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Food, Glorious Food! Energy budget and reproductive potential of critically endangered leatherback turtles explored with mechanistic modeling

Anna A. Ortega [a,c,*,1], Jeanette Wyneken [b], Nicola Mitchell [a], George Shillinger [c], Nina Marn [d,a,**,1]

[a] UWA Oceans Institute and School of Biological Sciences, The University of Western Australia, Crawley, Perth, 6009, Western Australia, Australia
[b] Florida Atlantic University, Dept. of Biological Sciences/FAU Marine Science Laboratory, Boca Raton, 33431-0991, FL, USA
[c] Upwell Turtle, 99 Pacific Street, Suite 375-E, Monterey, 93940, CA, USA
[d] Rudjer Boskovic Institute, Division for Marine and Environmental Research, Bijenicka cesta 54, Zagreb, 10000, Croatia

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ABSTRACT

In ectotherms such as sea turtles, energy acquisition requires a combination of sufficient food resources and access to suitable temperatures. Leatherback turtles (*Dermochelys coriacea)* , though partially endothermic, are highly migratory and little is known about their energy acquisition. Existing knowledge is based on a few studies of juvenile leatherbacks in captivity that remained relatively small and did not reach sexual maturity while under observation. To bridge this gap, relevant physiological data have been extrapolated to the full lifecycle using Dynamic Energy Budget (DEB) theory. DEB theory provides the basis of mechanistic modeling presented here to (i) predict functional and life history traits for Northwest Atlantic (NWA) leatherback turtles, (ii) elucidate the effects of food availability and sea temperature on those traits, and (iii) use the model to predict traits for another (East Pacific, EP) population of leatherback turtles. Model simulations with warmer temperatures and more abundant food conditions ($f \geq 0.882$) led to younger age at puberty, larger size, and higher reproductive potential. Scaled food availability lower than $f = 0.882$, corresponding to a resource limitation of > 15%, resulted in insufficient energy for leatherbacks to attain sexual maturity. Resource limitation hypothesized for the EP population was simulated as a 5% reduction in food availability, which, combined with a 1 °C warmer temperature possibly experienced by leatherbacks in the Pacific, successfully reproduced the observed data pattern. Namely, the model predicted that, under these conditions and while sharing the same physiological parameters as the NWA leatherbacks, the EP individuals would mature slightly earlier and at a similar size, would grow less after puberty (resulting in a smaller ultimate size), and would have a similar (seasonal) reproductive output as the NWA leatherbacks. Our findings highlight the need for a deeper understanding of the specific food and temperature conditions that individuals encounter along their migratory routes.

1. Introduction

The persistence of a population hinges on the ability of individuals to acquire energy to grow and produce offspring within their lifetime. The relationship between environmental factors and the impact of abiotic and biotic factors on reproductive potential are not well-understood for many species. These relationships are particularly difficult to study in migrating sea turtles, which spend most of their lives at sea and take over a decade to attain sexual maturity. Energy budget models have been used to investigate variations in food availability and temperature for different sea turtle species, specifically green (*Chelonia mydas*; Stubbs et al., 2020), loggerhead (*Caretta caretta*; Hatase and Tsukamoto, 2008; Marn et al., 2017a), and leatherback (Wallace et al., 2006a) sea turtles. These models indicate that although both rising temperatures and increased food supply generally lead to enhanced reproductive output (Marn et al., 2017a), stressors such as frequent marine heatwaves can limit food resources and consequently diminish reproductive potential of individuals (Stubbs et al., 2020). Furthermore, some individuals, due to

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[*] Corresponding author at: UWA Oceans Institute and School of Biological Sciences, The University of Western Australia, Crawley, Perth, 6009, Western Australia, Australia.

[**] Corresponding author at: Rudjer Boskovic Institute, Division for Marine and Environmental Research, Bijenicka cesta 54, Zagreb, 10000, Croatia.
E-mail addresses: anna.ortega@research.uwa.edu.au (A.A. Ortega), nmarn@irb.hr (N. Marn).

[1] These authors contributed equally to this work.

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environmental constraints, might already be smaller in specific populations (Wallace et al., 2006a; Hatase and Tsukamoto, 2008; Marn et al., 2018).

Leatherbacks are somewhat different to other sea turtles, as they are ectothermic early in life but exhibit partial endothermy as they grow bigger and are capable of moving across greater distances and depths (Davenport et al., 1990; Bostrom and Jones, 2007; Davenport et al., 2009; Bostrom et al., 2010). Partial endothermy makes ontogenetic shifts in thermal sensitivity complex to model and complicates predictions of temperature-dependent life history traits, as influence of temperature on growth and reproduction is likely to decline with increasing body size. Nevertheless, some populations might be experiencing resource limitation (Wallace et al., 2006b), making them more vulnerable than others to further environmental perturbations.

Contrary to static energy budget models published for green turtles and leatherback turtles (Hatase and Tsukamoto, 2008; Wallace et al., 2006a), energy budget models for green turtles and loggerhead turtles (Marn et al., 2017b; Stubbs et al., 2019) have been built using the Dynamic Energy Budget (DEB) framework (Kooijman, 2010). DEB models are full-life cycle models that, by employing biologically relevant parameters and modeling the key metabolic processes, enable simulating individual growth and reproduction over the whole lifespan. This framework has been used to fit data and explain energy allocation for > 7000 species with a low median relative error (0.07; Marques et al., 2018; AmP, 2025). DEB models are responsive and can therefore serve to investigate not only the effects of different levels of temperature and resource availability on the individual, but also the effects of changes in these environmental conditions. The simplest type of DEB models – the standard ('std') model – have been successfully applied to explain energy acquisition throughout a full life span for all seven sea turtle species (Add-my-Pet collection of model parameters and underlying data AmP, 2025), albeit with differing levels of detail.

A DEB leatherback model initially available in the AmP collection (AmP entry: Kooijman and Kearney, 2023) used data from two different leatherback populations: the Northwest Atlantic (NWA) and the East Pacific (EP); we will refer to this model as the '2023 leatherback model'. There is evidence that the NWA and EP populations are demographically different, exhibit different migratory behavior, and interact with different levels of environmental resources (Wallace et al., 2006b). For loggerhead turtles, two populations (North Atlantic and Mediterranean) experiencing different environmental pressures required population-specific sets of model parameters to realistically represent their growth rates and reproduction (Marn et al., 2018). Differences between the growth and reproduction of the NWA and EP populations of leatherback turtles have not been examined in detail but are potentially important given their contrasting population trajectories (Wallace et al., 2013). Furthermore, the 2023 leatherback model lacked detailed data on reproduction, which is crucial for making informed predictions about the interplay of environmental cues and reproductive output.

Here, we explore to what extent a well-parameterized DEB model of a leatherback turtle can: (i) predict functional and life-history traits, including reproductive potential, of leatherback turtles; (ii) elucidate the effects of environmental conditions (food availability and temperature) on those traits; and (iii) predict traits for two distinct (NWA and EP) leatherback turtle populations. We use the 2023 leatherback model as a starting point which we complement with previously unpublished growth data and updated published information on reproduction. We then use the reparameterized model to simulate a range of realistic food and temperature scenarios and predict selected life-history traits, including reproductive potential. We start by explaining the DEB principles and then move on to applications; more details are provided in the Appendix A, and for a deeper understanding of DEB models applied to sea turtle species, the reader is referred to examples for loggerhead (Marn et al., 2017a,b, 2018) and green turtles (Stubbs et al., 2019, 2020).

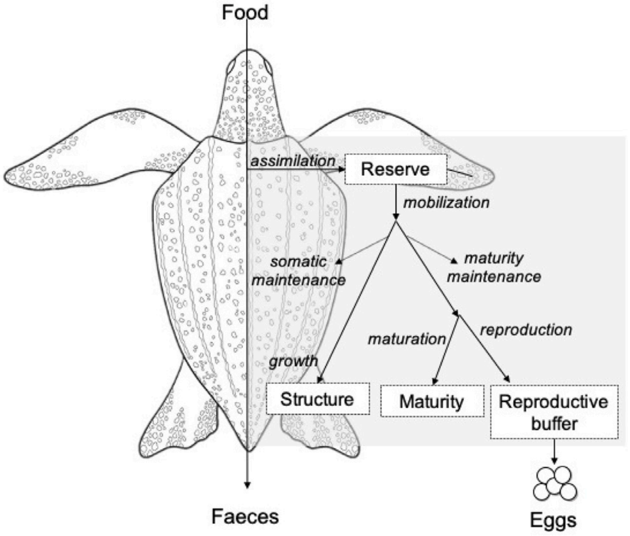


Fig. 1. Energy flows within the standard DEB model overlaid upon a dorsal view of a leatherback sea turtle. Four state variables (reserve, structure, maturity, and reproductive buffer) are denoted within rectangles. Utilization of the mobilized reserve follows the kappa rule. Processes are listed in Table 1.

2. Methods

2.1. The Dynamic Energy Budget (DEB) model

We use the standard Dynamic Energy Budget (DEB) model to track the turtle's physiology and to simulate the responses to environmental cues. Briefly, DEB theory provides a mechanistic framework to describe the assimilation and utilization of energy by individuals over their lifetime (Kooijman, 2010; Jusup et al., 2017). Energy is used for maintenance, growth and reproduction, and the energy fluxes are sensitive to both the state of the individual and the environment which the individual inhabits (Nisbet et al., 2000; Kooijman, 2001, 2010; Jusup et al., 2017). The individual's physiology (life stage, size, nutritional status) and the environment (food availability and temperature) will determine its reproductive potential, which we define as the relative capacity to produce viable offspring. Food availability is expressed as a value between 0 (no food) and 1 (abundant food), and is defined as a Holling-Type II response, $f = x/(1+x)$, where x is some measure of food abundance scaled by the species- (and food-) specific half-saturation constant (Kooijman, 2010, see also Table 1-Assimilation). Temperature affects all rates equally through an Arrhenius relationship, implemented into a DEBtool function named `tempcorr.m` (Kooijman, 2010; DEBtool, 2025).

The state of an immature individual is fully defined by three state variables (energy reserves E, structure L^3, and maturity E_H), while a reproductive buffer (E_R) is an additional state variable tracked for (sexually mature) adults; Fig. 1 provides a schematic representation of state variables and their dynamics; Table 1 lists the processes, and Appendix A provides further details. In a DEB model, energy is allocated in accordance with the κ-rule, in which κ represents the fixed proportion of the mobilized energy allocated to somatic maintenance and growth. The remainder of mobilized energy (1- κ) is allocated to maturity maintenance, and maturation or reproduction depending on the life stage: subadults (embryos and juveniles) allocate energy to maturation, while adults allocate to reproduction. Energy allocated to reproduction is first accumulated in a reproduction buffer (E_R) and then converted into eggs once a threshold is reached, linking maternal energy status to clutch production. DEB models are therefore often applied to understanding female reproductive capacity under the

Table 1
Energy flows denoted universally $\dot{p}_*$ (unit $\mathrm{J\,d^{-1}}$;).
Source: Modified from Marn et al. (2017b).

