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

Nina Marn^{a,*}, Marko Jusup^b, Tarzan Legović^a, S.A.L.M. Kooijman^c, Tin Klanjšček^a

^a*Rudjer Bošković Institute*

Bijenička cesta 54, HR-10002 Zagreb, Croatia

^b*Center of Mathematics for Social Creativity, Hokkaido University*

12-7 Kita Ward, Sapporo 060-0812, Japan

^c*Vrije Universiteit Amsterdam*

De Boelelaan 1105, 1081 HV Amsterdam, Netherlands

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

*nina.marn@gmail.com

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

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 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

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

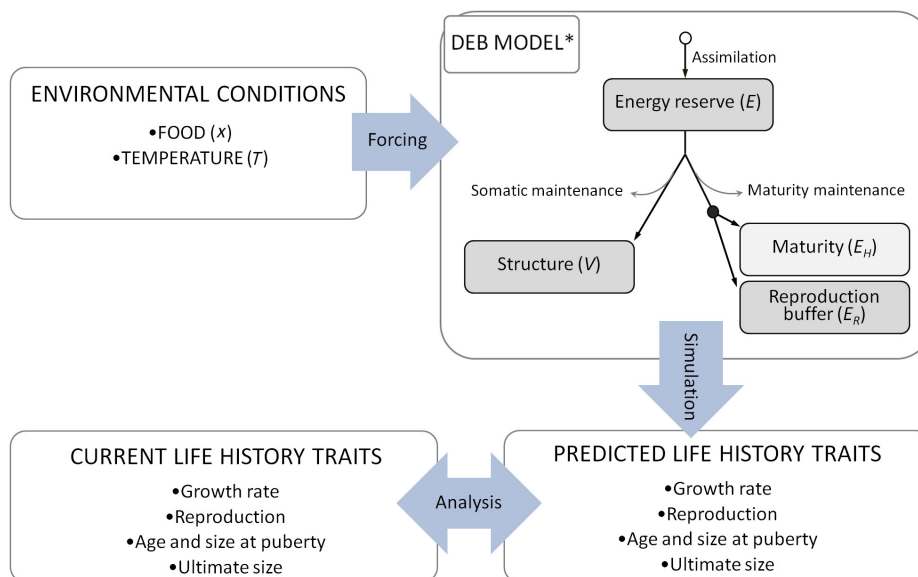


Figure 1: Schematic presentation of the study setup. Main environmental forcing factors are (scaled) food density (x) and temperature (T) which vary between simulations, but are kept constant throughout each simulation of the turtle’s life-cycle. Simulated and analyzed traits included growth rates, reproduction 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 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 κ -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 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)	κ_X	0.8	-
Energy conductance	\dot{v}	0.0708	cm d^{-1}
Allocation fraction to soma	κ	0.6481	-
Reproduction efficiency	κ_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	d^{-1}
Specific cost for structure	$[E_G]$	7847	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	δ_{SCL}	0.3744	-
Specific densities	d_V, d_E	0.28	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, $\dot{h}_a = 1.85e - 010 \text{ d}^{-2}$; Gompertz stress coefficient, $s_G = 0.0001$

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

In subsequent analyses, K and $\{\dot{p}_{Am}\}$ were assumed constant throughout the turtle life cycle, meaning that only changes in food *quantity* were taken into account, while food quality was assumed to be constant. This was a simplification. The effects of food quality could be accounted for by modifying $\{\dot{p}_{Am}\}$ by a dimensionless food quality parameter (see Section 2 in [52]); food of better quality would result in a higher assimilation flow (see Equation 1). The effect on the assimilation would, however, be difficult to differentiate from the effect of changes in food density (Equation 1) because 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. Pecquerie¹ were used with
 253 permission.

