e.g., (re)evaluating the IUCN criteria [34] and the  
797 current assessment of the North Atlantic population (regional management  
798 units) as “low risk-high threat” [1].

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## 805 **Appendix A. Comparison of modeled and measured growth rates**

806 Several studies reporting growth rates of North Atlantic loggerhead tur-  
807 tles [9, 11, 61, 14] were used to obtain a set of values recorded in the field  
808 (Table A.2). We narrowed our literature search by focusing on studies re-  
809 porting length as SCL (straight carapace length), and growth rates calculated  
810 from direct measurements rather than growth models or skeletochronology.  
811 Where length measurements and time intervals were reported in addition  
812 to growth rates (e.g., in Refs. [11, 61]), raw data was used to calculate the  
813 growth rates and descriptive statistics (average, standard deviation, mini-  
814 mum, and maximum of the size class). Size classes were set as in Ref. [14]  
815 (30-39 cm, 40-49 cm etc.), and a growth rate was assigned to a specific size  
816 class based on the mean of the SCL at initial capture and SCL at recapture  
817 [11, 14].

818 Based on the size range represented in the studies (30-110 cm SCL), we  
819 randomly chose 3000 combinations of two carapace lengths that fall within  
820 the 30-110 cm range, and treated them as “length at capture” and “length at  
821 recapture”. For the combinations that were less than 50 cm apart (largest

822 length difference in the studies [9, 11, 61, 14]), we simulated 15+15 sub-  
823 sets of environments: 15 environments were set up with equidistant scaled  
824 food densities (15 values for scaled food density ranging from 0.25% to 300%  
825 of the current one), but with a single temperature (currently experienced  
826 by North Atlantic loggerhead turtles,  $T_C = 294.95$  K), and 15 environments  
827 were set up with equidistant temperatures (15 values ranging from 287.15 K  
828 to 303.15 K), but with a single (current) scaled food density. Food availabil-  
829 ity ( $f$ ) and temperature correction were calculated using Equations 2 and  
830 3, respectively (see Subsection 2.2 for details). In total, simulations were  
831 performed for 2664 combinations of carapace lengths. Because each combi-  
832 nation had a set of values for environments differing in temperature and a  
833 set of values for environments differing in food availability, one combination  
834 of carapace lengths corresponded to roughly 30 individuals experiencing dif-  
835 ferent environmental conditions. Size class was assigned based on the mean  
836 of the two lengths (as in Refs. [11, 61]), and the descriptive statistics for all  
837 growth rates within a size class was then calculated (Table A.2).

838 The two subsets of simulated environments represent environments that  
839 are favorable for growth and reproduction of loggerhead turtles either due  
840 to temperature (21.8° C) or due to food availability ( $f = 0.81$ ) (or both).  
841 One would therefore expect that the range of predicted growth rates would  
842 include the growth rates recorded in nature. This was indeed the case for  
843 most size classes (Table A.2). Interestingly, within size classes for which  
844 more than two literature sources were available (50-79 cm), growth rates  
845 closer to the low end of the predicted range belonged to the samples which  
846 included or focused on loggerhead turtles inhabiting colder North Atlantic  
847 areas (north of Florida, [61, 14]), while growth rates close to the high end of  
848 the predicted range belonged to loggerhead turtles inhabiting warmer areas  
849 (south of Florida [9, 11]) with possibly also higher food availability.

850 Such a favorable agreement between model predictions and data obtained  
851 in the field corroborates the hypothesis of the strong causal relationship be-  
852 tween the two environmental factors and biological properties of loggerhead  
853 turtles, as well as provides additional support to the validity of our mecha-  
854 nistic model and study setup.

## 855 **Appendix B. Implications for climate change**

856 Climate change might affect sea turtles at sea by changing the tempera-  
857 ture and/or food availability in feeding and/or breeding areas [2, 39]. Here

Table A.2: Growth rates obtained by model simulations (column 2) and growth rates reported in literature (columns 3-6). All growth rates are for straight line carapace length (SCL) and divided into 10-cm size classes by mean SCL [11, 14].