Assimilation $\dot{p}_A = \{\dot{p}_{Am}\} f L^2$	Is the fraction of the daily feed ration that gets fixed into reserve, where $\{\dot{p}_{Am}\}$ (unit $\mathrm{J\,cm^{-2}\,d^{-1}}$) is the surface area-specific maximum assimilation rate and f is the scaled functional response equivalent to the ratio of the actual and the maximum feeding rate of an individual. The scaled functional response quantifies food availability (i.e., $f = 1$ under unlimited food availability and $f = 0$ when food is unavailable) and in many cases can be written as $f = x/(1+x)$, with x being the food density scaled by the half-saturation constant of the type-II saturating function (see p. 32 of Kooijman (2010) for details).
Mobilization $\dot{p}_C = E(\dot{v}/L - \dot{r})$	Is the flow of energy mobilized from reserve to power metabolic processes, where parameter $\dot{v}$ (unit $\mathrm{d^{-1}}$) is the energy conductance and, for $[E] = E/L^3$, the specific growth rate is $\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_M]/\kappa}{[E]+[E_G]/\kappa}$. Here, $[\dot{p}_M]$ (unit $\mathrm{J\,cm^{-3}\,d^{-1}}$) is the volume-specific somatic maintenance rate. Mobilized reserve is partitioned according to the κ-rule: fixed fraction κ is allocated to satisfy the organism's somatic needs (somatic maintenance and growth), whereas the rest is allocated to maturity maintenance and maturation (before puberty) or reproduction (after puberty).
Somatic maintenance $\dot{p}_M = [\dot{p}_M] L^3$	Is the flow of mobilized reserve energy needed to maintain the structure of given size L^3.
Growth $\dot{p}_G = \kappa\dot{p}_C - \dot{p}_M$	Is the flow of mobilized reserve energy invested into the increase of structure after satisfying the somatic maintenance needs.
Maturity maintenance $\dot{p}_J = \dot{k}_J E_H$	Is a flow (analogous to somatic maintenance) that quantifies the mobilized reserve energy necessary to maintain the current level of maturity. Parameter $\dot{k}_J$ (unit $\mathrm{d^{-1}}$) is called the maturity maintenance rate coefficient.
Maturation $\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$, $(E_H \leq E_H^p)$	Is the flow of mobilized reserve energy towards increasing the level of maturity (E_H), after satisfying the maturity maintenance, $\dot{p}_J$.
Reproduction $\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$, $(E_H = E_H^p)$	Is the switch in investment of energy at the onset of the adult stage when the level of maturity reaches E_H^p, when the organism starts to invest energy into reproduction instead of maturation. Hence, reproduction starts and maturity stops increasing.

assumption that eggs are fertile. The important implication of the κ-rule is that growth and reproduction do not directly compete for resources.

The model recognizes three distinct life stages that differ in energy acquisition and allocation: an embryo does not feed nor reproduce, a juvenile feeds but does not reproduce, and the adult feeds and allocates to reproduction (Kooijman, 2010). Transitions between life stages (embryo to juvenile, and juvenile to adult) occur at fixed levels of maturity: 'birth' and 'puberty', respectively. These maturity thresholds are species-specific and can be estimated from life history data, as can other parameters linked to maintenance, growth, and reproduction (see Section 2.2). Even though distinct sea turtle life stages (hatchling, posthachling, yearling, juvenile, subadult etc.) could be mapped with corresponding maturity thresholds (e.g., hatching defined for green and loggerhead turtles, Stubbs et al., 2019; Marn et al., 2017b, or a whole developmental map for frogs provided in Augustine, 2017), we opted to define three sea turtle stages due to data scarcity: embryo (from egg deposition to hatching), juvenile (from hatching to maturation), and adult (from maturation onward), with 'birth' and 'puberty' as corresponding transitions (as per DEB conventions).

Generally, individuals of the same species share the same traits, which will result in species-specific parameters of the DEB model. However, as there are seven recognized subpopulations of leatherbacks (NMFS and USFWS, 2020), inter-individual variability is likely to exist between (sub)populations, as has been shown for loggerheads (Marn et al., 2018). While life history data exist for each leatherback population, the extent of those data vary, with the most extensive data being available for the Northwest Atlantic (NWA) population (especially regarding growth) due to decades of small scale captive rearing efforts (e.g., Jones et al., 2000 in Florida), with husbandry methods being refined over time. Consequently, we parameterize the leatherback DEB model using NWA data but also compare the model predictions to data available for the EP population, assessing the applicability of the model to both populations.

2.2. Incorporation of physiological data for leatherbacks

Values for DEB model parameters were previously estimated for leatherback sea turtles, and results submitted to an online collection (2023 leatherback model in AmP collection: Kooijman and Kearney, 2023) . Parameterization was done based on values from literature (NWA and EP), and on experimental growth data for captive-reared NWA individuals presented in Jones (2009). We sourced additional (previously unpublished) data on captive growth obtained from a program at Florida Atlantic University. As part of this program, leatherback hatchlings were reared in 2009, 2013, 2014 and 2023 with the intention of releasing them as small juveniles (120–500 g). Turtles were reared at three different feeding regimes (combinations of mahi-mahi *Coryphaena hippurus* and human infant formula), with temperature maintained between 21 °C and 24 °C. These data were combined with published fecundity data, and with revised literature values to form a calibration dataset for NWA leatherbacks (Table 2). The average environmental conditions assumed for the NWA basin were $f = 0.9$, $T = 21.13$ °C, the latter based on an average of water temperatures at the edges of the NWA leatherback range: high latitude (Casey et al., 2014) and low latitude (Southwood et al., 2005).

To parameterize the model, the available data generally need to be linked to model state variables and processes: reserve and structure together constitute the physical volume of the organism (joined by the reproductive buffer in adults), and maturity tracks the developmental stage. Physical length is linked to structural length via an auxiliary parameter called 'the shape coefficient'. To incorporate the slight change in shape (length–width relationship) that occurs between early life and adulthood of leatherbacks (Pate and Salmon, 2017; Salmon and Scholl, 2014), we included a correction function for this auxiliary parameter. A constant ratio of reserve and structure (so-called 'weak homeostasis', Kooijman, 2010) was assumed throughout life in order to calculate wet weight of a turtle, thus implying that a turtle will experience a roughly constant relative food availability throughout its life. The condition of the mother at egg formation was used to calculate initial energy in an egg (the 'maternal effect' assumption, Kooijman, 2010). To compare embryo respiration data to model predictions, we summed the model predictions for energy dissipated as overheads of growth and maintenance during embryonic development. All parameter estimation was performed in Matlab R2017a, using the standardized DEBtool routines (DEBtool, 2025, last download: 2025/04/15) for parameter estimation. The parameter set of the 2023 leatherback model (AmP entry: Kooijman and Kearney, 2023) was used as initial parameter values.

2.3. Model evaluation

Goodness of fit and realism of parameters were assessed within the DEBtool (2025) and AmPtool (2024) software. For goodness of fit, we calculated the mean relative error (MRE) and symmetric mean relative error (SMSE). These two metrics are generally used in statistical

Table 2
Datasets used for NWA leatherback model parameterization.

Data type	Description	Source	Data and predictions
Life-history traits.	Age and size at life events (hatching, puberty, ultimate), reproduction rate, assimilation rate.	Values sourced from literature or as mean values of data; focus on NWA population, with average temperature in the NWA assumed as 21.13 °C.	Table 3 and A.1.
Growth in length and weight, length - weight relationship	Captive growth of hatchlings up to 150 days, for year 2009, 2013, 2014, and 2023. Feed composition varied between the years (modeled via a year-specific scaled functional response f), and temperature was maintained between 21 °C and 24 °C.	Unpublished data (J. Wyneken, Florida Atlantic University, Marine Futures Lab).	Panels B to D in Fig. 2.
Length - fecundity	Straight carapace length (SCL, cm) of wild nesting females related to the number of eggs per clutch.	Tucker and Frazer (1991) and Hirth (1987)	Panel A in Fig. 2
Growth in length and weight	Captive growth up to 2 years, data after 1.3 years dominated by 2 individuals	Table 3.1 in Jones (2009) and Jones et al. (2011)	Fig. A.1
Growth in length and weight, length - weight relationship	Data for captive reared and wild leatherbacks compiled by T. T. Jones	All in Jones (2009): Table 3.2 - captive animals; Table 3.3 - wild strandings or bycatch; Fig. 3.2 - adult data, skeletochronology	Panels A to C in Fig. A.2
Embryo respiration	O_2 consumption rate during incubation at 30 °C, initial egg mass 85.53 g; hatchling mass 45.69 g wet, 9.776 g dry	Thompson (1993)	Panel D in Fig. A.1.

estimation to quantify the difference between model predictions and the empirical data. MRE can range from 0 to ∞, and quantifies the over- or under-prediction of data, whereas the SMSE is a distance measure, and weights data and predictions "symmetrically", averaging the squared errors. In both cases, smaller values indicate better fit. Goodness of fit was also assessed visually by comparing the data and model predictions. We computed implied properties for the species and compared estimated parameter values to those of other sea turtle species by using dedicated outputs of the `estim_pars` DEBtool routine (DEBtool, 2025).

Finally, the traits of leatherbacks and other turtle species were evaluated in multidimensional space by multidimensional scaling (MDS) implemented into AmPtool (Kooijman et al., 2021, see also Appendix A.3). MDS can in principle be performed with as many traits as desired. Within MDS, 'traits' are either parameters (e.g. κ, $[\dot{p}_M]$) or other properties (traits) of a species (e.g. ultimate weight, maximum reproduction) as predicted by the model (Kooijman et al., 2021). We selected 13 traits on which to perform the comparison. Our choice was based on preliminary analysis of parameters differing between the current and the 2023 model (AmP: Kooijman and Kearney, 2023), and on the focus of this study (reproductive potential and size traits of leatherbacks). The selected traits include six model parameters (somatic maintenance rate, conductance, allocation to soma, maximum reserve density, supply stress, precociality coefficient) and seven life-history traits (age at puberty, age at birth, age at puberty, maximum lifespan, maximum wet weight, wet weight at birth and at puberty, and maximum reproduction at ultimate size).

Conductance ($\dot{v}$), allocation to soma (κ), and somatic maintenance rate ($[\dot{p}_M]$) are primary parameters of the model and define energy mobilization ($\dot{v}$), allocation (κ), and use ($[\dot{p}_M]$; Tables 1 and 4). Maximum energy density ($[E_m] = \{\dot{p}_{Am}\}/\dot{v}$) is a compound parameter positively linked to the ability to withstand prolonged periods of starvation. Supply stress ($s_s = \dot{p}_J \cdot \dot{p}_M^2/\dot{p}_A^3$) is a compound parameter indicating where a species is on the supply–demand spectrum (Lika et al., 2014). That is, how resilient a species is to resource fluctuations: lower values relate to the ability to deal with low food conditions by reducing growth and reproduction (Lika et al., 2014; Marn and Kooijman, 2022). The precociality coefficient (s_H^{bp}) is the ratio of maturities at birth and at puberty. This trait accounts for the discrepancy between large adults and small eggs; a smaller value has been shown to align with long-lived and slow-maturing species like sea turtles (Marn and Kooijman, 2022). Life-history traits include some quantities readily measured for leatherbacks (e.g., wet weight at hatching, i.e. birth in model context) and some that are extremely hard to measure (e.g., age at puberty and reproductive output at ultimate size). Observations are not directly used for MDS — rather, the model predictions for the traits are used to enable comparison among species for which these data would potentially be lacking (Kooijman et al., 2021).