¹IRD Brest, laure.pecquerie@ird.fr

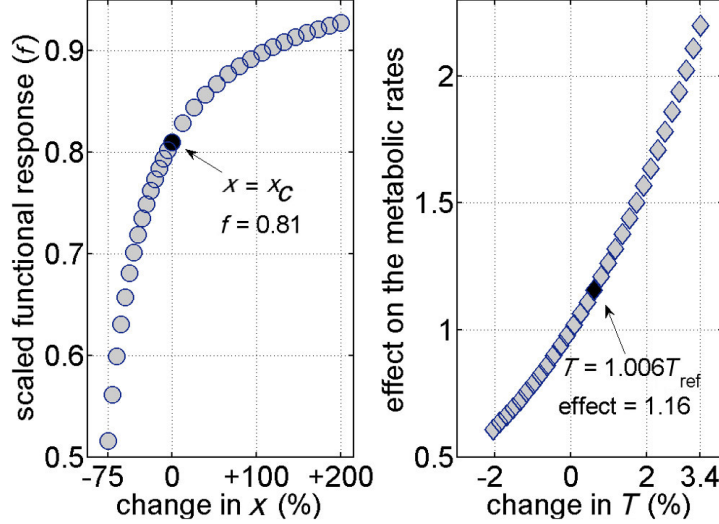


Figure 2: Simulated environmental factors: scaled food density (x , left panel) and temperature (T , right panel) on the x-axes, plotted with the corresponding scaled functional response (f , Equation 2) and the effect on metabolic rates (Equation 3) on the y-axes (see Subsection 2.1 for details). Scaled 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_{ref}) than an analogous increase (resulting in a 60% faster rate relative to the rate at T_{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-

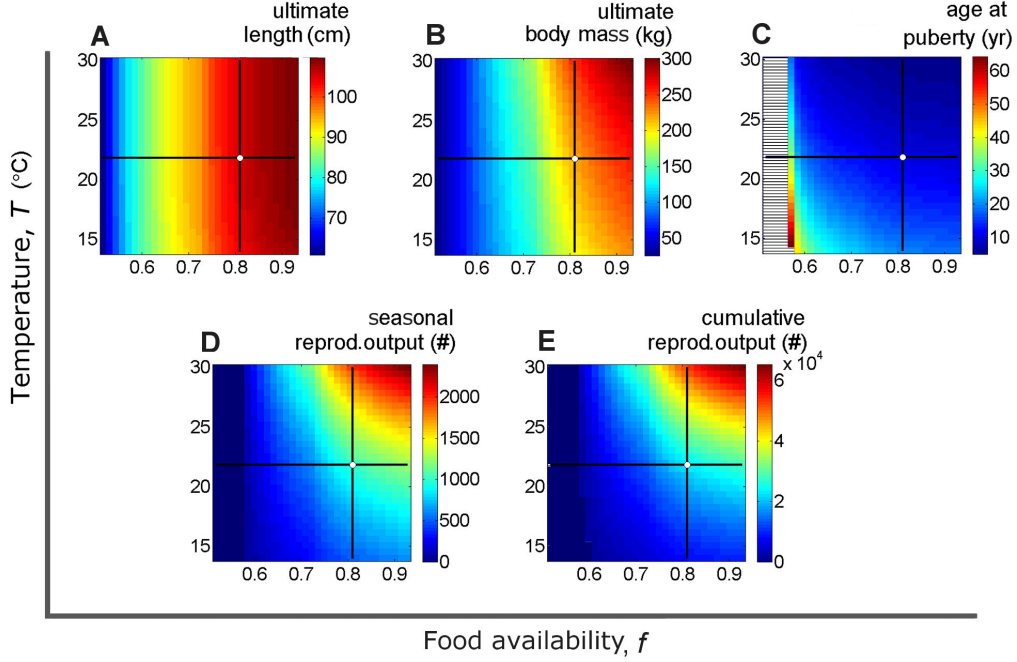


Figure 3: The effects of the environment on the selected life history traits of North Atlantic loggerhead turtles. Food availability (scaled functional response, f) is on the x-axis and temperature (T , denoted in degrees Celsius) is on the y-axis. Values of the traits are represented by colors; see 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)