Mean SCL size class (cm)	Growth rate (cm year <sup>-1</sup> )				
	Simulation (This study)	Bjorndal et al. [14]	Snover et al. [61]	Bjorndal and Bolten [11]	Mendonça [9]
<b>30 – 39</b>	<b>7.83 ± 2.59</b> (1.26-15.96) <i>N</i> = 2250	<b>5.90</b> (2.90 & 8.90) <i>N</i> = 2	–	–	–
<b>40 – 49</b>	<b>6.49 ± 2.26</b> (0.52-13.49) <i>N</i> = 5463	–	–	<b>15.67 ± 1.34</b> (14.81 17.21) <i>N</i> = 3	–
<b>50 – 59</b>	<b>5.24 ± 1.88</b> (0.19-11.07) <i>N</i> = 10904	<b>2.40 ± 2.50</b> (-1.40-12.60) <i>N</i> = 47	<b>2.14 ± 0.79</b> (1.26-2.76) <i>N</i> = 3	–	<b>7.40 ± 1.40</b> <i>N</i> = 2
<b>60 – 69</b>	<b>3.99 ± 1.48</b> (0.07-8.65) <i>N</i> = 14621	<b>1.50 ± 1.50</b> (-0.80-8.80) <i>N</i> = 196	<b>2.68 ± 1.56</b> (0.78-4.16) <i>N</i> = 6	–	<b>6.00 ± 2.30</b> <i>N</i> = 7
<b>70 – 79</b>	<b>2.83 ± 1.12</b> (0.08-6.26) <i>N</i> = 13941	<b>1.10 ± 1.10</b> (-0.50-5.80) <i>N</i> = 130	<b>2.15 ± 1.60</b> (1.02-3.28) <i>N</i> = 2	<b>5.16</b> (4.56 & 5.77) <i>N</i> = 2	<b>5.00 ± 3.50</b> <i>N</i> = 4
<b>80 – 89</b>	<b>1.78 ± 0.81</b> (0.07-3.82) <i>N</i> = 6732	<b>1.20 ± 1.40</b> (-0.70-2.50) <i>N</i> = 129	–	–	–
<b>90 – 99</b>	<b>1.14 ± 0.59</b> (0.03-2.34) <i>N</i> = 1273	<b>0.20 ± 0.50</b> (-0.80-2.20) <i>N</i> = 41	–	–	–
<b>100 – 109</b>	<b>0.58 ± 0.21</b> (0.16-0.99) <i>N</i> = 66	<b>0.20 ± 0.10</b> (0.10-0.30) <i>N</i> = 3	–	–	–

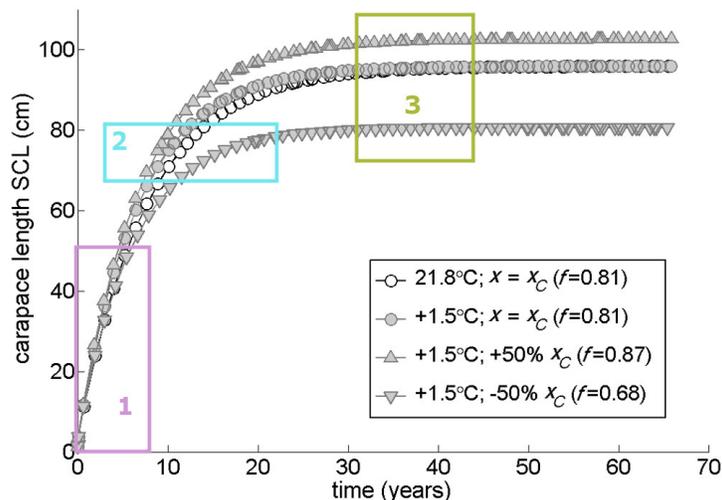


Figure B.7: Simulating possible scenarios resulting from climate change. Environmental factors were assumed to change relative to the current ones: an increase of temperature alone by  $1.5^{\circ}\text{C}$  from  $21.8^{\circ}\text{C}$  (scenario A) and the same temperature increase accompanied with a 50% increase (scenario B) or decrease (scenario C) of scaled food density from the current value,  $x_C$ . Enumerated rectangles mark three situations useful for studying and conserving loggerhead turtles in the context of climate change—see text for details.

858 we present an analysis of three possible scenarios relative to the conditions  
 859 assumed as current for North Atlantic loggerhead turtles, to illustrate how  
 860 the results from this study may be used for conservation purposes and for  
 861 studying the effects of climate change on loggerheads (and other sea turtles).