2.4. Simulating a range of constant food and temperature conditions

The parameterized model was used to run simulations under a range of environmental conditions including those theoretically more favorable (warmer sea with more food) or less favorable (colder sea with less food) than default NWA conditions. The default (scaled) average food availability in the NWA (x_{NWA}) was back-calculated from the estimated scaled food availability ($f = x/(x+1)$, with $f_{NWA} = 0.9$). The x_{NWA} was then modified to simulate a range of values between half and double the amount, corresponding to f ranging between 0.818 and 0.947. Temperature used for simulations ranged between 14 °C and 28 °C, to capture the (environmental) range of temperatures experienced by NWA leatherback turtles (Casey et al., 2014; Southwood et al., 2005).

While general patterns are, in fact, pre-determined by the generic model equations (more energy provided as input will lead to higher reproduction as an output), the amplitude of the resulting changes depends on the (species-specific) parameter values and was thus far not explored for leatherback turtles. Species-specific simulations enable: (i) quantifying how variation in environmental conditions affects growth, maturation, and reproduction, and (ii) identifying conditions (or thresholds) at which reductions in food availability or suboptimal temperatures could lead to substantial reproductive reductions (Marn et al., 2017a; Stubbs et al., 2020).

Simulations ran for 35 years (approximately one lifespan, NMFS and USFWS, 2020); under constant environmental conditions, with a remigration interval of 2.5 years for NWA leatherbacks (NMFS and USFWS, 2020). Outputs included six life-history traits: age at puberty, length at puberty, ultimate weight, ultimate length, seasonal reproductive output at maximum size, and cumulative (lifelong) reproductive output. Subsequently, these traits were analyzed with the expectation that individuals most beneficial to population viability would be large females reproducing at a younger age and females that reach larger sizes, experiencing optimal environments.

2.5. Evaluating the inter-population transferability of the DEB model

Model predictions obtained with the NWA specific parameter set were compared to the observed life-history traits of EP leatherback

Table 3

Comparison between observations and model predictions (RE stands for relative error) for NWA leatherback turtles at the indicated temperature and the assumed scaled functional response $f = 0.9$.

Data & Description	Unit	Value used	Prediction (RE)	Reference
ab, Age at hatching[a] (29.88 °C)	day	63	52.85 (0.161)	NMFS and USFWS (2020)
ap, Age at puberty (21.13 °C)	year	19.25	15.53 (0.193)	NMFS and USFWS (2020)
am, Life span (21.13 °C)	year	30.25	30 (0.008)	NMFS and USFWS (2020)
Lb, straight carapace length at hatching[a]	cm	6.18	5.65 (0.085)	Jones (2009), Wyneken (unpublished)
Lp, SCL at puberty	cm	125.6	131.7 (0.049)	NMFS and USFWS (2020) and Avens et al. (2009)
Ultimate SCL	cm	151.07	133.6 (0.115)	NMFS and USFWS (2020)
Wwb, wet weight at hatching[a]	g	46.03	45.48 (0.012)	Thompson (1993) and Hsu (2020); Wyneken (unpublished);
Wdb, dry weight at hatching[a]	g	9.776	13.64 (0.396)	Thompson (1993)
Wwi, ultimate wet weight	kg	370	439.5 (0.188)	Paladino et al. (1996), Lutcavage et al. (1992) and Wood (1982)
Ri, max reproduction rate[b] (21.13 °C)	egg/day	0.4147	0.4094 (0.013)	NMFS and USFWS (2020)
pXm, max adult intake of jellyfish[c] (20 °C)	W/kg	1.13	0.8115 (0.281)	Wallace et al. (2006b)

[a] We assumed that hatching (leaving the egg or nest) coincides with birth in DEB theory (the moment when an individual stops relying on embryonic energy reserves and starts feeding), despite there usually being 5–7 days of sea turtle hatchlings relying on external yolk sac (see also Stubbs et al., 2019; Marn et al., 2017b). The assumption applies also to Lb, Wwb and Wdb.

[b] Ri based on updated averages of clutch frequency (5), clutch size (81.74), and remigration interval (2.7) for the NW Atlantic stock.

[c] Average required feeding rate for St. Croix (NWA) leatherbacks for a 2.85 year remigration interval is 127 kg/d. Leatherback prey energy content is assumed to be 310 kJ/kg wet mass (Davenport and Balasz, 1991) and mass of adult is assumed as 400 kg: 127/400*310000/24/60/60 W/kg. See Appendix A.1). 2023 model: about 350 kg, 82 kg jelly fish/d for 250–450 kg turtle at 200 J/g = 82/350*200000/24/60/60 = 0.54 W/kg (Kooijman and Kearney, 2023, AmP entry).

population. Based on the results of model simulations and default environmental conditions assumed for the NWA basin ($f = 0.9$, $T = 21.13$ °C), we trialled several combinations of food availability and temperature, and assessed the most likely combination of environmental conditions that reproduced the observed EP traits. As remigration intervals are different between the two populations, in the simulations we used 2.5 years for the NWA population and 3.5 years for the EP population (NMFS and USFWS, 2020). Goodness of fit was assessed by calculating relative errors between data and predictions.

3. Results

3.1. Data and goodness of fit

Several data used in the initial 2023 leatherback model (AmP entry: Kooijman and Kearney, 2023) were replaced or modified for this study, mostly because NWA specific values were preferred, or because updated values became available (Table A.1). Supplementing the data of the 2023 model with additional data on early growth and reproduction increased the completeness score of the entry from 2.8 to 3 (Lika et al., 2011). Overall MRE and SMSE values were higher than those of 2023 model, indicating a poorer fit: MRE = 0.122 compared to 0.064, and SMSE = 0.132 compared to 0.008. The poorer fit was mostly due to newly added early growth data which showed relatively high inter-individual variability (Fig. 2b–d). The predictions (i.e., relative errors, RE) for life-history trait data used in model estimation were comparable, with most RE values in both cases (2023 and new model) having values <0.15 (Table A.1). The exception was the ultimate weight, which was predicted well in the 2023 model (RE = 0.01) but is now overpredicted by roughly 20%. This is due, in part, to the updated data value (370 kg now vs. 420 kg previously; see Appendix A.1 for rationale) and changed model parameters, but it might be due to the modeling approach, which we explore further in the Discussion.

3.2. Model parameters and implied traits

The new parameter set differed most from the initial 2023 parameter set in the following parameters: higher kappa ($\kappa = 0.63$ now vs. 0.25 previously), implying a higher proportion of mobilized energy allocated to growth as opposed to development and reproduction, higher energy conductance ($\dot{v} = 0.14$ cm d^{-1} now vs. 0.06 cm d^{-1} previously) and higher volume-specific maintenance rate ($[\dot{p}_M] = 47.06$ J cm^{-3} d^{-1} now vs. 34.97 J cm^{-3} d^{-1} previously), implying a faster energy turnover through increased energy mobilization and utilization. This was combined with a lower maximum specific assimilation rate ($\{\dot{p}_{Am}\} = 3780$ J cm^{-2} d^{-1} now vs. 4307 J cm^{-2} d^{-1} previously), implying a lower relative potential for assimilating energy. Compared to other sea turtle species, most new parameters were more closely aligned with other sea turtle species than were the 2023 model parameters (Table A.2), including the zoom factor (z), a proxy for relative physical size which is now highest for leatherbacks, the largest sea turtle species. The new combination of $\{\dot{p}_{Am}\}$ and $\dot{v}$ resulted in a lower reserve capacity ($[E_m] = \{\dot{p}_{Am}\}/\dot{v}$) than in the 2023 model, implying a shorter period of coping with starvation, but the new $[E_m]$ value was still up to 3 x higher than the value estimated for other sea turtles (Table A.2).

Being a full life-cycle model, the parameterized model enabled assessing hard-to-measure traits of interest, i.e., implied traits at typical environmental conditions (one of the automated model outputs available in DEBtool routines, DEBtool, 2025). The supply stress (s_s) value for leatherbacks is 0.1397, which is much higher than the median for all sea turtles (0.0560; Marn and Kooijman, 2022); this extremely high value places the leatherbacks at the top of the demand spectrum (Lika et al., 2014), and suggests they are very sensitive to resource fluctuations. A low precociality coefficient (s_H^{bp}) value implies that the leatherbacks require substantial energetic investment after hatching to reach maturity. Leatherbacks showed a smaller value than all other sea turtle species, suggesting that leatherback hatchlings require the greatest investment to reach maturity when compared to other sea turtle species. Other implied traits, such as lifetime reproductive output and maximum reproductive output at ultimate size, suggest that female NWA leatherbacks, experiencing the default NWA food availability and temperature, are capable of producing a relatively large number of offspring: 370 eggs per reproductive year (on average every 2.5 years), and 2171 eggs over their lifetime.

Results of multidimensional scaling (MDS) position the leatherbacks close to other sea turtles, yet they are different with respect to the explored traits (Fig. 3). More in-depth analysis (see Appendix A.3) suggests that particular traits position sea turtles in general, and leatherbacks in particular, in the bottom right corner of the MDS 2-dimensional plot. These traits are weights (at birth and at ultimate size), age at puberty, lifespan, maximum reserve density, and somatic maintenance rate. In other words, sea turtles cluster together as slow-maturing, long-living, relatively large individuals with relatively high metabolism and good ability to withstand food shortages (high reserve capacity).

