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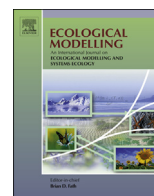
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Environmental effects on growth, reproduction, and life-history traits of loggerhead turtles



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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 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.

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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 (Wallace et al., 2011). 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 (Chaloupka et al., 2008; Hawkes et al., 2009; Robinson et al., 2009; Witt et al., 2010). 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 (Salmon and Scholl, 2014), 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 (Stokes et al., 2006; Braun-McNeill et al., 2008) or between (Mendonça, 1981; Piovano et al., 2011) populations, most often differences in growth rates have been either partially (Mendonça, 1981; Braun-McNeill et al., 2008; Piovano et al., 2011) or mostly (Bjorndal and Bolten, 1988; Bjorndal et al., 2000, 2003,

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2013) 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 (Godley et al., 2007), and/or exhibit fidelity to specific feeding areas (Pajuelo et al., 2012; Pikesley et al., 2015). Growth can be up to 30% faster in a neritic habitat (Snover, 2002 as cited in Peckham et al. (2011)). As neritic habitats are characterized by food of higher energy content and higher temperatures (Peckham et al., 2011), the higher growth rate in a neritic habitat further supports the thesis that food and temperature are the chief determinants of loggerhead turtle growth.

Reproduction is the other individual-based biological process that is extremely important for resilience and survival of a species (Koot, 2001). A direct correlation between growth rates and reproduction output has already been suggested (Iverson, 1992; Bjorndal et al., 2013), but not quantified. Different habitats, characterized by food and temperature, have been linked to drastically different adult sizes and different reproduction patterns, with the environmental factors hypothesized to be the major causes of the variability (Hawkes et al., 2006; Chaloupka et al., 2008; Hatase and Tsukamoto, 2008; Peckham et al., 2011; Vieira et al., 2014). The length of the remigration interval (period between two nesting seasons) has been found to correlate with the average sea surface temperature (SST) (Solow et al., 2002), similarly as the periods between two clutch depositions within a single nesting season (Sato et al., 1998; Hays et al., 2002; Mazaris et al., 2008). Large scale environmental fluctuations, such as the North Atlantic Oscillation and the El Niño Southern Oscillation have also been shown to account for a large part of nesting variability (Saba et al., 2007; Reina et al., 2009; Houtan and Halle, 2011).

Climate change, in addition to strongly affecting nesting and breeding sites (e.g., via changes in sea and sand temperature or in nesting beach areas susceptible to inundation) and potentially changing the spatial distribution of loggerhead turtles (Hawkes et al., 2009; Witt et al., 2010), will also affect temperature and/or food availability in oceanic and coastal feeding sites of loggerhead turtles (Hawkes et al., 2009; NOAA, 2013), thus affecting growth, reproduction, and other biological processes. Effects that global climate change might have on loggerhead turtles have received increased attention in the last decade (e.g., Hawkes et al., 2007b; Chaloupka et al., 2008, see also Hawkes et al., 2009; Witt et al., 2010 for a review). Slow-acting threats such as the climate change are, however, hard to study on a short time scale for which data is available (Keith et al., 2014), especially when trying to understand the balance between beneficial and detrimental effects caused by the same change. For example, higher SST might be beneficial by triggering an earlier nesting season with an increase of hatchling survival (Mazaris et al., 2008) and shorter internesting intervals (Sato et al., 1998), but also detrimental by causing some populations of loggerhead turtles to decline due to changes in resource availability (Chaloupka et al., 2008); understanding the combined effect is much more complicated than understanding each effect alone. The omnivorous loggerhead turtles feeding on various invertebrates are considered more resilient to changes in resource availability compared to specialized species such as leatherback, hawksbill, or herbivorous green turtles (Chaloupka et al., 2008; Hawkes et al., 2009), but a trophic mismatch is possible, especially for oceanic life stages of loggerhead turtles (Hawkes et al., 2009).

Furthermore, mechanisms by which changes in food availability and temperature *independently* affect the biological processes are extremely hard to study empirically for a long lived, large, and widely distributed species such as the loggerhead turtle. Hence, these mechanisms have only partially been explored and remain largely unquantified. Mechanistic deterministic models can generally help, especially with quantifying the consequences of a wide range of environmental conditions and with predicting the biolog-

ical responses of individuals to environmental change (Chaloupka et al., 2008; Keith et al., 2014), but have not been used to investigate effects of environmental factors on loggerhead turtles.

Adopting the hypothesis that food availability and temperature are the two key environmental factors that determine the physiological processes and life history traits of loggerhead turtles, we use a previously constructed and calibrated mechanistic model of the North Atlantic loggerhead turtle (Marn et al., 2017) to decipher the effects of the two environmental factors (food availability and temperature) on biological traits of the loggerhead turtle.

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

2. Methods

Physiological processes of loggerhead turtles were simulated using a mechanistic model based on Dynamic Energy Budget (DEB) theory (Kooijman, 2010) – a metabolic theory successfully applied to almost 700 animals from all major taxa (see the [Add-my-pet-collection](http://www.bio.vu.nl/thb/deb/DEB_papers.pdf)), and used in over 500 publications (see http://www.bio.vu.nl/thb/deb/DEB_papers.pdf for a complete list). Model setup is explained in Section 2.1. The predicted properties were analyzed in the context of currently experienced environmental conditions, and compared to the properties reported in literature. In addition to investigating life history traits, we also analyzed scaling of body mass with carapace length, and scaling of reproduction output with carapace length for a reduced set of environments. Schematic presentation of the study setup can be found in Fig. 1. To reduce variability that could be introduced by differences between populations, only one, the North Atlantic population, was studied (see also Hedges, 2007). Environmental conditions were simulated as a range of deviations from current food availability (estimated from available data Marn et al., 2017) and a range of ecologically realistic average sea surface temperatures from Hawkes et al. (2007a). Exact environmental simulation setup is explained in Section 2.2.

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

Biology of loggerhead turtles was studied by following physiological processes (such as growth, maturation, and reproduction), and life-history traits (growth rates, age and size at puberty, size of fully grown adults – ultimate size, relationships between length and mass, and length and reproduction output). We predicted the processes and the traits at a given food level and temperature using a mechanistic model (Marn et al., 2017) based on a general metabolic theory (Dynamic Energy Budget – DEB theory, see Nisbet et al., 2000, 2012; Kooijman, 2001; Sousa et al., 2008, 2010; Jusup et al., 2017 for in-depth discussion). Relevant DEB-related terms and concepts are briefly presented (following the length-energy framework in Kooijman (2010)) in the next four paragraphs. Detailed description of the standard DEB model for the North Atlantic loggerhead turtle, including the model's parameterization and validation, can be found in Marn et al. (2017).

The North Atlantic loggerhead turtle can be described well by the simplest (standard) form of DEB models (Marn et al., 2017). The standard DEB model recognizes *three life stages* of an individual – embryo (does not feed or reproduce), juvenile (feeds but

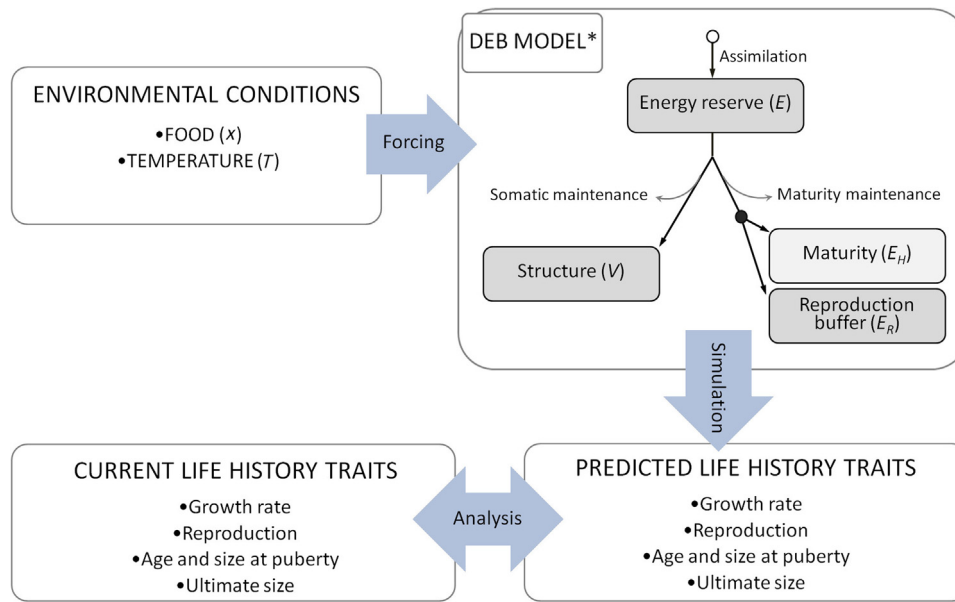


Fig. 1. Schematic presentation of the study setup. Main environmental forcing factors are (scaled) food density (x) and temperature (T) which vary between simulations, but are kept constant throughout each simulation of the turtle's life-cycle. Simulated and analyzed traits included growth rates, reproduction 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 Section 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. (2017). The main parameters of the model from Marn et al. (2017) are listed in Table 1.