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

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

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

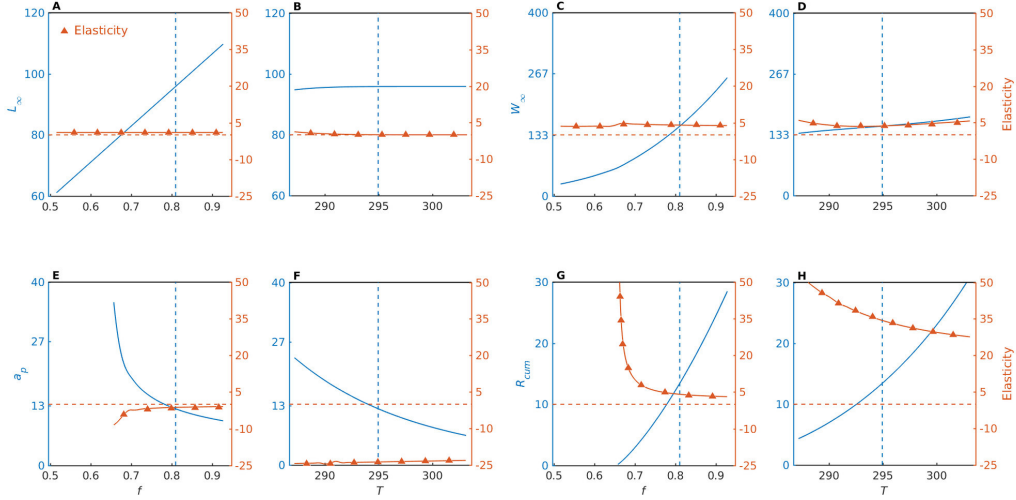


Figure 4: Elasticity analysis, showing the relative change of a life history trait (on the left y-axis), if the forcing variable (on the x-axis) changes by 1%. The horizontal dashed line marks elasticity equal to zero, which means that the life-history trait is independent of the forcing variable. If 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 ≥ 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.

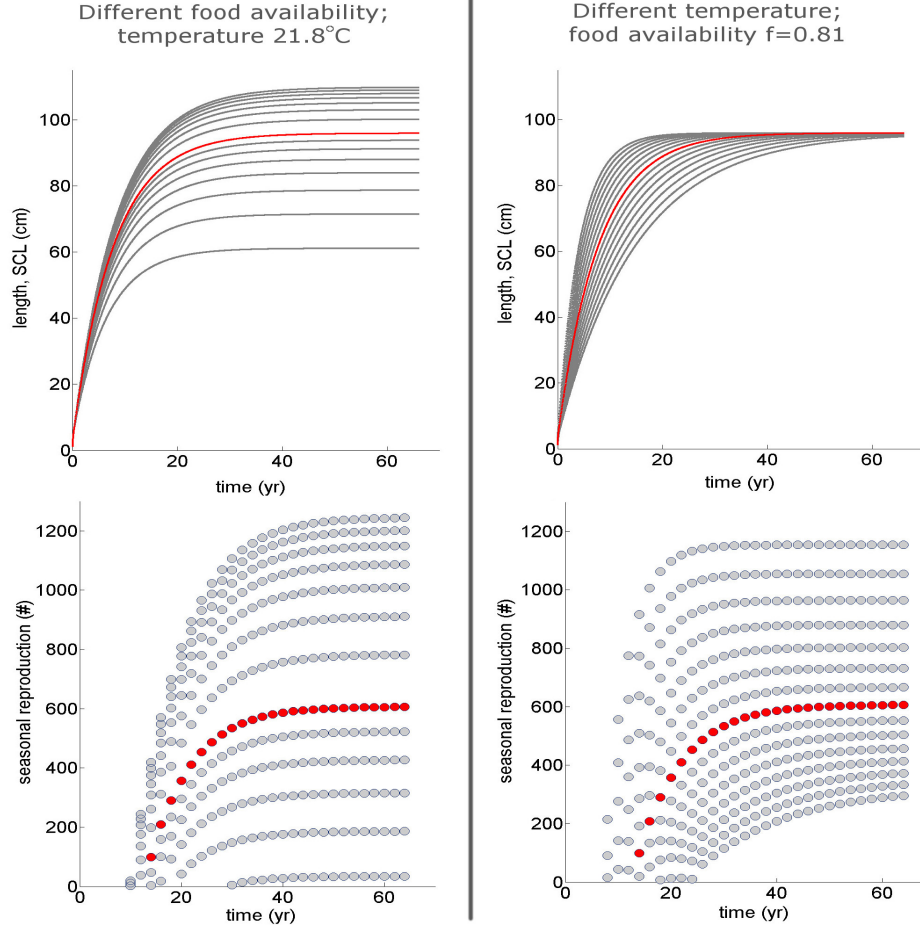


Figure 5: Growth curves (top two panels) and biannual reproduction curves (bottom two panels) predicted for a subset of environments differing in food availability or temperature. Left panels: Food availability ranging from $0.516 \leq f \leq 0.927$ at $T = T_C = 294.95$ K (21.8°C). Right panels: temperature ranging from 287.15 K (14°C) to 303.15 K (30°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.