3.3. Model simulations

Taken together, the simulations highlighted a range of environmental conditions which could support leatherback females to mature and

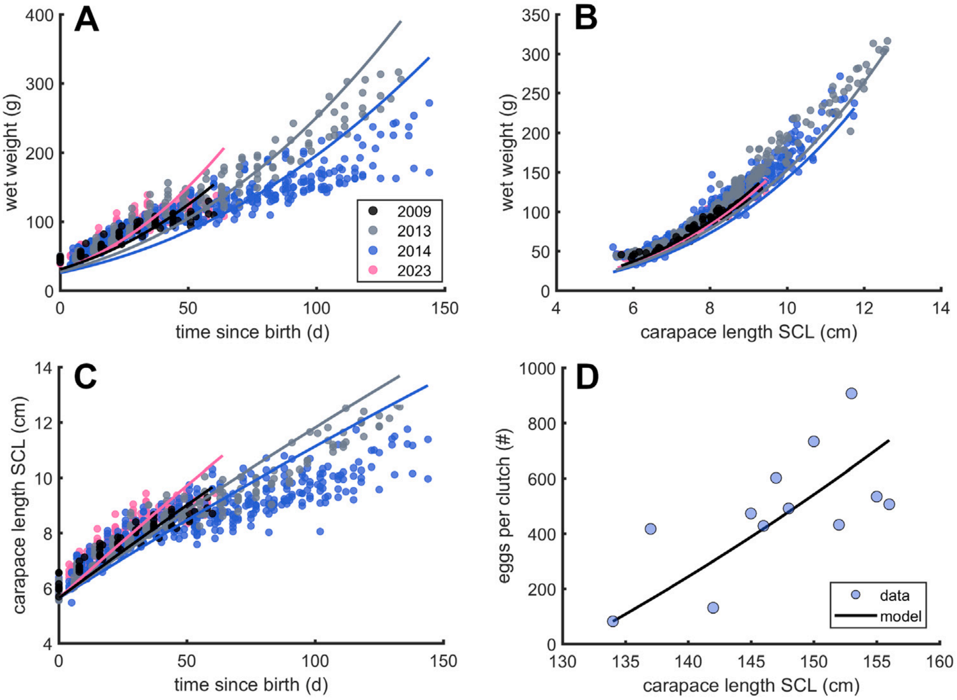
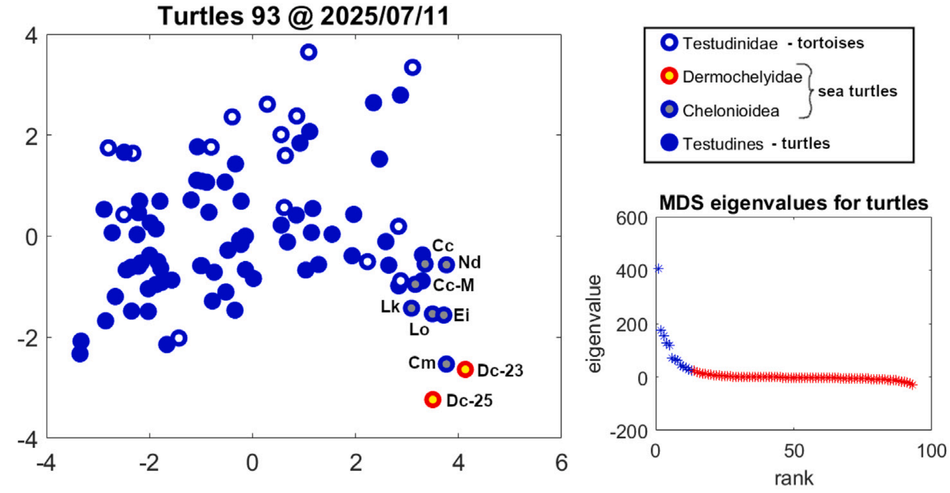


Fig. 2. Model predictions for four univariate datasets added to the 2023 DEB model for *D. coriacea* (AmP entry Kooijman and Kearney, 2023). **(A)** wet weight of captive neonates from age 0–150 days. **(B)** wet weight and carapace length (SCL, cm) of captive neonates. **(C)** carapace length (SCL, cm) of captive neonates from age 0–150 days. For panels A-C year class/diet and DEB model predictions to these data are color coded. Data source: Unpublished data, J. Wyneken, Florida Atlantic University, Florida, United States of America. Experimental design based on laboratory records of diet and temperature in different years: 2009: f = 0.5269, T = 21.5 °C; 2013: f = 0.4441, T = 22 °C; 2014: f = 0.3975, T = 21.5 °C; 2023: f = 0.4985, T = 24 °C. As turtles age, the increase in mass and length slows — partially due to a deliberate food reduction not explicitly modeled in this study, and partially due to physiology. **(D)** the relationship between carapace length (SCL, cm) and reproductive output (eggs per clutch) of wild nesting females. Data from Hirth (1987) and Tucker and Frazer (1991). For model predictions we conservatively assumed 5 nests per season per female with nesting seasons 2.7 yrs apart, with $f = 0.9$.



Cc: Caretta caretta (North Atlantic), Cc-M: C. caretta (Mediterranean), Nd: Natator depressus,
Lk: Lepidochelys kempii, Lo: L. olivacea, Ei: Eretmochelys imbricata, Cm: Chelonia mydas,
Dc-23: Dermochelys coriacea (2023), Dc-25: D. coriacea (2025-this study)

Fig. 3. Multidimensional scaling (MDS) of leatherbacks (red-centered dots) and other turtle species was performed based on 13 traits: seven life history traits as predicted by the model (age at birth and puberty, weight at puberty and ultimate size, and reproductive output) and six metabolic traits represented by primary and compound model parameters, such as maintenance rate and maximum reserve density. Plot with eigenvalues in the bottom right corner suggests that the 1st eigenvalue (corresponding to the x-axis) has the strongest contribution to the overall position of a species in the MDS plot, whereas the 2nd eigenvalue (y-axis) and 3rd eigenvalue (z-axis) contribute less. Number of eigenvalues is determined by the number of explored traits, as these define the n-dimensional space within which the comparison is made. In our case, this is a 13-dimensional space; we show here the first two dimensions (x and y), and the 3-dimensional image is available in Supplementary Material as an interactive figure. Generally, based on the MDS of selected traits, sea turtles (labeled dots) cluster together as slow-maturing, long-lived, relatively large individuals with relatively high metabolism and good ability to withstand food shortages (high reserve capacity). See text and Appendix A.3 for further details.

Table 4
List of primary and auxiliary parameters for the Northwest Atlantic leatherback turtle (*Dermochelys coriacea*) estimated using the covariation method (Lika et al., 2011), unless specified differently.

Parameter	Symbol	*D. coriacea*	Unit
Maximum specific assimilation rate	$\{\dot{p}_{Am}\}$	3780.30	$\mathrm{J\,d^{-1}\,cm^{-2}}$
Digestion efficiency (of food to reserve)	κ_X	0.28	–
Energy conductance	$\dot{v}$	0.14	$\mathrm{cm\,d^{-1}}$
Allocation fraction to soma	κ	0.63	–
Volume-specific somatic maintenance	$[\dot{p}_M]$	47.06	$\mathrm{J\,d^{-1}\,cm^{-3}}$
Specific cost for structure	$[E_G]$	7812	$\mathrm{J\,cm^{-3}}$
Maturity at birth	E_H^b	4.76e+04	J
Maturity at puberty	E_H^p	1.24e+09	J
Weibull aging acceleration	$\ddot{h}_a$	8.72e–10	$\mathrm{d^{-2}}$
Arrhenius temperature	T_A	8000	K
Shape coefficient - posthatch and juvenile	δ_M	0.38	–
Shape coefficient - late juvenile and adult	δ_M	0.34	–
Delay until start of development, at 20 °C	t_0	76.88	d

All rates are given at reference temperature $T_{ref} = 273\,\mathrm{K}$, and food availability $f = 0.9$, unless otherwise specified. Centimeters in units are referring to (surface area or volume of) structure. Auxiliary parameter zoom factor = 51. For a full set of parameters and comparison to previous entry, see Table A.2 in the Appendix.

reproduce, as well as theoretically achievable ranges for simulated life-history traits (Figs. 4, A.3 and A.4, and Tables A.3 and A.4 in Appendix A.2). Some traits were impacted more by food availability than by temperature: length at puberty L_p was predicted to fall within a narrow range of 131 cm to 133 cm SCL; ultimate length L_i ranged between 122 cm to 140 cm SCL, depending on the simulated food availability (Fig. 4B and D). Some traits exhibited a high sensitivity to both environmental factors: age at puberty ranged between <10 yr to >30 yr (Fig. 4A), and the reproductive output between <50 eggs/season to > 2500 eggs/season at ultimate size (Fig. 4E). Warmer temperature was generally linked to a younger age at puberty and higher reproductive output (see also Table A.4 in Appendix A.2). Reproductive output (maximum seasonal and cumulative) peaked under the highest food and temperature conditions: the maximum value suggested that given sufficient food and high temperatures for growth (100% more food than the NWA average corresponding to scaled food availability $f = 0.947$, and average temperature of 28 °C), and while assuming no deleterious effects of high temperature, adult females could produce up to 2 700 eggs every 2.5 years, i.e. 26 000 eggs in their lifetime, likely resulting also in shorter remigration intervals (Fig. 4E and F).

The new parameter set enabled simulating a range of realistic environmental conditions, unlike the 2023 (AmP) parameter set where in preliminary simulations even a minor (<5%) reduction in food availability resulted in individuals acquiring insufficient energy to sexually mature. Simulations did, however, suggest a potential resource limitation for leatherbacks: food reduction of −15% (relative to the NWA average food availability), corresponding to a scaled functional response $f = 0.884$, was the minimum scaled functional response for attaining sexual maturity (puberty) (Fig. 4). Food reduction >10% ($f = 0.890$) would likely result in prolongation of remigration intervals, as the females would be able to produce only 30 eggs every 2.5 years (see also Table A.3 in Appendix A.2). Similarly (within the maturation and reproduction context), temperatures below 15 °C would prolong the period required to mature to almost 30 years, and lower the seasonal reproductive output (at maximum size) to < 300 eggs at the default NWA value $f = 0.90$ (Table A.4), with periods even longer and reproductive output lower at reduced food availability (Fig. 4E).

3.4. *Predicting EP leatherback traits with NWA parameter set*

Life-history data for EP leatherbacks were available for age and size at hatching (i.e., birth in the model context), age and length at puberty, ultimate length and weight, and maximum annual reproductive output; relevant data for NWA and EP leatherbacks are summarized in Table 5. Given these (limited) data, we focused on reproducing the trends; EP leatherbacks are somewhat smaller at hatching and at ultimate size, but of comparable size at puberty. Age at puberty is marginally lower for EP leatherbacks, and their maximum seasonal reproductive output is slightly higher but comparable to that of NWA leatherbacks. Environmental conditions that would theoretically reproduce this pattern are resource limitation combined with warmer temperatures, which would be possible considering a wider tropical area in the Pacific than in the Atlantic Ocean (Kenyon, 2017), and a possible resource limitations experienced by EP leatherbacks along their migratory routes (Wallace et al., 2006b). Indeed, simulating a slight (5%) reduction in food availability and assuming that EP leatherbacks experience on average ≈1 °C warmer temperature (22.5, °C), the model predicts hatching at a slightly smaller size, earlier maturation at a similar size, attainment of a smaller ultimate size, and more reproduction each nesting season, the latter after correcting for the observed remigration intervals which differ between the two populations (Table 5). A stronger food reduction hinders the maturation of EP leatherbacks, and a much higher temperature would result in an overprediction of the reproductive output. Despite a higher seasonal reproductive output, the cumulative reproductive output of EP leatherbacks is predicted to be lower than that of NWA leatherbacks (Table 5).

4. Discussion

As environmental conditions experienced by different subpopulations of the same species differ, so too do their demography and life history traits. Most critical for conservation focus are the reproductive traits of a population, of which we highlight six that directly influence a population's longevity. It is important to note that population density affects both resources and mate availability, which are also crucial to viability but outside the scope of this study. Understanding the relationship between reproductive traits and environmental conditions could be crucial when making conservation decisions, and when deciding whether or not these relationships can be extrapolated between data-rich and data-deficient subpopulations (Caro and O'Doherty, 1999; Che-Castaldo and Neel, 2012).