does not reproduce), and adult (feeds and reproduces). Transitions (birth and puberty, respectively) between life stages occur when the amount of energy, measured in Joules, cumulatively invested into increase in complexity (maturation), reaches a certain threshold. The variable tracking the investment is called maturity, and its thresholds – maturity at birth and maturity at puberty – are expressed in Joules (J). Within the DEB-framework, an individual (turtle) is defined by *three state variables* that change with time: In addition to 'maturity' (symbol E_H , unit J), the standard DEB model tracks 'structure' (symbol V , unit cm^3) and 'energy reserve' (symbol E , unit J) (Fig. 1). When food is abundant, all three state variables increase with time until puberty, after which maturation ceases and the energy is directed into reproduction. The energy committed to reproduction is tracked by an auxiliary state variable, 'reproduction buffer' (symbol E_R , unit J); the energy accumulated in the buffer is utilized for egg production prior to nesting. To calculate the reproduction output, we assumed that nesting occurs every two years (Tiwari and Bjorndal, 2000) if there is enough energy stored in the reproduction buffer to produce at least one egg (210 kJ; Hays and Speakman, 1991).

Structure, energy reserve (and the reproduction buffer in the adult stage) contribute to the biomass of a turtle. Structure and energy reserve were converted to length and mass of the individual using standard auxiliary equations (Kooijman, 2010; Marn et al., 2017). Age at puberty corresponds to the age at which the 'maturity at puberty' threshold is reached (Kooijman, 2010), which is earlier than the actual first reproductive event.

Processes and parameters. Energy reserve in DEB models serves as a buffer between the individual and the environment during short-term environmental fluctuations. Adults and juveniles assimilate energy from the environment into the reserves, from which energy can be utilized for maintenance, growth, maturation, and reproduction even during food shortages. Energy utilization and allocation among processes will depend on parameter values (see Lika et al., 2011 for an example of parameterization). The main parameters of the model, estimated for the loggerhead turtle by Marn et al. (2017) are listed in Table 1.

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 Marn et al. (2017). Rate parameters are listed at the reference temperature $T_{ref} = 273$ 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	$\{\hat{p}_{Am}\}$	906.1	$\text{J d}^{-1} \text{cm}^{-2}$
Digestion efficiency (of food to reserve)	κ_X	0.8	–
Energy conductance	\dot{i}	0.0708	cm d^{-1}
Allocation fraction to soma	κ	0.6481	–
Reproduction efficiency	κ_R	0.95	–
Somatic maintenance	$[\hat{p}_M]$	13.25	$\text{J d}^{-1} \text{cm}^{-3}$
Maturity maintenance rate coefficient	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, $\{\hat{f}_m\} = 6.51 \text{d}^{-1} \text{cm}^{-2}$; Defecation efficiency (of food to feces), $\kappa_F = 0.1$; Reproduction efficiency, $\kappa_R = 0.95$; Maturity maintenance rate coefficient, $k_j = 0.002 \text{d}^{-1}$; Weibull aging acceleration, $h_a = 1.85e-010 \text{d}^{-2}$; Gompertz stress coefficient, $s_G = 0.0001$.

DEB theory relies on a κ -rule (Kooijman, 2010; Jager et al., 2013; Nisbet et al., 2016), which guarantees that maturation and growth do not compete. Structure and maturity both require maintenance (named somatic and maturity maintenance, respectively). Somatic maintenance has absolute priority: energy investment into growth, maturation, and reproduction is possible only after maintenance has been paid. Note that energy reserve and the reproduction buffer do not require maintenance in DEB models.

Assimilation of energy from the environment into the turtle, i.e., the amount of energy per unit of time that will be transformed into

energy reserve (Kooijman, 2010) is determined by the assimilation flux, \dot{p}_A :

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

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

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

Quantity f is a saturating function of food density which has a minimal value of zero when no food is available, and a maximal value of 1 when food is abundant. The scaled functional response can also be defined as a fraction of the maximum feeding rate of an individual of the given size (Kooijman, 2010; Jusup et al., 2014), depending not only on the environment but also on the physiology of an individual. Scaled functional response for North Atlantic loggerhead turtles, marked hereafter as f_C , was estimated as $f_C = 0.81$ (Marn et al., 2017); the corresponding x_C can then be back-calculated using Eq. (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 Kooijman (2015)); food of better quality would result in a higher assimilation flow (see Eq. (1)). The effect on the assimilation would, however, be difficult to differentiate from the effect of changes in food density (Eq. (1)) because both effects act to reduce assimilation flux, i.e., reduce f . In other words, predictions for an environment with lower food quality would be qualitatively indistinguishable to predictions for an environment with lower food quantity presented herein.

The other environmental factor that will strongly influence the energy budget and biology of ectothermic organisms such as sea turtles is temperature. DEB theory argues that changes in temperature equally affect all metabolic rates (see Section 1.2 in Kooijman (2010)). Because the body temperature of juvenile, sub-adult and moderately active adult chelonid turtles corresponds to the surrounding water temperature (Read et al., 1996) (as would be expected for an ectotherm), we used the sea surface temperature as a proxy for body temperature. The average temperature experienced by the loggerhead turtles was set to 21.8 °C (Hawkes et al., 2007b, 2011) ($T_C = 294.95$ K). All rates and parameters of DEB models are generally expressed at a reference temperature of 20 °C ($T_{ref} = 293.15$ K) (Kooijman, 2010); for consistency, we adhere to the principle. Correction for the effect of temperature is done using the Arrhenius equation (from Eq. (1.2) in Kooijman (2010)):

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

where $C(T)$ is the correction factor for a certain temperature T , and T_A is the Arrhenius temperature equal to 7000 K for loggerhead turtles (Marn et al., 2017). For example, the assimilation flux (Eq. (1)) at temperature T is: $\dot{p}_A(T) = \dot{p}_A(T_{ref}) \times C(T)$.

2.2. Simulating the environment

Simulations were performed over a 31×31 grid of different environmental conditions using 15 equidistant values higher and 15 equidistant values lower than the current values for scaled food density (x_C) and temperature (T_C). In total, 961 environments were

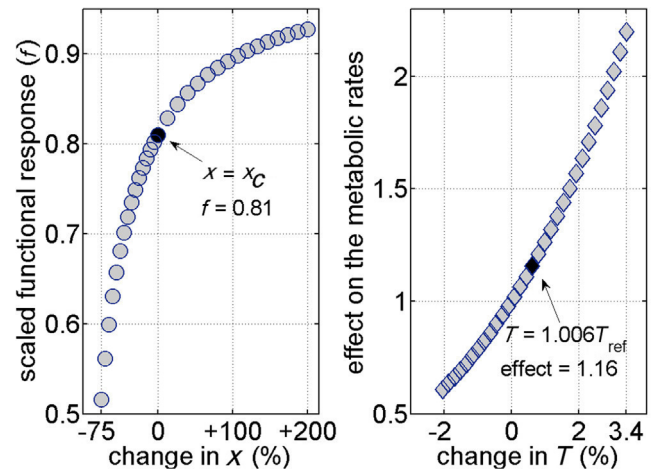


Fig. 2. Simulated environmental factors: scaled food density (x , left panel) and temperature (T , right panel) on the x -axes, plotted with the corresponding scaled functional response (f , Eq. (2)) and the effect on metabolic rates (Eq. (3)) on the y -axes (see Section 2.1 for details). Scaled food 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 ($T_{ref} = 293.15$ K = 20 °C) – the temperature at which all DEB rate parameters are generally given (Kooijman, 2010). 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.

thus simulated as possible combinations of food density and temperature. During each simulation, which lasted a turtle's lifetime of 65 years, the environment was assumed to be constant.

Values for scaled food density (x) ranged from a decrease of 75% to an increase of 200% relative to the current scaled food density ($0.25x_C$ to $3x_C$). Eq. (2) was employed to turn each simulated food density into the scaled functional response (f) (Fig. 2, left panel), which was then used as a proxy for food availability. Explored scaled food densities ranged from those resulting in a very high scaled functional response ($f > 0.9$) to those identified in the preliminary analysis as unable to sustain reproduction ($f \leq 0.6$). We assumed that values outside this range are rarely (if ever) present in nature: scaled functional responses close to the maximum are reached only at extremely high food densities (for example, $f = 0.999$ for loggerhead turtles is reached at a scaled food density 22 times higher than the currently estimated density, x_C), and values lower than the simulated ones would imply extinction due to lack of reproduction.