862 In all three scenarios, we assumed that the sea temperature increased  
 863 for  $1.5^{\circ}\text{C}$  [39, 32]. Scaled food density was assumed to remain the same  
 864 (scenario A), increase by 50% (scenario B), or decrease by 50% (scenario C).  
 865 Otherwise, identical setup as in the main text (see Section 2.1) was used to  
 866 map the changes in the environment to the biological traits of loggerhead  
 867 turtles. Conditions assumed as current comprised of temperature  $T_C$  and  
 868 scaled food density  $x_C$  (see Section 2 for details).

869 The growth curves generated by the model (Figure B.7) under the tem-  
 870 perature increase of  $1.5^{\circ}\text{C}$  imply that: (i) if food availability remains the  
 871 same, there should be a visible effect on age-length curves, but no effect on  
 872 the size range of individuals in a given population, and (ii) if food availability  
 873 does change, the size range of individuals should also be affected.

874 The said effects of increased temperature are not always easy to spot as  
875 illustrated by the enumerated rectangles in Figure B.7. In Rectangle 1, pre-  
876 dicted growth curves are so close to each other that they all fall within the  
877 range of reported growth rates. Therefore, one cannot easily distinguish be-  
878 tween the growth curve at the higher temperature and same food availability  
879 (scenario A) and the growth curve at higher temperature and higher food  
880 availability (scenario B). It is even harder to distinguish the growth curve  
881 under current environmental conditions from the one at higher temperature  
882 and lower food availability (scenario C), thus indicating that an increase in  
883 temperature can, up to a point, mask a decrease in food availability.

884 In Rectangle 2, changes in food availability and temperature have a syn-  
885 ergistic effect on growth. Given the model predictions that loggerhead turtles  
886 reach puberty at around 76-78 cm SCL (see Subsection 3.1), age at puberty  
887 strongly varies between scenarios, ranging from around 9 years to more than  
888 18 years. Age at puberty is a trait with an important role in population  
889 dynamics wherein the differences this big may separate prosperous from de-  
890 clining populations.

891 In Rectangle 3, as individuals approach their ultimate size, the effects  
892 of temperature on growth and size of individuals diminish. By contrast,  
893 food availability has a pronounced effect, suggesting that, e.g., longitudinal  
894 datasets of adult size distributions within a population may contain infor-  
895 mation on changes in food availability in an area.

896 **Appendix C. Additional results on life-history traits**

Table C.3: Model predictions for a subset of 15 environments differing in food availability; temperature fixed at 21.8°C (vertical lines in Figure 3). Food availability, modeled using the scaled functional response ( $f$ ), was calculated for each environment via scaled food density ( $x$ , Equation 2), which was obtained by modifying the current scaled food density ( $x_C$ ) by a factor given in column one (e.g., a factor of 3 means a 200% larger scaled food density, and a factor of 0.25 means 75% lower scaled food density compared to the current one). The corresponding scaled functional response is given in column two, and the selected life history traits in the following columns. Lengths are straight carapace lengths (SCL); mass refers to body mass. Reproduction output is expressed as number of eggs (#). Due to a relatively high  $f_C$  and the saturating relationship between  $x$  and  $f$  (Eq. 2, Figure 2.2), food density, e.g., 50% *lower* than  $x_C$  had a much stronger effect on the traits than food density 50% *higher* than  $x_C$ . Results for  $x_C$  ( $f = 0.81$ ) are indicated in bold.

Factor for $x_C$	$f$ (-)	Age puberty (yr)	Length puberty (cm)	Mass puberty (kg)	Length ultimate (cm)	Mass ultimate (kg)	Reprod. seasonal (#)	Reprod. cumul. (#)
3	0.927	9.72	76.48	71.93	109.75	258.39	1244	28497
2.71	0.920	9.83	76.49	71.62	108.92	250.99	1201	27483
2.43	0.912	9.97	76.51	71.24	107.91	242.20	1150	26270
2.14	0.901	10.16	76.54	70.77	106.66	231.59	1087	24795
1.86	0.888	10.41	76.57	70.18	105.07	218.52	1010	22965
1.57	0.870	10.77	76.61	69.40	102.97	202.07	911	20636
1.29	0.846	11.33	76.67	68.33	100.09	180.79	782	17581
<b>1</b>	<b>0.810</b>	<b>12.34</b>	<b>76.77</b>	<b>66.77</b>	<b>95.87</b>	<b>152.34</b>	<b>606</b>	<b>13419</b>
0.89	0.792	12.97	76.82	65.99	93.73	139.10	523	11454
0.79	0.770	13.88	76.89	65.05	91.15	124.07	427	9203
0.68	0.743	15.34	76.98	63.89	87.96	106.93	316	6617
0.57	0.709	18.17	77.10	62.44	83.92	87.35	186	3669
0.46	0.664	28.71	77.28	60.57	78.64	65.08	34	509
0.36	0.604	-	-	-	71.44	45.37	0	0
0.25	0.516	-	-	-	61.07	26.09	0	0