For sea turtle species, the standard DEB model has increased understanding of the energetics and life-cycle of loggerheads and green turtles (Marn et al., 2017b; Stubbs et al., 2019), and how reproduction and growth are influenced by environmental cues and anthropogenic stressors (Marn et al., 2017a, 2018; Stubbs et al., 2020; Marn et al., 2020). Our updated DEB model for leatherback sea turtles, based on reproduction data specific to the NWA population, was able to achieve a good overall fit with realistic parameters. The model could be expanded in the future by explicit modeling of the partial endothermy shown by leatherbacks, but also provides useful information in its current, simplified form. We now have an enhanced understanding of the relationship between food availability, temperature, and leatherback reproductive traits, including the DEB model's ability to capture the observed inter-populational differences in life-history and reproductive traits by simulating resource limitation and warmer temperatures for EP leatherbacks.

4.1. *The model as a good representation of a leatherback turtle*

While incorporation of additional data resulted in a mathematically poorer model fit (higher MRE and SMSE), the data are now specific to a (sub)population and more extensive than the datasets used to fit the 2023 leatherback model. This updated parameter set is considered more realistic in the sense that parameter values fall within the range for other sea turtles and result in model predictions that fit the observed data. In cases where DEB parameter estimation relies primarily on trait data at a specific time point (such as age at birth or size at puberty), as was the case in the 2023 leatherback model, energy conductance, zoom

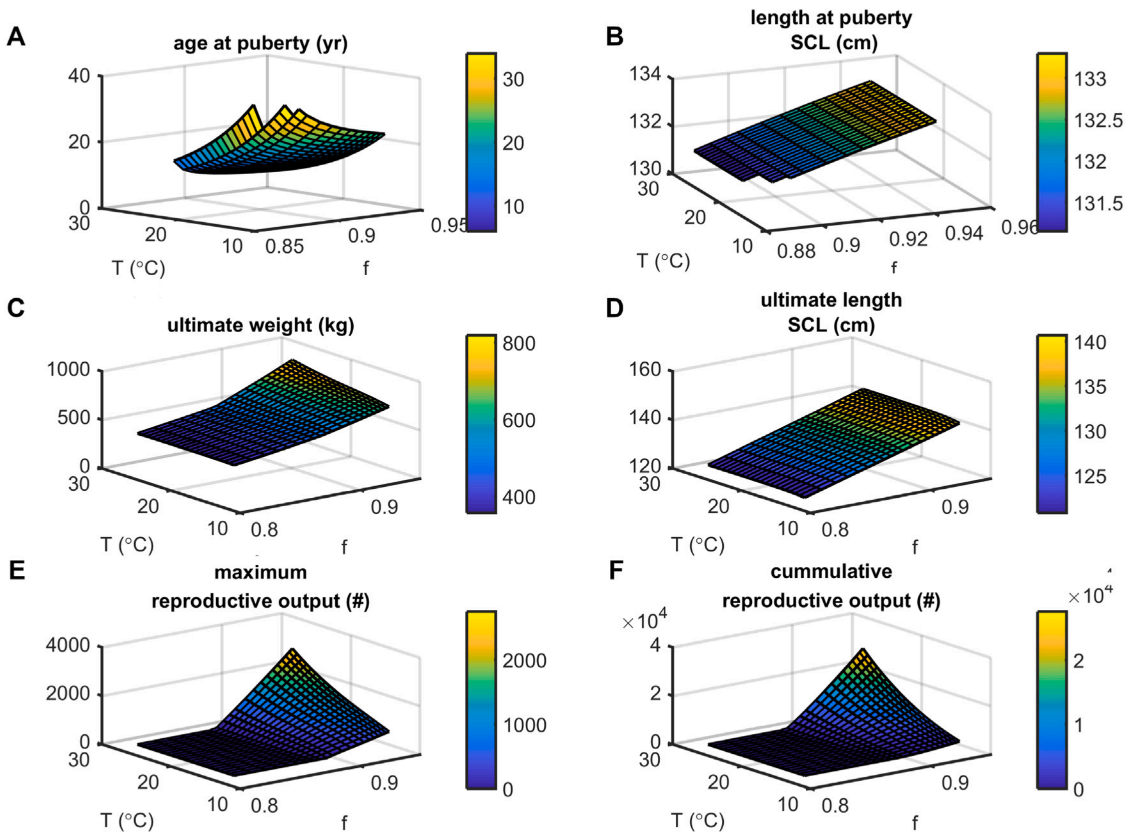


Fig. 4. 35-year simulations for a *D.coriacea* DEB model. The effect of (constant) food availability (f) and temperature (T) conditions on horizontal axis is represented for **(A)** age at puberty (year), **(B)** length at puberty (cm straight carapace length (SCL)), **(C)** ultimate weight (kg), **(D)** ultimate length (cm SCL), **(E)** maximum reproductive output (eggs per nesting season), and **(F)** cumulative reproductive output (eggs in a life time). The subplot title corresponds to the vertical (y-)axis of each subplot, and results are visualized using the color scales to the right of each plot. In sum, higher food availability is associated with greater length at puberty (B) and ultimate length (D); the combination of higher food availability and warmer temperatures is associated with younger age at puberty (A), greater ultimate weight (C), and larger both maximum (E) and cumulative (F) reproductive output. While food availability plays a role in all traits, the combined impact of more food and higher temperatures is most pronounced for age at puberty (A) and reproductive output (E, F).

factor, kappa, maturity at birth, and the shape coefficient are likely to be most sensitive to the inclusion of additional more elaborate and varied data (Lika et al., 2011). These are, in fact, the parameters for which values changed the most during model reparameterization from 2023 to this study.

The precociality coefficient for the leatherbacks is lower than for the other (sea) turtle species, suggesting that the difference between the size of hatchlings and adults is greater, and therefore, more energetic investment is required to reach adulthood for leatherbacks. As leatherbacks are the largest sea turtle species, this is not surprising, coupled with the subset of their life history traits that align with r-selected traits, such as the production of many eggs. The r/K framework characterizes species by their reproductive strategies, ranging from high-fecundity, low-investment r-strategists to low-fecundity, high-investment K-strategists (MacArthur and Wilson, 2001). Leatherbacks – like other sea turtles – have a maternal investment strategy that depends on many smaller eggs rather than fewer large eggs (Wallace et al., 2007), which potentially compensates for low survival rates of eggs and hatchlings in all species (Hirth et al., 1993). The relatively low ratio of maturity at birth and puberty is a trait of sea turtle species which enables the combination of large adults and many small offspring, while following a general pattern of ultimate mass of adults being proportional to the overall mass of offspring produced (Marn and Kooijman, 2022). Animals with larger maximum body size are expected to have higher reserve capacity ($[E_m]$), as this relates to the ability to tolerate fluctuations in food availability (Augustine et al., 2019). The reserve capacity of leatherbacks is multiple times higher than that of other sea turtles (Table A.2), reflecting the fact that the leatherbacks are the longest migrating sea turtle species, capable of traversing entire oceans between nesting years (Shillinger et al., 2008; Fossette et al., 2010).

Our model with the updated parameter values generally produces predictions that match the observed life-history traits and patterns well (size and age at relevant life events, growth, length-weight, and length-fecundity relationships, see Results). Ultimate weight is a notable exception, as there is a discrepancy between a datapoint and the corresponding model prediction. While it is true that there is substantial variation in the reported values for ultimate weight in leatherbacks (ranging from 300 kg to over 900 kg; see Appendix A), and we have selected a relatively small value of 370 kg for model calibration, there is also a mismatch between the data and predictions for the length-weight relationship for some datasets (Fig. A.2B). Therefore, the overprediction of almost 20% (Table 3) could reflect a suboptimal model setup. Furthermore, under the current setup, while length at puberty is predicted reasonably well, the weight at puberty predicted for the two leatherback populations surpasses the selected ‘ultimate’ weight (Table 5). We accommodated for a possibility of a change in shape (length–width relationship) occurring between early

Table 5

Predictions obtained using the *D. coriacea* DEB model parameterized on input data from the Northwest Atlantic (NWA) population, compared to independent life history data for the East Pacific (EP) leatherback population. Predictions were obtained by assuming that the NWA turtles experience slightly higher food availability ($f = 0.9$ vs. $f = 0.895$) and slightly lower temperatures than EP turtles (Kenyon, 2017; T = 21.13 °C vs. T = 22.5 °C).

Life-history trait	Prediction for NWA (f = 0.9, T = 21.13 °C)	Prediction for EP (f = 0.895, T = 22.50 °C)	NWA data	EP data	Reference (EP)
Age at puberty (yr)	15.51	14.73	19.25	18.50	Avens et al. (2020) in NMFS & USFWS, 2020
SCL at puberty (cm)	131.7	131.5	125.6	129.7[b]	Avens et al. (2020) in NMFS & USFWS, 2020
Weight at puberty (kg)	497.31	493.12	NA	NA	NA
Ultimate SCL (cm)	133.6	132.9	151.1	145.33	Stewart et al. (2007)
Ultimate weight (kg)	544.61	536.99	323	268	Wallace et al. (2005)
Maximum seasonal reproduction[a]	370	417	408.7	466	NMFS & USFWS, 2020
Cumulative reproduction	2171	1754	NA	NA	NA
SCL at birth (cm)	5.65	5.65	6.18	5.68	Bandimere et al. (2021)
Hatchling weight (g)	45.48	45.28	46.03	41.06	Bandimere et al. (2021)

[a] Remigration interval simulated as 2.5 years for the NWA population and 3.5 years for the EP population (NMFS and USFWS, 2020). If the same (2.5 years) remigration interval assumed, EP leatherbacks would produce around 300 eggs per nesting season.

[b] Mean SCL from EP nesting beaches.

life and adulthood of leatherbacks (Pate and Salmon, 2017; Salmon and Scholl, 2014), but the estimated parameter values do not substantially differ (0.34 and 0.38, Table 4). Other sources of this discrepancy could concern the way that the blubber and carapace (shell) have been handled. In the current model setup – due to (i) the lack of precise data on relative contributions of carapace and blubber to total weight, and (ii) motivation to keep the model relatively simple and straightforward – the contribution of carapace and blubber to the total body mass is considered constant throughout life, and these structures are not modeled explicitly. Considering the relative size of carapace and blubber, and the important physiological role they play (not only in size but also in thermoregulation, Greer et al. 1973, Davenport et al. 2009), it could be beneficial to expand the model and track the blubber and carapace explicitly.

4.2. Effect of food and temperature on growth, development, and reproduction of leatherbacks

Our measure of optimal reproductive capability combines younger age at puberty, longer length (at puberty and at ultimate size), greater ultimate weight, larger maximum reproductive output, and larger cumulative reproductive output, i.e., traits better suited to sustaining a population. We showed a direct relationship among these traits (as predicted by the DEB model) and a range of simulated temperature and food availability used as model inputs during a lifespan of leatherback turtles (Fig. 4). In doing this, we have identified ranges and combinations of relative food availability and temperature which would support maturation and reproduction of leatherback females.