Values for temperature ranged from 287.15 K to 303.15 K (14 °C to 30 °C; Hawkes et al., 2007a, 2011). Metabolic rates were corrected for each simulated temperature using Eq. (3) (Fig. 2, right panel). The loggerhead turtles in the North Atlantic rarely experience sea temperatures outside this range, even during winter (Hawkes et al., 2007a), with adults being more efficient than juveniles in keeping their body temperature close to optimal values (Hochscheid et al., 2007; Hawkes et al., 2011).

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

Each environment was simulated for a duration of 65 years, corresponding to the age of the oldest recorded loggerhead turtle (Georgia Sea Turtle Centre). Simulations presented here therefore implicitly assume that loggerhead turtles keep their food intake and body temperature relatively stable through out their life. This simplification is justified in the sense that the turtles (i) modulate food intake by adapting searching activities to satisfy their energy needs and (ii) stabilize experienced temperature by following thermoclines (Hawkes et al., 2011; Scales et al., 2015). Habitat shifts during a life-time (such as those from a pelagic to a neritic environment; Bolten and Witherington, 2003) are therefore not explicitly modeled. Although beyond the scope of this study, the model in principle allows exploring changes in the average conditions at some point in the life cycle. All simulations were performed in Matlab R2011b. Modified “EVHR” scripts by L. Pecquerie¹ were used with permission.

3. Results

3.1. Selected life-history traits

The patterns that emerge while predicting the selected life-history traits (age and length at puberty, length and mass of fully grown adults, and seasonal and cumulative reproduction output of fully grown adults) in the simulated 31×31 environmental grid of food density and temperature reveal which of the two environmental characteristics (food availability or temperature) has the predominant effect on a specific life-history trait (Fig. 3). For example, values for a trait predominantly affected by food availability (plotted on the x-axis) will vary from left to right, but remain constant from top to bottom. Analogously, if trait values vary from top to bottom, but not from left to right, temperature (plotted on the y-axis) has the predominant effect on the trait. A diagonal pattern suggests that the trait is simultaneously affected by both environmental conditions.

Food availability strongly affects length of a fully grown adult (ultimate length), which varied between 61 and 110 cm straight carapace length (SCL) for the set of simulated environments (Figs. 3A and 4A). Temperature, by contrast, does not affect the ultimate length an individual can reach (Sousa et al., 2008; Kooijman, 2010; Jusup et al., 2017, see also Figs. 4A and 5, top left panel). However, because growth is slower at lower temperature (Fig. 5, top left panel), an individual might die before reaching its ultimate length. This is mirrored in our results: the duration of simulations corresponds to the maximum life span, so the realized ultimate length is smaller at lower temperatures.

Length at puberty generally exhibits limited variation with food availability: predicted values range from 76.6 cm SCL to 77.2 cm SCL, and are not affected by temperature (Tables C.1 and C.2 in Appendix C). A similar effect of food availability (but not temperature) on mass at puberty is observed, with a relatively narrow range of predicted values (Tables C.1 and C.2 in Appendix C).

A predominant effect of food availability, but also a relatively strong effect of temperature, are predicted for mass of fully grown adults (ultimate mass) (Figs. 3B, 4C and D). Predictions for ultimate body mass in the environments differing in food availability have a wider range than those for the environments differing in temperature (compare Table C.1, column 7 and Table C.2, column 4 in Appendix C). This was expected because food availability affects the maximal reachable ultimate length (and body mass scales approximately with length cubed; Wabnitz and Pauly, 2008), whereas the temperature generally does not affect the ultimate length (but can

slow down growth, see above). To explain why temperature, somewhat counter-intuitively, has a relatively large effect 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 (Fig. 3C–E, see also Fig. 4E–H). Predictions for age at puberty range from 5.5 years to >60 years (Fig. 3C). 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 years; Table C.1, 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 years; Table C.2, 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.1 and C.2 in Appendix C, respectively, see also Fig. 4G and H). The reproduction buffer can be a substantial part of adult sea turtle's body mass (Iverson, 1992), but it is unlikely that it would reach the 43 kg predicted for warm environments with high food availability. Rather than accumulating such a large reproductive buffer, the turtle is more likely to reproduce annually if conditions are so favorable.

3.2. Growth and reproduction rates

Predicted growth curves in Fig. 5 (top two panels) show faster growth at higher food availability and temperature with one notable difference: increased food availability positively affects the size of fully grown adults (Fig. 5, top left panel), whereas the temperature does not. At lower temperatures, however, it takes more time to become a fully grown individual (Fig. 5, top right panel).

Predicted reproductive output increases with both food availability and temperature (Fig. 5, bottom two panels, see also Fig. 4G and H), with the range of the predicted values larger in the subset of environments differing in food availability (Fig. 5, bottom left panel). Interestingly, the model predicts a very similar seasonal reproduction output for lower temperature and higher food availability as it does for higher temperature and lower food availability, highlighting a synergistic effect of the two environmental factors on reproduction. For example, a fully grown adult turtle has an almost identical reproduction output in an environment characterized by temperature of 21.8 °C and food availability $f \approx 0.87$, as it

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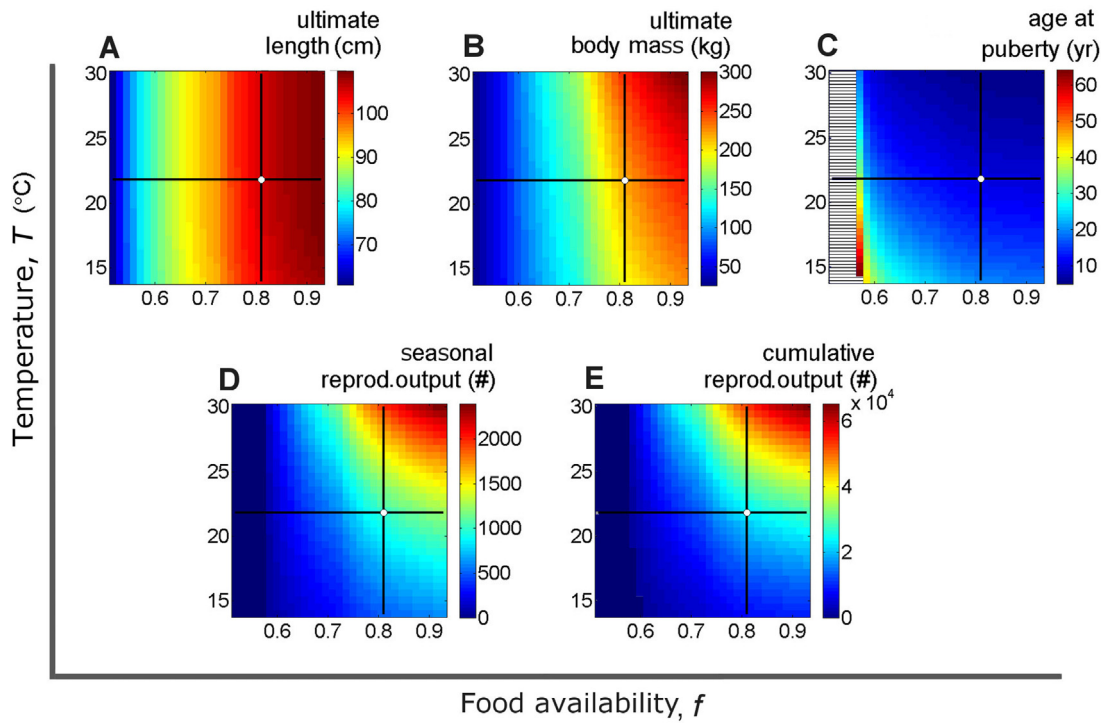


Fig. 3. The effects of the environment on the selected life history traits of North Atlantic loggerhead turtles. Food availability (scaled functional response, f) is on the x-axis and temperature (T , denoted in $^{\circ}\text{C}$) is on the y-axis. Values of the traits are represented by colors; see 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 the 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 (Hawkes et al., 2007a, 2011; Marn et al., 2017). (Simulation setup explained in Section 2.2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