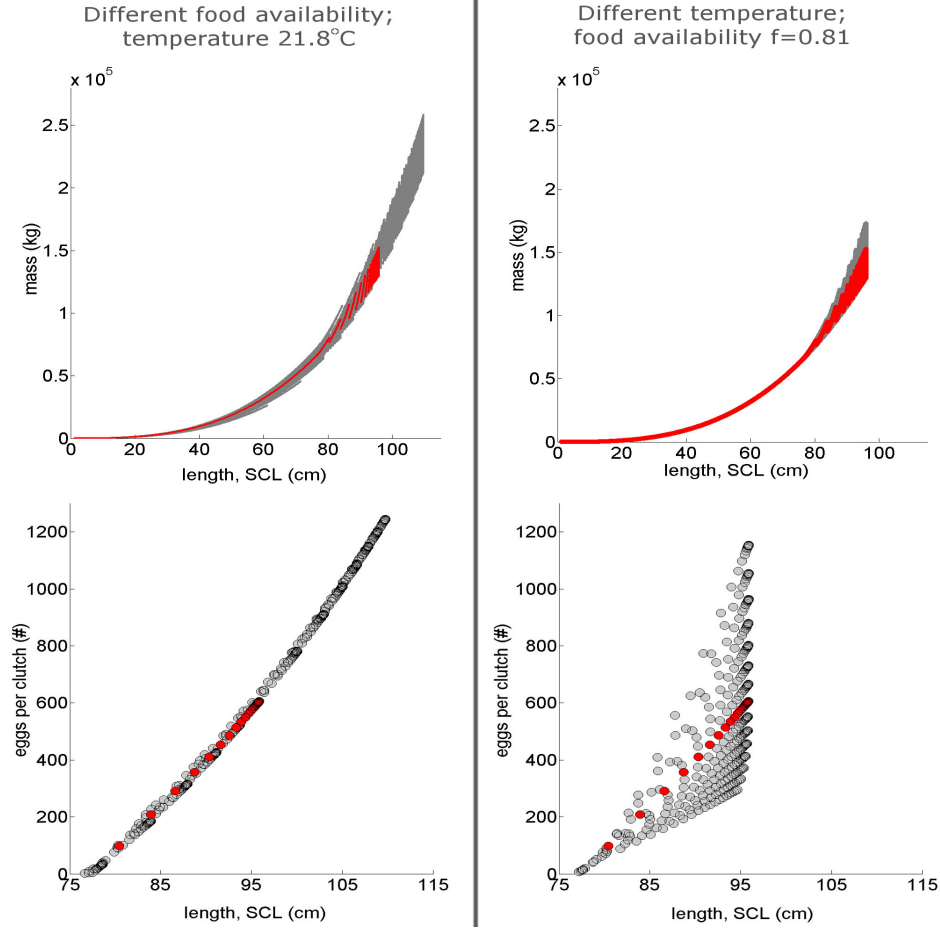


Figure 6: The relationship between carapace length and body mass (top two panels), and carapace length and seasonal (biannual) reproduction output (bottom two panels) as predicted for a subset of environments differing in food availability or temperature. Left panels: Food availability ranging from $0.516 \leq f \leq 0.927$ at $T = T_C = 294.95$ K (21.8°C). Right panels: temperature ranging from 287.15 K (14°C) to 303.15 K (30°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 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

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

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

5. Conclusion

Mechanisms by which environmental factors (food availability and temperature) affect physiological processes are crucial for studying correlations between environmental trends or oscillations and growth rates, reproduction output, or other life history traits of sea turtles (e.g., [26, 29, 31]), as well as for using the conclusions from those studies for conservation activities. We investigated environmental effects on biology (processes and life history traits) of North Atlantic loggerhead turtles using a mechanistic model [35] based on Dynamic Energy Budget (DEB) theory [36]. Our study relies on the model developed by Marn et al. [35], which successfully reproduced the full life cycle and general ecological properties of North Atlantic loggerhead turtles. Marn et al. [35], however, focused on the energy budget of the loggerhead 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 size was the same as when temperature was lower. Higher food availability and higher temperature resulted in a lower age at puberty, and a higher reproduction output (seasonal and cumulative) of individuals. The predictions for the reproduction output differed by two orders of magnitude over the simulated range of food densities, and one order of magnitude over the range of simulated temperatures, suggesting a strong effect of both food availability and temperature on the reproduction output. On a population level, environments with higher food availability might be correlated with a higher reproduction output because individuals can grow to a larger size, and because more energy can be (continuously) invested into reproduction. Warmer environments, by contrast, might result in a higher reproduction output because of the positive effect of higher temperature on physiological rates (earlier onset of reproduction, shorter remigration and inter-nesting intervals, etc). Reduction in food availability adversely impacted all life history traits in the simulations, and food level reductions below 50% of the current (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. This practice may be appropriate when the environment is fluctuating randomly and numbers are large (creating a random error in scaling). However, if the environmental change has a trend (e.g., due to climate change), indiscriminately using scaling could result in misleading conclusions; for example, 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 com-
767 pensation 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].