This direct relationship between the environment (i.e. food availability and temperature) and the traits corresponds to findings from a loggerhead and green turtle DEB model, which showed faster maturation (younger age at puberty) and a higher reproductive output when either food availability or temperature was increased (Marn et al., 2017a; Stubbs et al., 2020). It is worth noting, however, that in the case of leatherback turtles, the effects of environmental temperature are likely to weaken with body size. This is because leatherback turtles develop partial endothermy as they grow, and are (as large juveniles and adults) able to maintain a body temperature higher than ambient temperature (Davenport et al., 1990; Paladino et al., 1990; Davenport et al., 2009; Bostrom and Jones, 2007; Bostrom et al., 2010). Furthermore, temperature was simulated as a constant, so neither long deep dives performed by both young and older individuals (into areas with substantially colder temperatures, Paladino et al., 1990), nor temperature changes experienced at certain points of the life cycle due to long term migrations, were taken into account. Simulation conclusions, especially those of temperature effects, should therefore be interpreted within the context of the ambient temperature not necessarily matching the temperature experienced by the turtle, as well as it not being constant.

The model outputs can, also in the current simplified model formulation, be used as inputs to a population model, thus identifying conditions capable of supporting a viable leatherback population. Different populations can experience differing levels of resources (Wallace et al., 2006b), which could result in resource limitation at the population level and cause some populations to be more vulnerable to extirpation than others (Wallace et al., 2006a; Hatase and Tsukamoto, 2008; Marn et al., 2018). Identifying such regions or populations can be aided by models such as the DEB model presented here, as sufficient reproductive output of individuals is dependent on their ability to assimilate enough energy to achieve a high reproductive potential during their lifetime.

4.3. Reproducing the observed inter-population variability: NWA model for EP population

Our results indicate that while subpopulation-specific data are best suited to predict parameters for that subpopulation, extrapolating to another subpopulation where data gaps exist may still be useful for decision-making, especially when a decision is needed before additional input data can be collected. Understanding the interplay of shifting food and temperature conditions in different populations could be crucial in conservation planning at the sub-population and population level, and potentially to actions aimed at enhancing reproductive potential of one population to contribute to the persistence of an entire species. In the absence of data specific to a subpopulation, conservation decisions are sometimes made using data from other subpopulations, or even other species (Caro and O'Doherty, 1999; Che-Castaldo and Neel, 2012; Kerr, 2021). All sea turtle species are long-lived and generate many eggs that are not cared for by the parents. Since sea turtles exhibit both r- and k-selected traits in this way, their reproductive traits are likely conserved (Miller, 2017; Marn and Kooijman, 2022). All sea turtle species exist in the same trait space in an MDS plot (Fig. 3), so inter-species variability may not affect reproduction dramatically.

Of the seven leatherback turtle populations, we focused on the NWA population which has the most data (types) available, but explored the applicability of the model also to the Critically Endangered EP population which may be experiencing resource limitations along their migratory routes (Wallace et al., 2006b). Simulating a slight resource limitation (reduction of 5% of the NWA default food availability, corresponding to scaled functional response of 0.895 compared to the 'default' value of 0.9) indeed resulted in a smaller ultimate size, and smaller lifetime reproductive output. The observed seasonal reproductive output of EP leatherbacks, however, is comparable to that of NWA leatherbacks. This was successfully reproduced by the same model when a 1 °C warmer temperature was assumed for EP leatherbacks (22.5 °C instead of 21.13 °C), and the observed remigration intervals of 3.5 years were used for the respective seasonal output calculations (Table 5). The assumption of slightly warmer temperature is not unrealistic, in the context of the Pacific Ocean having a wider region of warmer water compared to the Atlantic (Kenyon, 2017), implying that EP leatherbacks have a relatively high probability of encountering warmer water than NWA leatherbacks during their migrations. Of course, the reality is more complex than our simulations: the El Niño/Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) have a complex relationship to SST within each basin, and environmental stochasticity plays an important role on food availability in both ocean basins (Ding et al., 2023), with cooler periods in the EP associated with more upwell/nutrients and warmer periods with deprivation – thus impacting also growth, reproduction, and remigration intervals of leatherbacks (see Saba et al., 2007).

4.4. Implications for conservation

Leatherback turtles have the longest migrations of all sea turtle species and could take almost three decades to mature (Avens et al., 2009), making them vulnerable to numerous threats throughout their lives. All seven leatherback turtle populations are in various stages of population decline (IUCN, 2018), despite regional conservation efforts since 1959 and global assessment efforts since 2003 (Carr, 1959; SWOT, 2003). Some input data for the leatherback model presented here were based on averages for females from various nesting beaches and subpopulations within the NWA, and the environmental conditions were simulated to be constant, and therefore not considering partial endothermy, within-seasonal variations or density-dependent food/partner availability. While annual averages of environmental conditions can be used to generate insights about the response of an individual to its environment, true conditions vary greatly in the wild.

Specifically, as a female leatherback hatchling leaves its nesting beach and returns to reproduce almost two decades later (NMFS and USFWS, 2020), it follows a unique migratory path that includes continuous variation in food availability and temperature. The ability to access suitable water temperatures and assimilate sufficient food is critical for survival to adulthood, yet this is not captured within our current model. To simulate oceanic environments more realistically, model forcing could be informed by an individual-based migration model for leatherbacks, such as the output from the Sea Turtle Active Movement Model (STAMM; Gaspar and Lalire, 2017; Lalire and Gaspar, 2019). These models incorporate daily choice of an individual turtle to move towards optimal temperature and food habitats when gradients exist, and could therefore provide realistic estimations of environmental conditions for turtles in different subpopulations. DEB model outputs could then be integrated with subpopulation-specific environmental conditions to provide insights on reproductive potential where extensive demographic data do not exist.

Understanding population responses becomes extremely relevant as the interplay of resource availability and temperature in the two oceans is likely to be shifting. For example, within 15 years the average remigration interval for EP leatherbacks has decreased from 3.7 to 3.3 years, while that for NWA leatherbacks has increased from 2 to 2.7 years (Wallace et al., 2006b; NMFS and USFWS, 2020). Mechanistic models, such as the one presented here, could be extremely useful for elucidating long-term and/or hard-to-observe changes, such as lifetime reproductive output. For example, our model predictions match the observations of a similar seasonal reproductive output of a NWA and EP female. However, the cumulative lifetime reproductive output is predicted to be 19% lower for an EP female due to resource limitations (Table 5). These types of metrics are hard to measure empirically, and could be obscured by more readily obtained short-term metrics, such as number of eggs or nests per female for a given season.

5. Conclusion

Here we demonstrate how incorporating population-specific data from literature and captive rearing facilities for a highly migratory species can alter the goodness of fit and output of a DEB mechanistic model. When put in context with other turtle species, leatherback turtles exhibit traits and parameters that are aligned to other sea turtle species but also stand alone, which may relate to their status as an exceptional species: the largest, deepest-diving, and longest-migrating of the extant sea turtle species. Food and temperature conditions affected reproductive traits, in which more abundant food and warmer temperatures corresponded with more optimal reproductive traits. However, by simulating constant environmental conditions over a lifespan, we lose the dynamic fluctuation of food and temperature that is realistic for migrating leatherbacks. Comparisons of the NWA to the EP population suggests that the EP population is experiencing resource limitation, combined with slightly warmer sea temperature. We provide insights about leatherback reproduction that are unattainable through field data collection methods, such as lifetime reproductive output. These (DEB) model outputs could inform conservation actions, particularly the understanding of how different nesting beach conditions or migratory paths could impact the reproductive output of females, and in turn, population viability in the face of threats such as climate change.

CRediT authorship contribution statement

Anna A. Ortega: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jeanette Wyneken:** Writing – review & editing, Data curation. **Nicola Mitchell:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **George Shillinger:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Nina Marn:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Model setup and additional results

A.1. Data preparation, model assumptions, parameters

We focused on the NWA population of leatherbacks as more data are available for this population. The existing (DEB-related) information for the leatherback turtle was already present in the Add-my-Pet (AmP) collection of data and DEB parameters (AmP entry: Kooijman and Kearney, 2023), and was used as a starting point and is referred to as '2023 leatherback model' in the manuscript; we present here the choices made and resulting differences compared to the 2023 model (i.e. AmP entry): data and predictions for both models are in Table A.1, and model parameters in Table A.2. We also list more general assumptions and choices made while parameterizing our (NWA) leatherback DEB model.

Hatching vs. birth. Lacking precise data, we assumed that hatching (leaving the egg or nest) coincides with birth in DEB theory (the moment when an individual starts feeding), thus assuming no substantial growth or development between hatching and the moment that the hatchling stops relying on the yolk sac. The assumption applies also to other data pertaining to hatching and birth (Lb, Wwb and Wdb). Egg weight was predicted in the model as initial wet weight (Ww0), but was ignored already in the 2023 model because it "needs detailed modeling of the contribution of water to weight" (AmP entry: Kooijman and Kearney, 2023)

Puberty. Mean maturation for NWA leatherbacks is set as 19.25 years, at mean water temp (21.13°) averaged between high latitudes (15–17 °C) and low latitudes (25–27.5°) water temperature mean values. Growth models in Zug et al. (1986) suggested a value between 6.8 and 16.1 yrs. Length at puberty (125.6 cm straight carapace length, SCL) was calculated based on an Avens 2020 study about mean age at maturation, which used ossicles as an estimate of age (minimum was 109.56 cm SCL). Mean maturation CCL for NWA is 129.2 cm converted to SCL = 125.6 using Avens 2009 methods (better regression fit than Jones et al. (2011) when tested on nesting female data).

Ultimate size $\mathbf{L}_i$ = 151.07 cm SCL, averaged from 19 different studies measuring the size of nesting females (Avens et al., 2020; NMFS and USFWS, 2020, and studies in Parham and Zug, 1997). Previous AmP entry (Kooijman and Kearney, 2023) used values from Girondot et al. (2021): Max SCL values for both sexes measured on the French Caribbean Atlantic coast (n = 300) ; even though this excludes first-time (smaller) nesters, the value might be inflated by few large individuals. Jones et al. (2011) reported Li around 140 cm SCL as obtained by the models. $\mathbf{Ww}_i$ = 370 kg. For ultimate size, we opted to use the average maximum size as opposed to the largest ever recorded individual, because we want the model to represent an average leatherback turtle. The value of 370 kg was selected based on several more recent Refs. Paladino et al. (1996), Lutcavage et al. (1992) and Harms et al. (2007) and informed by historic records (Eckert and Luginbuh, 1988, Guiness book of records). Paladino et al. (1996) report values of 13 adult female leatherback turtles (*D. coriacea*) found nesting in 1990, 1991, and 1992, at their nesting beaches near Tortuguero (Limon Province, Costa Rica, NWA) and Playa Langosta (Guanacaste Province, Costa Rica, EP). In their Table 1 they report values for all turtles regardless of the location, and list several mean values: 354 kg (n = 10), 366 kg (n = 10), and 300 kg (n = 3). Lutcavage et al. (1992) report weights of five adult females on Tortuguero beach, Costa Rica: 320 kg, 315 kg, 370 kg, 355 kg, 350 kg (mean 342 +/−23 kg). Harms et al. (2007) report 10 adult females nesting on Trinidad weighing between 242 kg to 324 kg. Guiness book of animal facts and feats (Gerald L Wood, 1982) cites Duron 1978 for a record of a captured male in a fishing net at Longeville, Vendee Dept, W France that was 800 kg, with two other records off of West France at 650 and 600 kg. The report by Eckert and Luginbuh (1988) states that "the largest ever recorded leatherback turtle was found dead on Harlech beach in Gwynedd, Wales. The animal, an adult male weighing 2016 pounds (916 kg), boasted a curved carapace length of 101 inches (256.5 cm); plastral length and width were 53 inches (134.6 cm) and 32 inches (81.3 cm), respectively. Foreflipper span, measured ventrally from flipper tip to flipper tip, was 94.75 inches(240.7 cm)". Value used in the 2023 model (Kooijman and Kearney, 2023) was 420 kg, Spotila (2004) obtained from the AnAge database (de Magalhaes et al., 2024).