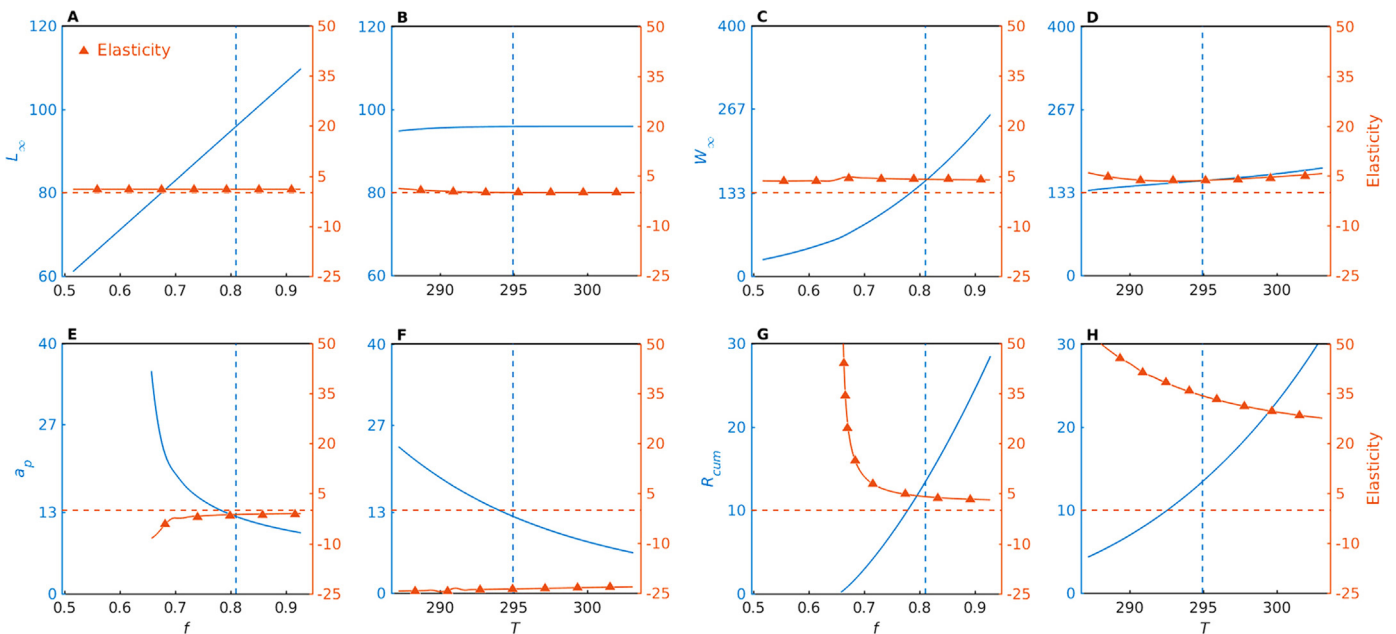


Fig. 4. Elasticity analysis, showing the relative change of a life history trait (on the left y-axis), if the forcing variable (on the x-axis) changes by 1%. The horizontal dashed line marks elasticity equal to zero, which means that the life-history trait is independent of the forcing variable. If elasticity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

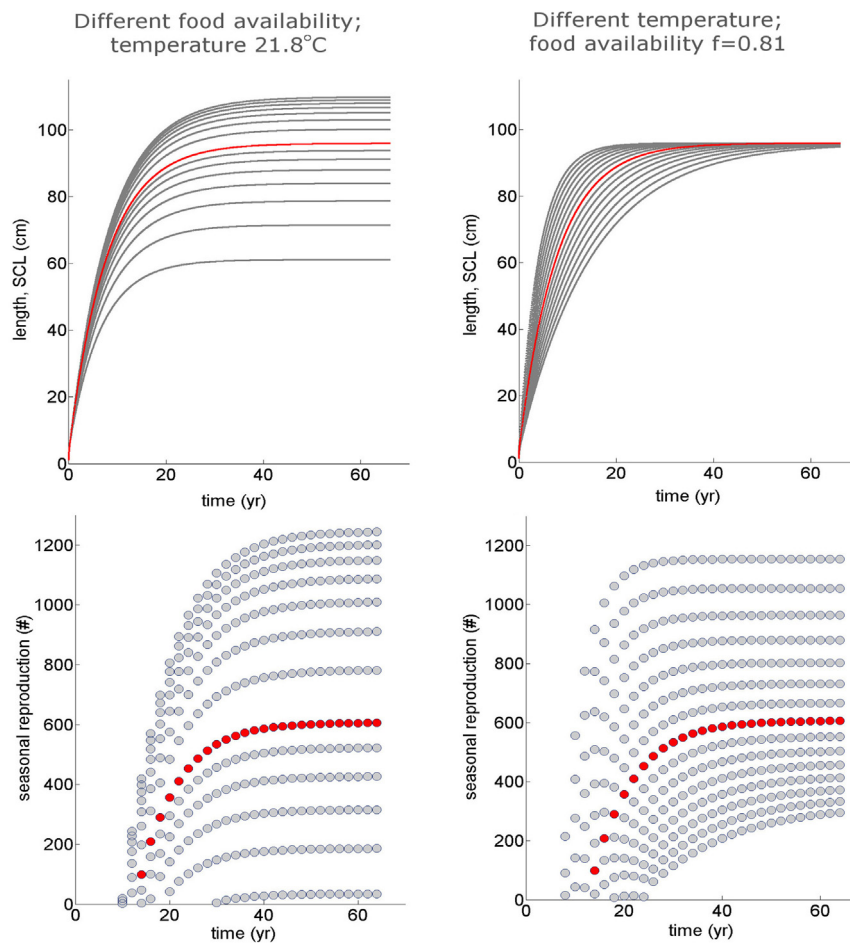


Fig. 5. Growth curves (top two panels) and biannual reproduction curves (bottom two panels) predicted for a subset of environments differing in food availability or temperature. Left panels: food availability ranging from $0.516 \leq f \leq 0.927$ at $T = T_C = 294.95 \text{ K}$ (21.8°C). Right panels: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

does in an environment with temperature of 30°C and food availability $f = 0.81$. Similarly, a fully grown adult turtle experiencing a temperature of 21.8°C and food availability $f \approx 0.7$, has an almost identical reproduction output as if experiencing a temperature of 14°C and food availability $f = 0.81$.

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

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

The seasonal biannual reproduction output and carapace length scale linearly in all simulated environments, but with markedly different patterns depending on whether food availability or temperature differ between the simulations (Fig. 6, bottom two panels).

When environments differ in food availability, the seasonal reproduction is seemingly completely positively related to the carapace length (Fig. 6 bottom left panel), suggesting that individuals of the same length will have the same seasonal reproduction output regardless of the experienced food availability. By contrast, when environments differ in temperature, individuals of a given carapace length produce more eggs in environments with higher temperatures (Fig. 6, bottom right panel). This implies that, when food is abundant, the available time (duration of the nesting season, duration of the inter-nesting period, etc.) becomes the limiting factor.

4. Discussion

Processes (growth, maturation, and reproduction), as well as life history traits (ultimate size, age and size at puberty, and the reproduction output), are affected by both the environment (temperature and food availability), and the individual characteristics (physiology of a loggerhead turtle). The DEB model helps disentangle the effects of the two causes of variability by conceptually separating the effects of physiology (represented by DEB model parameter values) from the effects of the environment (food availability and temperature). By fixing the physiology, and only varying environmental conditions, our results demonstrate the extent to which two environmental factors (food availability and tempera-