799 6. Acknowledgments

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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

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

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

Such a favorable agreement between model predictions and data obtained in the field corroborates the hypothesis of the strong causal relationship between the two environmental factors and biological properties of loggerhead turtles, as well as provides additional support to the validity of our mechanistic model and study setup.

Appendix B. Implications for climate change

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

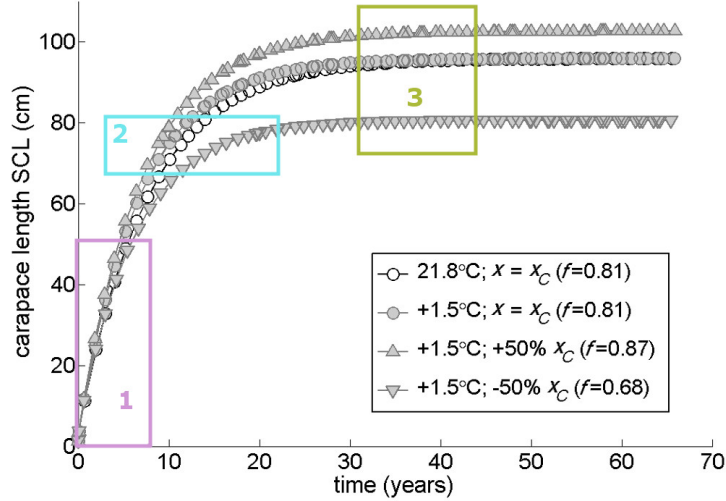


Figure B.7: Simulating possible scenarios resulting from climate change. Environmental factors were assumed to change relative to the current ones: an increase of temperature alone by 1.5°C from 21.8°C (scenario A) and the same temperature increase accompanied with a 50% increase (scenario B) or decrease (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°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°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.

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
1	0.810	12.34	76.77	66.77	95.87	152.34	606	13419
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
21.80	12.34	95.87	152.34	606	13419
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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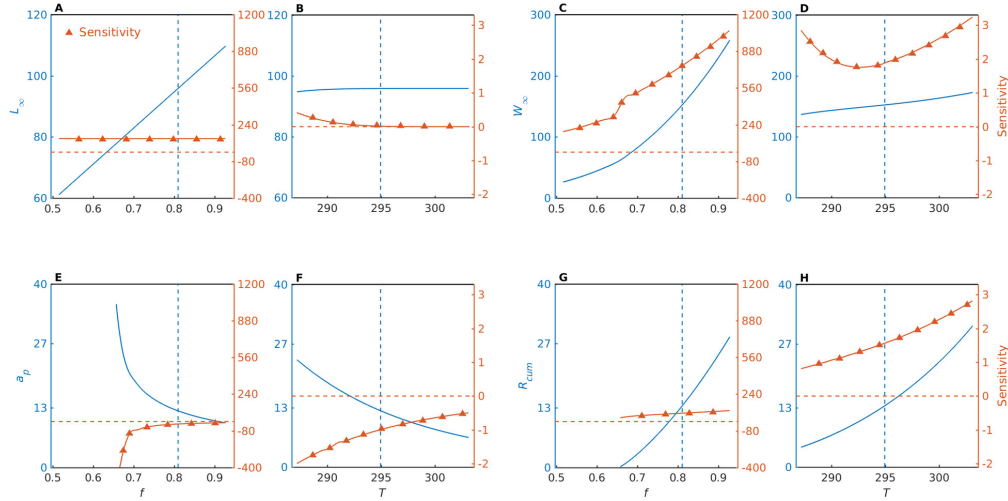


Figure C.8: Sensitivity analysis showing the change of a life history trait given a small change in the forcing variable (f or T). The horizontal dashed line marks zero sensitivity, i.e., where life-history traits are independent of the forcing variable. If sensitivity is a non-zero constant, then life-history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

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