Reproduction. Maximum reproductive output value was based on updated averages of clutch frequency (5 clutches per season), clutch size (81.74 eggs per clutch), and remigration interval (2.7 years) for the NW Atlantic stock (NMFS & USFWS 2020), which provided averages for several nesting beaches within the NW Atlantic. For simulating the seasonal and total (lifelong) reproductive output of EP leatherbacks, a remigration interval of 3.5 years was used (NMFS & USFWS 2020), and no inference on clutch size was made.

Mass-specific rates. Mass-specific metabolic rate provided in Jones (2009) for turtle of about 350 kg was assumed in the 2023 model (AmP entry Kooijman and Kearney, 2023) to correspond to the assimilation rate, because investment into growth and reproduction were assumed negligible (= no energy fixed in structure or gametes, and therefore no corresponding overheads contributing to metabolic rate). In the 2023 model this data point was ignored because of inconsistency with other data and because allometric correction was applied for obtaining the specific rate, but value is provided in Table A.1 for reference. The maximum adult intake of jellyfish (0.54 W/kg) was provided by the same author (Jones, 2009) for a turtle of about 350 kg, where 82 kg jelly fish/d for 250–450 kg turtle with 200 J/g food was calculated as = 82/350*200 000/24/60/60 W/kg (AmP entry Kooijman and Kearney, 2023). This value was replaced with 1.14 W/kg based on work by Wallace et al. (2006b): energy budget calculations between EP and NWA leatherbacks, suggesting that average required feeding rate for St. Croix (NWA) leatherbacks for a 2.85 year remigration interval is 127 kg/d. Leatherback prey energy content was set to 310 kJ/kg wet mass based on Davenport and Balasz (1991). Assuming the same ingestion rate of 82 kg jellyfish/day, the updated calculation for a 400 kg turtle would be: 82/400*310 000/24/60/60 W/kg = 0.7355 W/kg, and with 127 kg/day ingestion rate: 1.14 W/kg.

Univariate datasets (Table 2). New data: previously unpublished data on growth sourced from captive rearing (J. Wyneken), and length-fecundity relationship (literature). Compared to 2023 model (AmP entry Kooijman and Kearney, 2023), we kept growth and biometry data (Tables 3.1, 3.2 and 3.3, and Figure 3.2 in Jones, 2009). However, we used partial data from Table 3.1 (where N>3), and tL1 data in the original entry had mixed captive and wild turtles- now revised.

Food availability. Scaled food (f) for the wild leatherbacks was assumed to be less than maximum (f = 0.9 instead of f = 1), and this value was applied for all calculations pertaining to wild turtles.

Table A.1
Comparison between observations and model predictions, at the temperature that had been used for the corresponding observation (see the online AmP files for details, 2023 model AmP entry: AmP, 2025), and the assumed scaled functional response $F = 1$ in the 2023 model, and $f = 0.9$ in the new model. We present the values (data and predictions) of the previous model version for context, designated as 2023. The relative error (RE) of the predictions is given next to each prediction.

Data & Description	Unit	Value used 2023 model	Prediction 2023 model (RE)	Value used Now	Prediction Now (RE)	Reference 2023 model
ab, Age at birth[a]	d	60	50.81 (0.15)	63	52.85 (0.161)	Jones (2009) and de Magalhaes et al. (2024)
ap, Age at puberty	yr	15.30	15.64 (0.02)	19.25	15.53 (0.193)	Jones (2009)
am, Life span	d	10 950	11 000 (0.01)	11 041	10 950 (0.008)	de Magalhaes et al. (2024)
Lb, straight carapace length at birth	cm	6.31	6.638 (0.05)	6.18	5.651 (0.085)	Jones (2009)
Lp, SCL at puberty	cm	121	140.7 (0.16)	125.6	131.7 (0.049)	Jones (2009)
Li, ultimate SCL	cm	175	142.7 (0.19)	151.07	133.6 (0.115)	Wikipedia *D.c.* entry
Egg weight[b]	g	85.5	55.72 (0.35)	83.59	54.9 (0.343)	Thompson (1993)
Wwb, wet weight at birth	g	46	43.41 (0.06)	46.22	46.03 (0.112)	Jones (2009)
Wdb, dry weight at hatching	g	9.776	9.551 (0.02)	9.776	13.64 (0.396)	Thompson (1993)
Wwi, ultimate wet weight	kg	420	426.2 (0.01)	370	439.5 (0.188)	de Magalhaes et al. (2024)
Ri, maximum reproduction rate[c]	#/d	0.3836	0.3791 (0.01)	0.4147	0.4094 (0.013)	Jones (2009)
pAm, Mass-specific metabolic rate[b],[d]	W/kg	0.4	0.1187 (0.70)	0.41	0.2263 (0.448)	Jones (2009)
pXm, Max. adult intake of jellyfish[e]	W/kg	0.54	0.5311 (0.02)	1.14	0.8115 (0.281)	Jones (2009)

References correspond to previous AmP entry (Kooijman and Kearney, 2023). For data sources corresponding to values used now, please refer to Table 3 in the main text.

[a] We assumed that hatching (leaving the egg or nest) coincides with birth in DEB theory (the moment when an individual starts feeding). The assumption applies also to other data pertaining to hatching and birth (Lb, Wwb and Wdb).

[b] Given relative weight of zero during parameter estimation. Also applies to data point for pAm. See text and online scripts (AmP entry: Kooijman and Kearney, 2023) for details.

[c] 2023 model: 8 clutches, 70 eggs/clutch, nesting each 4 yr. New model: Clutch frequency = 5/year, clutch size = 81.74 eggs/clutch, remigration interval = 2.7 years.

[d] Comment (2023 model): about 350 kg; assumed that metabolic rate (measured) corresponds to assimilation rate (calculated) and other dissipation is negligible. Datapoint disregarded already by 2023 authors due to inconsistency; provided here for reference.

[e] Comment (2023 model): about 350 kg, 82 kg jelly fish/d for 250–450 kg turtle with 200 J/g = 82/350*200000/24/60/60 W/kg; updated to 127 kg food/day for 400 kg turtle with 310 J/g; see Appendix A.1.

Table A.2
List of primary and auxiliary parameters for all seven sea turtle species: **Dc** - *Dermochelys coriacea* (Amp entry: Kooijman and Kearney, 2023), *D. coriacea* (this study), **Cc** - *Caretta caretta* (Marn et al., 2020), **Cm** - *Chelonia mydas* (Stubbs et al., 2019), and parameter values taken from AmP (2025): **Lk** - *Lepidochelys kempii*, **Lo** - *Lepidochelys olivacea*, **Nd** - *Natator depressus*, **Ei** - *Eretmochelys imbricata*.

Parameter	Symbol	Dc (2023)	Dc (2025)	Cc	Cm	Lk	Nd	Lo	Ei	Unit
Max. assimilation rate[a]	$\{\dot{p}_{Am}\}$	4307.95	3780.3	906.1	900.96	728.426	786.249	971.923	1716.37	$\mathrm{J\,d^{-1}\,cm^{-2}}$
Digestion efficiency	κ_X	0.22346	0.2788	0.8	0.8	0.8	0.8	0.8	0.8	–
Energy conductance	$\dot{v}$	0.06278	0.139	0.0681	0.1015	0.0424	0.1262	0.05756	0.043761	$\mathrm{cm\,d^{-1}}$
Allocation fraction to soma	κ	0.2502	0.6349	0.7286	0.7067	0.6929	0.8459	0.89429	0.91807	–
Volume-spec. somatic maint.	$[\dot{p}_M]$	34.97	47.06	11.20	12.80	20.17	18.38	32.38	59.45	$\mathrm{J\,d^{-1}\,cm^{-3}}$
Cost for structure	$[E_G]$	5770.67	7812	7322	7845	7840.77	7816	7354.52	7833.92	$\mathrm{J\,cm^{-3}}$
Maturity at birth	E_H^b	55.77	47.58	25.350	37.654	13.24	37.4	4.785	2.017	e+03 J
Maturity at puberty	E_H^p	14.78	12.35	0.98750	2.4972	0.3648	0.5899	0.2554	0.3292	e+08 J
Weibull aging acceleration	$\dot{h}_a$	15.73	6.881	1.1120	0.3789	14.21	0.1874	3.273	1.811	e–10 $\mathrm{d^{-2}}$
Arrhenius temp.	T_A	8000	8000	7200	7680	8000	6274	8000	8000	K
Density (structure, reserve)	$d_V = d_E$	0.22	0.3[b]	0.28[c]	0.3	0.3	0.3	0.3	0.3	–
Max. reserve capacity	$[E_m]$	68.619	27.912	6.230	16.885	39.221	13.305	8.8783	17.179	e+03 J
Precociality coefficient	s_H^{bp}	0.4203	0.3852	2.567	1.508	3.629	6.340	1.874	0.612	e–04 J
Supply stress[d]	s_s	0.0452	0.1397	0.0630	0.0643	0.0768	0.0723	0.0583	0.0537	
Shape coefficient, SCL	δ_M	0.21687	0.3813[e]	0.3744	0.3852	0.3629	0.4252	–	0.2351	–
Delay until start of development (at 30 °C)	t_0	20.53	31.58	–	12.79	33.91	27	–	–	d

All rates are given at reference temperature $T_{ref} = 273\,\mathrm{K}$. Primary and auxiliary parameters for which the default values were used are listed below. For notation rules see `www.bio.vu.nl/thb/deb/deblab/`.

Default parameters: Max. searching rate, $\{\dot{F}_m\} = 6.5\ \mathrm{l\,d^{-1}\,cm^{-2}}$; Defaecation efficiency (of food to faeces), $\kappa_P = 0.1$; Reproduction efficiency, $\kappa_R = 0,95$; Maturity maint. rate, $\dot{k}_J = 0.002\,\mathrm{d^{-1}}$; Gompertz stress coefficient, $s_G = 0.0001$.

[a] Indirectly estimated primary parameter, $\{\dot{p}_{Am}\} = L_m^{ref} z[\dot{p}_M]/\kappa$,using the estimated value Cc: $z = 44.32$, Cm: $z = 49.73$; Lk: $z = 25.02$, Dc: $z = 51.57(2025) z = 30.82$ (2023).