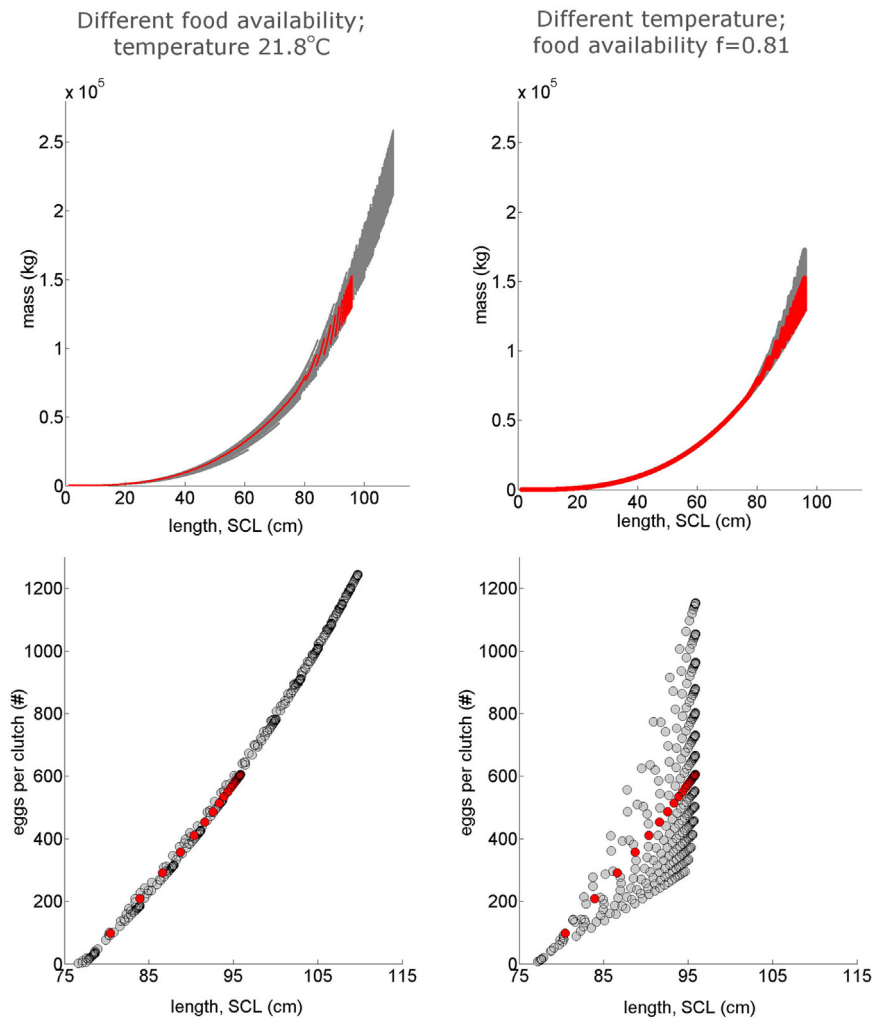


Fig. 6. The relationship between carapace length and body mass (top two panels), and carapace length and seasonal (biannual) reproduction output (bottom two panels) as predicted for a subset of environments differing in food availability or temperature. Left panels: food availability ranging from $0.516 \leq f \leq 0.927$ at $T = T_C = 294.95 \text{ K}$ (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.

ture) can affect the processes and the life history traits. Below, we put the results into the context of existing knowledge and data.

4.1. The non-linear relationship between the two studied environmental factors and the physiology of loggerhead turtles

Defining the relationships between environmental factors and the resulting life-history traits (Section 2.1) was the baseline for predicting the effects of the environmental conditions on the observable biological quantities. Ranges of the simulated temperature and food availability, albeit somewhat arbitrarily chosen, are realistic: the simulated temperature range has been reported for North Atlantic loggerhead turtles (Hawkes et al., 2007a), and the simulated food density ranges from values at which reproduction is impossible (implying extinction), and values giving functional response very close to the maximal. The non-linear relationships for the dependence of the scaled functional response on (scaled) environmental food density (a proxy for food availability, Eq. (2)), and of the metabolic rates on temperatures (Eq. (3)) were taken from the thoroughly tested DEB theory (Kooijman, 2010; Jusup et al., 2017).

The current food availability was estimated to be relatively high ($f_C = 0.81$; Marn et al., 2017), and, because food availability is a saturating function of scaled food density (Eq. (2), Fig. 2, left panel),

reducing scaled food density has a much stronger effect on the predicted traits than increasing it by the same relative amount. If food availability is low to begin with, even a small further reduction of food density results in a large decrease in the scaled functional response (Fig. 2), and a strong negative effect on the biological traits. The consequences of reduced food availability in areas where food availability is relatively low (e.g., in the Mediterranean Sea and oceanic habitats; Zenetos et al., 2002; Peckham et al., 2011) may, therefore, be more dramatic than in areas with high food availability.

The exponential relationship between temperature and physiological rates (Eq. (3)) results in a relatively large effect of a small temperature change on metabolic rates: for the range of simulated temperatures, the rates were suggested to be as much as 40% smaller and up to 120% greater than the rates at the reference temperature of $293.15 \text{ K} = 20^\circ \text{C}$ (Fig. 2, right panel). Although the change may seem drastic, it is still realistic. If we assume loggerhead turtles experience a temperature of around 20°C in the oceanic habitat (Peckham et al., 2011), and then move to a neritic habitat characterized by 24°C (Peckham et al., 2011), the model predicts an increase in metabolic rates by almost 40%. This prediction is consistent with the noted “up to 30% faster growth” in a

neritic habitat reported by Snover (2002) (as cited in Peckham et al. (2011)).

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

Growth rates generally differ between life stages and between populations (genetic stocks) of loggerhead turtles (Mendonça, 1981; Piovano et al., 2011; Bjorndal et al., 2013). However, similar growth rates were also reported between individuals belonging to different populations and/or life stages (Bjorndal and Bolten, 1988; Bjorndal et al., 2003, 2013) suggesting a strong influence of extrinsic (e.g., environmental) factors. Growth estimates derived from capture-mark-recapture data (e.g., Mendonça, 1981; Bjorndal and Bolten, 1988; Casale et al., 2009), growth marks on the bones (e.g., Snover et al., 2007; Braun-McNeill et al., 2008; Casale et al., 2011a), or length frequency analyses (e.g., Bjorndal et al., 2000; Casale et al., 2011b) should therefore be interpreted in the context of the environmental data, with possibly special emphasis on the conditions present during the initial part of the development (Madsen and Shine, 2000; Metcalfe and Monaghan, 2001; Stokes et al., 2006). The intertwining effect of food availability and temperature on growth curves (and thus growth rates) of identical individuals reproduced by the model (Fig. 5, top two panels) highlights why a direct comparison of growth data could be misleading.

Different environmental conditions may result in practically indistinguishable growth rates. For example, in warmer environments with low food availability growth rates of sea turtles might decrease between 50 cm and 60 cm straight carapace length (SCL) (this study) because individuals approach ultimate size (von Bertalanffy, 1950; Mendonça, 1981; Bjorndal et al., 2013). In an environment with high food availability but low temperature, our results show that growth rates might decrease around the said size range due to a decrease in temperature. The inter-dependency of growth and environmental conditions can be reconstructed with the help of a DEB model (Pecquerie et al., 2012; Jusup et al., 2014) by combining, e.g., the environmental data, our mechanistic model for loggerhead turtles, and skeletochronology.

The model can be (partially) validated by calculating the growth rates plotted in Fig. 5, and comparing them with literature. For example, the model predicts that growth from 25 cm to 75 cm SCL requires between 7 and 19 years (when food availability is varied at temperature of 21.8°C), and between 5 and 18 years (when temperature is varied at $f=0.81$). The low ends of the predicted ranges correspond to environments characterized by warm temperatures and high food availability; an example of such an environment could be the Southern Bahamas, where extremely fast growth was observed. Two loggerhead turtles needed just 3 to 4 years to grow from 25 cm to 75 cm SCL (Bjorndal and Bolten, 1988).

The average prediction in simulated environmental subsets is around 10 years to grow from 25 cm to 75 cm SCL. This is consistent with the observed time needed for the Florida population, for which estimates indicate 10 (von Bertalanffy model) to 16 years (logistic model) are needed to achieve the same growth (Frazer and Ehrhart (1988) in Bjorndal and Bolten (1988)). Available information for a different size span (growth from 50 cm to 75 cm SCL) is also in agreement with our results: Mendonça (1981) calculated that Florida loggerheads need 5 years to grow from 50 cm to 75 cm SCL, whereas the average time predicted by the model for the simulated subset of the environments is around 6.5 years (between 3 and 12 years for varying food, and between 4 and 14 for varying temperature). A more elaborate report on the predicted growth rates (in cm year^{-1}) in the context of literature values can be found in Appendix A.

A direct comparison of the reproduction output predicted by the model and the values reported in literature is complicated by the

many uncertainties that plague *in situ* observations of the total seasonal reproduction output (and thus also the cumulative reproductive output) of an individual female (Hays and Speakman, 1991; Tiwari and Bjorndal, 2000; Tucker, 2010). Examples where annual reproduction output is reported or calculated are rare, but available information corroborates our results: we predict that mass of the reproduction buffer (when reproduction is biannual) is between 2% and 25% of the ultimate mass, which is consistent with approximately 10% of the total body mass reported for annual clutch mass of marine, freshwater, and terrestrial turtles (Iverson, 1992).

Seasonal and cumulative reproduction output of individuals in our study was positively affected by both food availability and temperature. The range of predictions was larger when environments differed in food availability than in temperature (Sections 3.1 and 3.2). The results therefore imply that sea turtles in warmer and energy richer neritic environments (Peckham et al., 2011) will have a larger reproduction output than those in an oceanic environment, but also that the simulated range of food availability has a stronger influence on the reproduction output than the simulated range of temperature. The reproduction output has indeed been linked to the type of habitat (oceanic vs neritic) (Hatase and Tsukamoto, 2008), with the dichotomy between smaller adult females having a smaller reproduction output and larger adult females having a larger reproduction output explained primarily by energy available for reproduction (Hatase and Tsukamoto, 2008).

While the link between food (energy) availability and reproduction output is straightforward, the link between temperature and reproduction reported in the literature is somewhat ambiguous: Chaloupka et al. (2008) hypothesized that loggerhead turtles with a higher reproduction output experienced environments with a higher food abundance and lower temperature than the loggerheads with a lower reproduction output, suggesting that the effect of temperature on reproduction output, if present at all, is minor. Furthermore, no correlation was found between temperature at the breeding sites and reproductive output (number of clutches per nesting season) (Mazaris et al., 2008), but the correlation was found between reproductive output and temperature at feeding sites (Mazaris et al., 2009). Loggerhead turtles spend just a fraction of their time at breeding sites where they do not feed. During this period the processes related to egg production (such as vitellogenesis) take place (Limpus, 1990; Blanvillain et al., 2011).