Table C.4: Model predictions for a subset of 15 environments differing in temperature; food availability fixed at  $f_C = 0.81$  (horizontal lines in Figure 3). Temperatures are expressed in degrees Celsius. Lengths are straight carapace lengths (SCL); mass refers to body mass. Reproduction output is expressed as number of eggs (#). Results for 21.8° C ( $T_C = 294.95$  K) are indicated in bold. Temperature had no predictable effect on length (76.9 cm SCL) and body mass (66.8 kg) at puberty, therefore the two traits were omitted from the table.

Temperature (°C)	Age puberty (yr)	Length ultimate (cm)	Mass ultimate (kg)	Reprod. seasonal (#)	Reprod. cumul. (#)
30.00	6.49	95.89	172.63	1154	30922
28.83	7.10	95.89	168.99	1055	27755
27.66	7.77	95.89	165.63	964	24839
26.49	8.51	95.88	162.53	880	22154
25.31	9.33	95.88	159.68	803	19685
24.14	10.23	95.88	157.05	732	17415
22.97	11.23	95.88	154.62	666	15331
<b>21.80</b>	<b>12.34</b>	<b>95.87</b>	<b>152.34</b>	<b>606</b>	<b>13419</b>
20.69	13.50	95.84	150.30	553	11750
19.57	14.78	95.80	148.33	503	10215
18.46	16.20	95.74	146.37	457	8809
17.34	17.75	95.62	144.32	414	7527
16.23	19.49	95.44	142.10	373	6354
15.11	21.40	95.17	139.58	333	5295
14.00	23.52	94.78	136.65	295	4343

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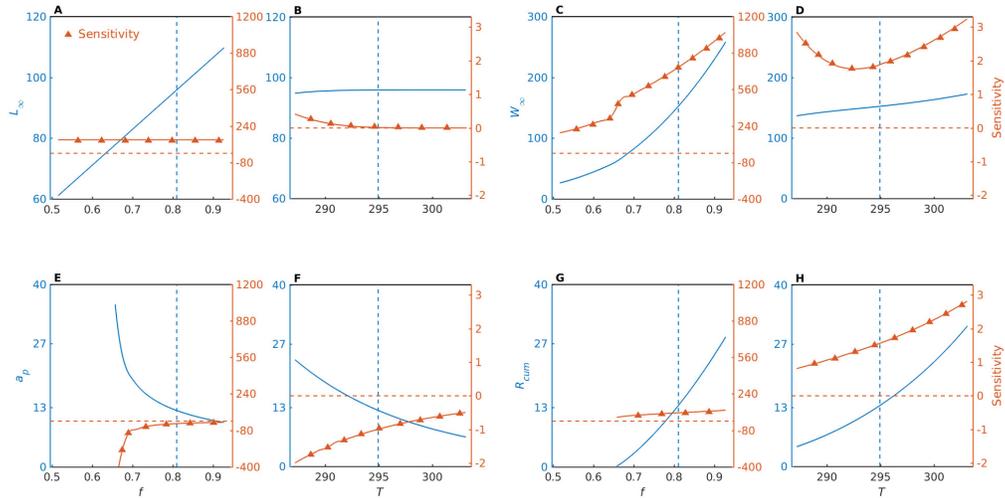


Figure C.8: Sensitivity analysis showing the change of a life history trait given a small change in the forcing variable ( $f$  or  $T$ ). The horizontal dashed line marks zero sensitivity, i.e., where life-history traits are independent of the forcing variable. If sensitivity is a non-zero constant, then life-history traits depend on the forcing variable, but the relationship is linear.

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