The apparent conflict can, however, easily be resolved by following the reasoning used for the model construction. The assumption made in our model was that the energy is assimilated from the environment and invested into the reproduction buffer continuously throughout the year (Kooijman, 2010), i.e., we do not differentiate between fractions of time at feeding and breeding sites. Higher energy investment into the reproduction buffer (and thus production of more eggs) predicted by the model can be a result of two distinct factors: (i) higher food abundance in the environment (more energy available for assimilation), and (ii) warmer environment (faster assimilation of energy and production of eggs). Areas of higher temperature could be combined with higher food quality (Peckham et al., 2011; Bjorndal et al., 2013), but do not need to in order to correlate with a higher reproduction output (more eggs per turtle) – such areas could affect metabolic rates just via temperature (Eq. (3), Table C.2). Either scenario would result in more energy being continuously invested into the reproduction buffer, thus increasing the reproductive output. In the context of continuous investment into reproduction, the predicted positive correlation of temperature and the reproduction output complies with the “capital breeders” hypothesis, where temperature at breeding sites may affect the timing of breeding events, but not the total energy committed to breeding (Hawkes et al., 2007b).

Furthermore, our results imply that increasing either temperature or food availability, in addition to increasing the reproduction

output, increases the growth rate and decreases age at puberty, i.e., increases the maturation rate (Figs. 3–6). This link has already been hypothesized by Iverson (1992), who noted that maturation rates and annual reproduction output could be directly linked to growth rates, i.e., the rate of energy acquisition.

Predictions for maturation rates, i.e., the time required to reach puberty varied greatly between simulated environments: predicted values were between 10 years and 15 years for most of the simulated range, but also values as small as 5.5 years were predicted for environments with high food availability and high temperature, and values larger than 40 years were predicted for environments with low food availability and low temperature (Fig. 3C). Mendonça (1981) estimated that loggerhead turtles needed between 10 and 15 years to reach puberty, but also noted that loggerhead turtles reared in captivity need 6–8 years, and loggerhead turtles in the Pacific 25–30 years to reach puberty (Refs. in Mendonça (1981)). Wild loggerhead turtles in the North Atlantic might need as long as 19 years to >35 years to mature (Snover, 2002; Braun-McNeill et al., 2008; Scott et al., 2012). It is reasonable to assume that captive-reared loggerhead turtles experience a higher average temperature and/or fewer exposures to low temperatures, as well as a higher food availability compared to those in the wild, making model predictions in excellent agreement with observed data.

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

The analyzed relationship of carapace length and body mass exhibited less variation across the simulated environments compared to the relationship of carapace length and seasonal reproduction output (Fig. 6). Limited variation in scaling of body mass with carapace length is in agreement with the empirical finding that a single curve explains the whole size range, with a high measure of goodness of fit even when data from more populations are pooled into analysis ($R^2 = 0.97$; Wabnitz and Pauly, 2008).

Scaling of seasonal reproduction output with carapace length should be interpreted with the assumption about biannual nesting in mind (Section 2, see also Section 4.4), but is nonetheless informative when analyzing the commonly reported relationship of carapace length and clutch size (e.g., Hays and Speakman, 1991; Tiwari and Bjorndal, 2000; Broderick et al., 2003). For example, our results imply that individuals of the same size will have a similar seasonal reproduction output regardless of the experienced food availability (Fig. 6, bottom left panel), suggesting a positive correlation between carapace length and clutch size. However, the reproduction output of an individual of a certain length strongly varies with temperature (Fig. 6, bottom right panel), suggesting that the positive correlation between carapace length and clutch size should have a large scatter. Since loggerhead turtles experience variable environmental factors, we expect to observe a positive correlation between carapace length and clutch size, with a large scatter or low goodness of fit measure; indeed, this is true: $R^2 = 0.30$ (Hays and Speakman, 1991), $R^2 = 0.29$ (Broderick et al., 2003), see also Fig. 1 in Tiwari and Bjorndal (2000).

Patterns in the scaling relationships also suggest two distinct mechanisms through which a warmer environment with more available food can result in a higher reproduction output: (i) higher food availability enables individuals to grow to a larger size, and larger size has a strong correlation to the seasonal and cumulative reproductive output; (ii) warmer temperature affects all metabolic rates (including food assimilation, energy mobilization, and chemical transformations; Kooijman, 2010), many of which are involved in production of eggs (Limpus, 1990; Deem et al., 2009). This is consistent with the empirical finding that a higher temperature at breeding sites correlates with the shorter period between two clutch depositions within a single nesting season (Sato et al.,

1998; Hays et al., 2002; Mazaris et al., 2008), probably by increasing the rate of processes related to vitellogenesis (Limpus, 1990). Hence, two individuals experiencing the same food availability, but exposed to different temperatures during the year, will have a different reproductive output: the individual that experienced higher temperature will have a higher reproductive output due to both having accumulated more energy for reproduction, and a faster vitellogenesis. This result implies that, at high energy accumulation rates (feeding in warm environments with abundant food), temperature at breeding sites may become the limiting factor in reproduction: higher temperature will result in a shorter period between two nest depositions within a nesting season, whereas lower temperature will require a longer nesting season.

4.4. Model considerations

We assumed a constant environment (characterized by constant food availability and temperature) for our simulations. Loggerhead turtles certainly do not experience the same environmental conditions during their entire life cycle, but the annual averages should not differ too much between the years. In the context of the simulation, the seasonal variation should mostly cancel out (months at higher-than-average temperature roughly canceling out months at lower-than-average temperature). The model in principle allows exploring fluctuations in the conditions, but the previous explorations of DEB models show that results for life history traits such as length and mass of fully grown adults would show the same patterns, and the growth and reproduction curves would include more fluctuations but would show the same general trend (Kooijman, 2010). Including changes in the average conditions at some point in the life cycle, e.g., to mirror the ontogenetic habitat shift (Bolten and Witherington, 2003) could make an informative extension of the standard model.

We assumed biannual reproduction and did not transform the predicted seasonal reproduction output into number of clutches (nests). In the field, most often a clutch size is used as a measure of the reproduction output of females (Tiwari and Bjorndal, 2000; Broderick et al., 2003), or nest counts in a nesting season are used for assessing the reproduction (nesting) activity of a specific population (e.g., Houtan and Halle, 2011). Transforming the seasonal biannual reproductive output (predicted by the model) to the number of nests per nesting season or number of eggs per clutch is complicated by the trade-off between the number of clutches (nests) per season, eggs per clutch, internesting intervals, and remigration intervals (Hays and Speakman, 1991; Iverson, 1992; Tiwari and Bjorndal, 2000). Generally, loggerhead turtles that are not first-time nesters have a modal value of 4–5 nests per nesting season (Tiwari and Bjorndal, 2000; Hawkes et al., 2005; Tucker, 2010), and nests with fewer than 50 eggs or more than 200 eggs are rarely observed in nature (Hays and Speakman, 1991; Margaritoulis et al., 2003; Miller et al., 2003), so a seasonal reproduction output of around 100 eggs (for first time nesters) up to around 1000 eggs would be realistic. By forcing the reproduction to occur every two years if there is enough energy in the reproduction buffer even for a single egg, and not limiting the number of eggs per season (see Section 2), unrealistically small and large seasonal reproduction outputs were predicted (Fig. 3D; Tables C.1 and C.2 in Appendix C). It is more likely that those loggerhead turtles with more energy available will have shorter remigration intervals (i.e., reproduce every year), whereas those with less energy available will have longer remigration intervals (i.e., reproduce three or more years apart) (Hatase and Tsukamoto, 2008). The reproduction output could be constrained by a minimal and a maximal seasonal outputs, and the remigration intervals allowed to correlate with temperature (Solow et al., 2002). It is likely that remigration intervals with a modal value of 2–3 years, yet ranging from 1 to 7 years (Broderick et al.,

2003) could be reproduced in such a way, and more realistic seasonal reproduction output values could be obtained. Nevertheless, we decided to implement a remigration interval of 2 years (Tiwari and Bjorndal, 2000). Even though this simplification occasionally resulted in predictions for a seasonal reproduction output smaller 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 (Hawkes et al., 2007b, 2009; Witt et al., 2010), so the research has been focused on distribution, temperature-dependent sex determination, and/or nesting activity (e.g., Chaloupka et al., 2008; Hawkes et al., 2009; Witt et al., 2010). 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., Sato et al., 1998; Saba et al., 2007; Houtan and Halle, 2011), 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 (Marn et al., 2017) based on Dynamic Energy Budget (DEB) theory (Kooijman, 2010). Our study relies on the model developed by Marn et al. (2017), which successfully reproduced the full life cycle and general ecological properties of North Atlantic loggerhead turtles. Marn et al. (2017), however, focused on the energy budget of the loggerhead turtles and the implied physiological properties such as the ability to cope with periods of starvation, giving a secondary role to the environment.

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

The DEB framework allowed us to map food density and temperature in the environment onto the energy budget of a loggerhead

turtle (Section 2.1) in a thermodynamically consistent and an empirically validated manner (Jusup et al., 2017). Relationships that play a critical role in the present analyses are (i) the saturating dependence of the scaled functional response (food availability, or food intake) of loggerhead turtles on food density and (ii) the exponential dependence of physiological rates on temperature.

Even though our predictions are based on the assumption that all loggerhead turtles have the same DEB parameters and only differ in state variables, the predictions successfully reproduced many patterns observed in nature (Sections 4.2 and 4.3). For example, we predict that the scaling of body mass with carapace length will have limited scatter, while the reproductive output will exhibit a large degree of scatter, a pattern observed in nature (Hays and Speakman, 1991; Tiwari and Bjorndal, 2000; Wabnitz and Pauly, 2008; Broderick et al., 2003). If, however, inter-individual variability were markedly higher in real life, we would expect a high degree of scatter in body mass vs. length as well. Therefore, the assumption that individuals are almost identical, but experiencing different environments, is more consistent with the observations than the assumption that differences between individuals are the chief drivers of differences between individual performance (growth, reproduction, etc).

Satisfactory agreement between simulations and available data over a range of food availabilities and/or temperatures also corroborated the hypothesis that two environmental factors – food availability and temperature – are the major cause of variability in biological properties of loggerhead turtles within a population (Sections 4.2 and 4.3). This conclusion may not apply when individuals of different populations (or life stages) are compared, yet the results of this study can serve as a good starting point for such comparisons (e.g., between individuals belonging to the North Atlantic and the Mediterranean populations, inhabiting markedly different habitats; Zenetos et al., 2002; Piovano et al., 2011).

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

Growth and reproduction curves predicted for simulated environments suggested faster growth and maturation in warmer environments with higher food availability (such as neritic habitats). Even though faster growth was 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.

The model provides a mechanistic context that can help interpret scaling of body mass and reproduction output with carapace length. Studies relying on such scaling (e.g., [Tiwari and Bjorndal, 2000](#); [Wabnitz and Pauly, 2008](#)) 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 declining food availability, the short term effects would be hard to detect because loggerhead turtles of a specific carapace length would still produce a corresponding number of eggs expected for that size ([Fig. 6](#), bottom left panel). Long-term effects might become visible decades later, as the size structure shifts toward smaller adults. Similarly, should temperature increase or decrease without a change in food availability, short term effects would show up as an increase or decrease in the reproduction output (number of eggs per nesting season, [Fig. 6](#), bottom right panel), even though the productivity of an area might not have been affected.

Our approach and results present a strong basis for future research. In addition to the scenarios of several constant temperatures and food densities tested in this study, temporary changes in temperature and/or food availability could be simulated. Loggerhead turtles are physiologically capable of withstanding prolonged periods of starvation ([Marn et al., 2017](#)), and compensatory growth has been observed in sea turtles experiencing an increased food level after a period of decreased food availability ([Roark et al., 2009](#)). The consequences of the compensation on the energy budget later in life are unknown ([Metcalf and Monaghan, 2001](#)), and could be studied using the DEB model presented here (e.g., see [Bavčević et al., 2010](#)). Our model is (in principle) also capable of taking into account the effects of changes in food quality and gut residence time, should specific feeding and digestion data become available to justify the added complexity of the model. Frequency and length of the migrations can also be integrated into the model by modifying the energy budget in response to the distance traveled as suggested in [Hatase and Tsukamoto, 2008](#). The added realism of the actually experienced environment might give a more realistic size and maturation predictions, and also account for some of the observed intra-population variability in the growth rates, size and age at sexual maturity. The added complexity, however, would ideally rely on significantly richer data sets than currently available.

Effects of long-term changes in environmental factors, such as those resulting from climate change, could also be investigated using the model, which could be driven by climate change scenarios to assess the possible consequences (see [Appendix B](#) for an illustrative example). For example, an increase in sea surface temperature may be considered positive because it increases growth rate and reproduction output, but positive effects on the population depend on food availability: large decreases in food availability may negate any positive effects of a temperature increase. Similarly, reduction in food availability may be compensated by increase in temperature, but only up to a point. Environmental change could also have a synergistic effect: increase in both food availability and temperature would considerably increase both the growth rate and reproduction.

Quantifying the effects on the population level requires a population dynamics model. The developed DEB model can be directly nested into a population dynamics model using, for example, physiologically structured approach of [De Roos and Persson \(2001\)](#), or individual-based approach of [Martin et al. \(2012\)](#). Subsequently, the coupled models could be employed to help the conserva-

tion efforts by, e.g., (re)evaluating the IUCN criteria ([Keith et al., 2014](#)) and the current assessment of the North Atlantic population (regional management units) as “low risk-high threat” ([Wallace et al., 2011](#)).

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Appendix A. Comparison of modeled and measured growth rates

Several studies reporting growth rates of North Atlantic loggerhead turtles ([Mendonça, 1981](#); [Bjorndal and Bolten, 1988](#); [Snover et al., 2007](#); [Bjorndal et al., 2013](#)) were used to obtain a set of values recorded in the field ([Table A.1](#)). We narrowed our literature search by focusing on studies reporting length as SCL (straight carapace length), and growth rates calculated from direct measurements rather than growth models or skeletochronology. Where length measurements and time intervals were reported in addition to growth rates (e.g., in Refs. [Bjorndal and Bolten \(1988\)](#), [Snover et al. \(2007\)](#)), raw data was used to calculate the growth rates and descriptive statistics (average, standard deviation, minimum, and maximum of the size class). Size classes were set as in [Bjorndal et al., \(2013\)](#) (30–39 cm, 40–49 cm, etc.), and a growth rate was assigned to a specific size class based on the mean of the SCL at initial capture and SCL at recapture ([Bjorndal and Bolten, 1988](#); [Bjorndal et al., 2013](#)).

Based on the size range represented in the studies (30–110 cm SCL), we randomly chose 3000 combinations of two carapace lengths that fall within the 30–110 cm range, and treated them as “length at capture” and “length at recapture”. For the combinations that were less than 50 cm apart (largest length difference in the studies; [Mendonça, 1981](#); [Bjorndal and Bolten, 1988](#); [Snover et al., 2007](#); [Bjorndal et al., 2013](#)), 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, $T_C = 294.95\text{K}$), 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 Eqs. (2) and (3), respectively (see [Section 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. [Bjorndal and Bolten \(1988\)](#), [Snover et al. \(2007\)](#)), and the descriptive statistics for all growth rates within a size class was then calculated ([Table A.1](#)).

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.1](#)).

Table A.1

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 (Bjørndal and Bolten, 1988; Bjørndal et al., 2013).

Mean SCL size class (cm)	Growth rate (cm year ⁻¹)				
	Simulation (this study)	Bjørndal et al. (2013)	Snover et al. (2007)	Bjørndal and Bolten (1988)	Mendonça (1981)
30–39	7.83 ± 2.59 (1.26–15.96) N = 2250	5.90 (2.90 & 8.90) N = 2	–	–	–
40–49	6.49 ± 2.26 (0.52–13.49) N = 5463	–	–	15.67 ± 1.34 (14.81 17.21) N = 3	–
50–59	5.24 ± 1.88 (0.19–11.07) N = 10,904	2.40 ± 2.50 (-1.40 to 12.60) N = 47	2.14 ± 0.79 (1.26–2.76) N = 3	–	7.40 ± 1.40 N = 2
60–69	3.99 ± 1.48 (0.07–8.65) N = 14,621	1.50 ± 1.50 (-0.80 to 8.80) N = 196	2.68 ± 1.56 (0.78–4.16) N = 6	–	6.00 ± 2.30 N = 7
70–79	2.83 ± 1.12 (0.08–6.26) N = 13,941	1.10 ± 1.10 (-0.50 to 5.80) N = 130	2.15 ± 1.60 (1.02–3.28) N = 2	5.16 (4.56 & 5.77) N = 2	5.00 ± 3.50 N = 4
80–89	1.78 ± 0.81 (0.07–3.82) N = 6732	1.20 ± 1.40 (-0.70 to 2.50) N = 129	–	–	–
90–99	1.14 ± 0.59 (0.03–2.34) N = 1273	0.20 ± 0.50 (-0.80 to 2.20) N = 41	–	–	–
100–109	0.58 ± 0.21 (0.16–0.99) N = 66	0.20 ± 0.10 (0.10–0.30) N = 3	–	–	–

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; Snover et al., 2007; Bjørndal et al., 2013), while growth rates close to the high end of the predicted range belonged to loggerhead turtles inhabiting warmer areas (south of Florida; Mendonça, 1981; Bjørndal and Bolten, 1988) 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 (Chaloupka et al., 2008; Hawkes et al., 2007a). Here we present an analysis of three possible scenarios relative to the conditions assumed as current for North Atlantic loggerhead turtles, to illustrate how the results from this study may be used for conservation purposes and for studying the effects of climate change on loggerheads (and other sea turtles).

In all three scenarios, we assumed that the sea temperature increased for 1.5 °C (Hawkes et al., 2007a; NOAA, 2013). Scaled food density was assumed to remain the same (scenario A), increase by 50% (scenario B), or decrease by 50% (scenario C). Otherwise, identical setup as in the main text (see Section 2.1) was used to map the changes in the environment to the biological traits of loggerhead turtles. Conditions assumed as current comprised of temperature T_C and scaled food density x_C (see Section 2 for details).

The growth curves generated by the model (Fig. B.1) under the temperature increase of 1.5 °C imply that: (i) if food availability remains the same, there should be a visible effect on age-length curves, but no effect on the size range of individuals in a given

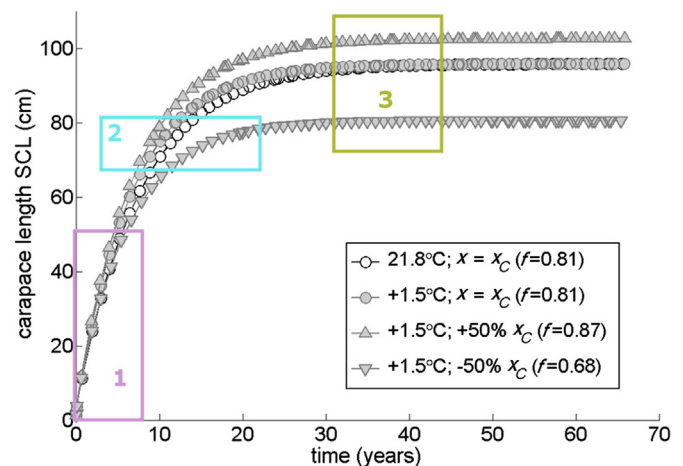


Fig. B.1. Simulating possible scenarios resulting from climate change. Environmental factors were assumed to change relative to the current ones: an increase of temperature alone by 1.5 °C from 21.8 °C (scenario A) and the same temperature increase accompanied with a 50% increase (scenario B) or decrease (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.

population, and (ii) if food availability does change, the size range of individuals should also be affected.

The said effects of increased temperature are not always easy to spot as illustrated by the enumerated rectangles in Fig. B.1. In Rectangle 1, predicted growth curves are so close to each other that they all fall within the range of reported growth rates. Therefore, one cannot easily distinguish between the growth curve at the higher temperature and same food availability (scenario A) and the growth curve at higher temperature and higher food availability (scenario B). It is even harder to distinguish the growth curve under current environmental conditions from the one at higher temperature and lower food availability (scenario C), thus indicating that an increase in temperature can, up to a point, mask a decrease in food availability.

In Rectangle 2, changes in food availability and temperature have a synergistic effect on growth. Given the model predictions that loggerhead turtles reach puberty at around 76–78 cm SCL (see Section 3.1), age at puberty strongly varies between scenarios, ranging from around 9 years to more than 18 years. Age at puberty is a trait with an important role in population dynamics wherein the differences this big may separate prosperous from declining populations.

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

Appendix C. Additional results on life-history traits

Table C.1

Model predictions for a subset of 15 environments differing in food availability; temperature fixed at 21.8 °C (vertical lines in Fig. 3). Food availability, modeled using the scaled functional response (f), was calculated for each environment via scaled food density (x , Eq. (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), Fig. 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 (years)	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	28,497
2.71	0.920	9.83	76.49	71.62	108.92	250.99	1201	27,483
2.43	0.912	9.97	76.51	71.24	107.91	242.20	1150	26,270
2.14	0.901	10.16	76.54	70.77	106.66	231.59	1087	24,795
1.86	0.888	10.41	76.57	70.18	105.07	218.52	1010	22,965
1.57	0.870	10.77	76.61	69.40	102.97	202.07	911	20,636
1.29	0.846	11.33	76.67	68.33	100.09	180.79	782	17,581
1	0.810	12.34	76.77	66.77	95.87	152.34	606	13,419
0.89	0.792	12.97	76.82	65.99	93.73	139.10	523	11,454
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.2

Model predictions for a subset of 15 environments differing in temperature; food availability fixed at $f_C = 0.81$ (horizontal lines in Fig. 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 (years)	Length ultimate (cm)	Mass ultimate (kg)	Reprod. seasonal (#)	Reprod. cumul. (#)
30.00	6.49	95.89	172.63	1154	30,922
28.83	7.10	95.89	168.99	1055	27,755
27.66	7.77	95.89	165.63	964	24,839
26.49	8.51	95.88	162.53	880	22,154
25.31	9.33	95.88	159.68	803	19,685
24.14	10.23	95.88	157.05	732	17,415
22.97	11.23	95.88	154.62	666	15,331
21.80	12.34	95.87	152.34	606	13,419
20.69	13.50	95.84	150.30	553	11,750
19.57	14.78	95.80	148.33	503	10,215
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

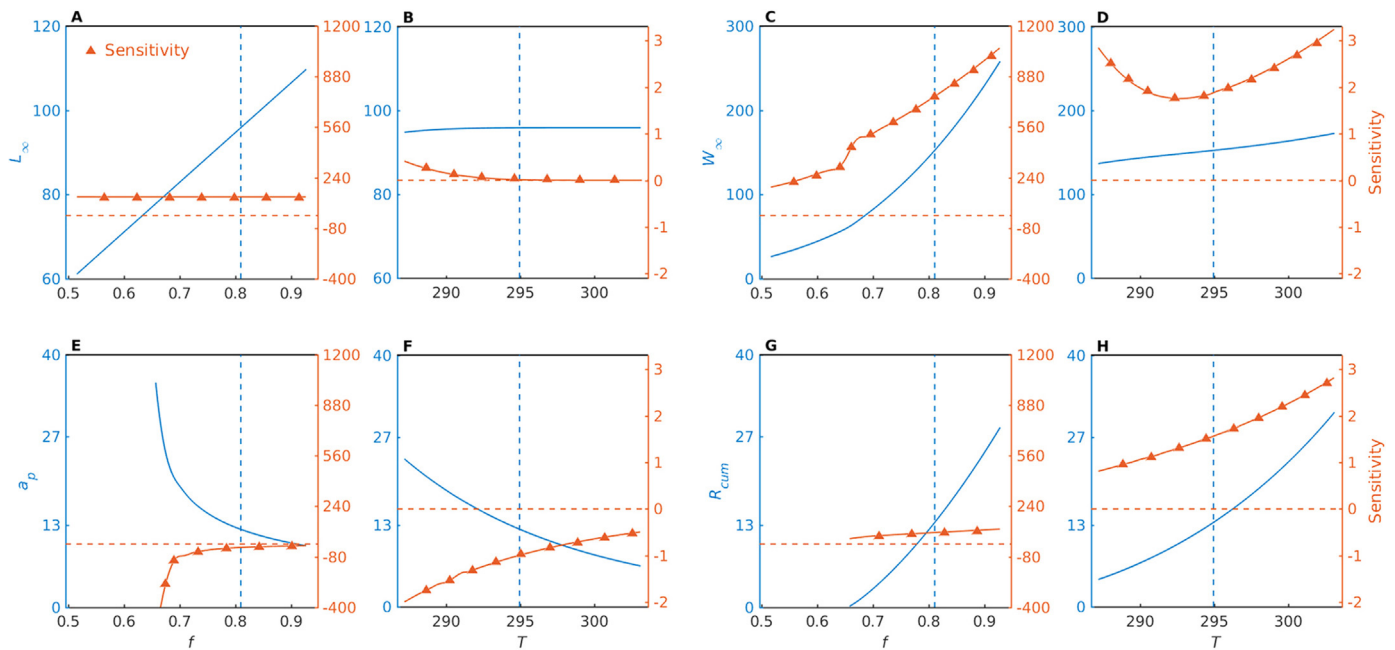


Fig. C.1. Sensitivity analysis showing the change of a life history trait given a small change in the forcing variable (f or T). The horizontal dashed line marks zero sensitivity, i.e., where life-history traits are independent of the forcing variable. If sensitivity is a non-zero constant, then life-history traits depend on the forcing variable, but the relationship is linear.

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