[b] Removed dV = dE = 0.22 as no reference was provided.

[c] See Marn et al. (2017b) for details.

[d] Supply stress calculated as $s_s = (k_J \cdot E_H^p \cdot [\dot{p}_M]^2)/(f^3 \cdot \{\dot{p}_{Am}\}^3)$, see Lika et al. (2014). Median value for sea turtles is 0.0560 (Marn et al., 2018).

[e] 0.3434 late juveniles and adults SCL > 39 cm.

A.2. Additional simulation results

Here we present model predictions for growth in length and weight, and reproductive output simulated for several selected (constant) food levels (Fig. A.3) and temperatures (Fig. A.4). Combination of food and temperature result in different values for tracked endpoints; see also 3D plot in the main text (Fig. 4).

A.3. Multidimensional scaling

We have applied multidimensional scaling (MDS) on trait-based distances between species (Kooijman et al., 2021) by using 13 traits,

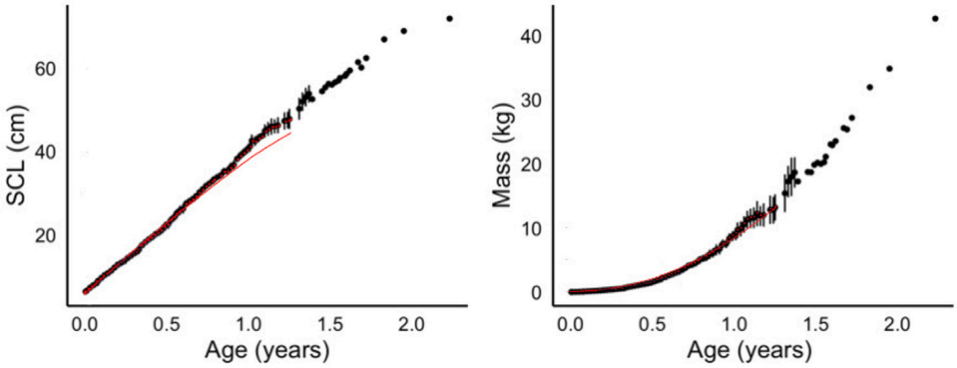

Fig. A.1. Growth of captive leatherbacks in length (SCL) and mass (kg) from Jones 2009 with standard deviations. The first data points are for 20 leatherbacks, but due to mortality, the sample size reduces to two individuals from 1.33 years, and to one individual from 1.39 years onward. DEB model predictions in red.

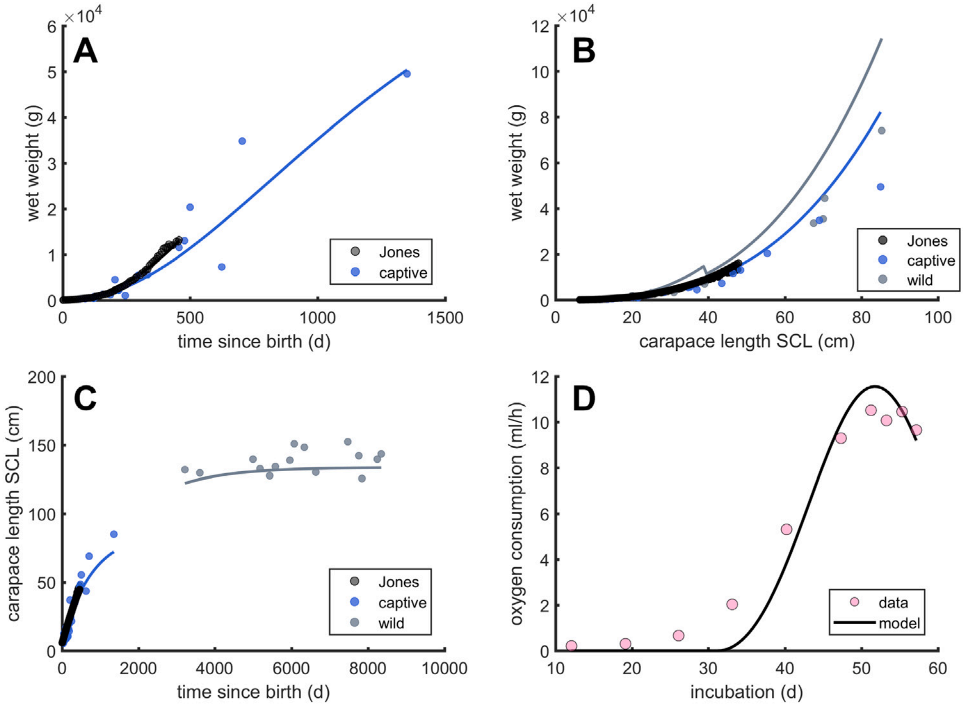

Fig. A.2. Data (dots) and model fits (lines) for data available in the 2023 model (Amp entry Kooijman and Kearney, 2023). **Panels (A-C)** Growth data compiled within Jones (2009) for length and weight over time. This compilation included literature review of leatherback growth in the wild and in captivity; data sources per data type (Jones/captive/wild) referenced as provided in Jones (2009): **tW and LW** (panels A and B): Jones (2009), *captive*: Deraniyagala, 1939, Bels et al. 1988, Phillips, 1977, Birkenmeier, 1970; *wild in panel B*: MTN(1996), Deraniyagala, 1939, J.Wyneken (unpublished), NOAA (NMFS/PIFSC), MTN(2004), M. Conti (pers.comm; note: now M. Koperski); **tL** (panel C): Jones (2009), *captive*: Deraniyagala, 1939, Bels et al. 1988, Frayr, 1970, Phillips, 1977, Birkenmeier, 1970; *wild*: Zug and Parham 1996 skeletochronology data cited in Jones (2009). Model predictions were obtained with the assumption that for the wild data the default conditions were experienced (f = 0.9, T = 21.13 °C), for captive data measured by Jones T = 24 °C and estimated f = 0.666, and for other captive data T = 24 °C and estimated f = 0.5845. **Panel (D):** oxygen consumption during incubation at 30 °C.
Source: Data from Thompson (1987).

but a different set and/or number of traits could have been chosen (see Kooijman et al., 2021). Selected traits were: maximum lifespan (a_m), age at puberty (a_p), age at birth (a_b), maximum wet weight (W_w^i), wet weight at puberty (W_w^p) and at birth (W_w^b), maximum reproduction at ultimate size (R_i), supply stress (s_s), ratio of maturity at birth and puberty (precociality coefficient $s_H^{bp} = E_H^b/E_H^p$), somatic maintenance rate ($[\dot{p}_M]$), conductance ($\dot{v}$), allocation to soma (κ), and maximum reserve density ($[E_m]$). It is relevant to note that the life-history traits, such as age and size at life events, are not as observed but as predicted by the model.

The MDS needs a matrix of distances between species as input. The matrix is created based on the symmetric bounded loss function (Marques et al., 2019), which simultaneously takes into account all analyzed traits: the number of rows in the matrix corresponds to the number of species (here - 93 species of turtles), and the number of relevant columns depends on the eigenvalues: typically only the first few columns are relevant because the second eigenvalue is much smaller than the first one etc. By correlating each trait with (relevant) eigenvalues, it is possible to determine which traits contribute the most to the observed pattern among species. MDS was performed using the in-built Matlab function `cmdsc.m`, and the correlation of trait distances with eigenvalues was performed using the DEBtool_M function `corr.m`. Please see Kooijman et al. (2021) for presentation and examples of MDS of animal traits in the context of DEB theory, and Marn and Kooijman (2022) for an in-depth analysis of DEB-traits, including the MDS analysis, of turtles, crocodiles and other reptiles.

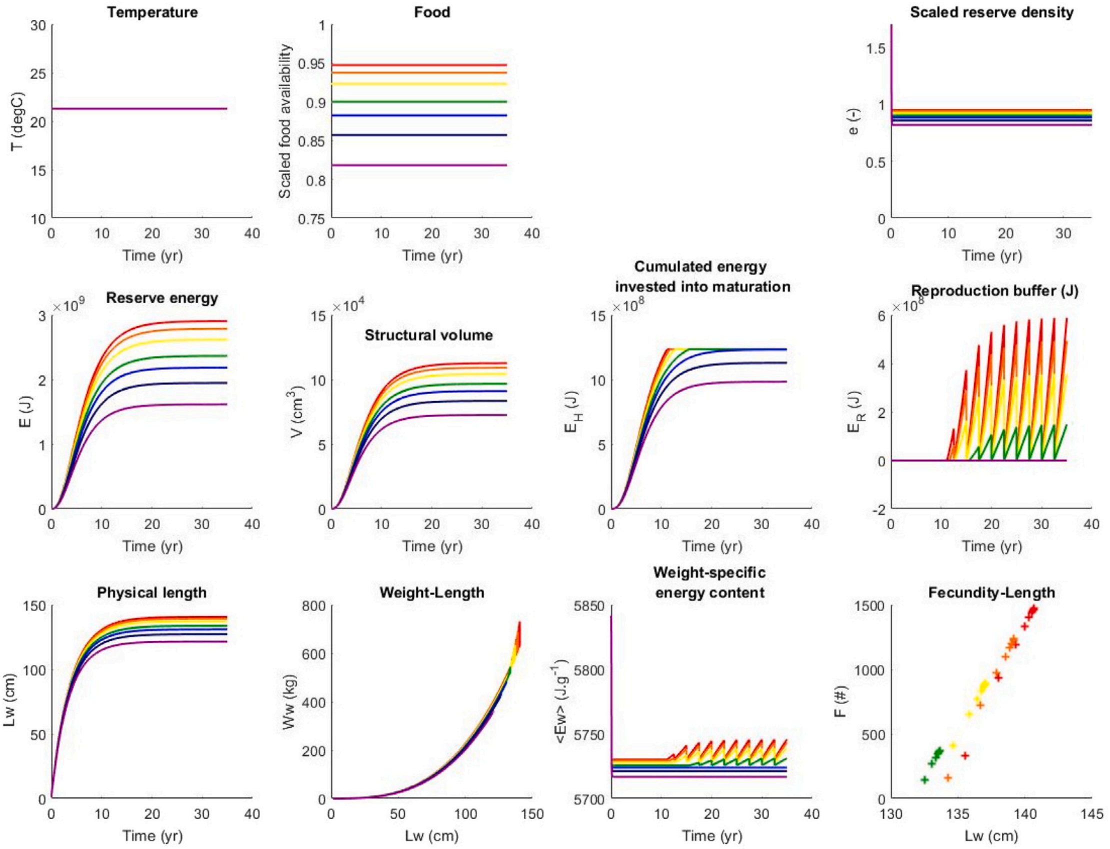

Fig. A.3. Simulations for growth and reproduction of NWA leatherback turtles for several food levels (half of the default available food in the NWA to twice as much food) under constant temperature (T = 21.12 °C). Simulation run for 35 years. Food availability has a strong effect on the size of the turtle and her reproductive output, with the two lowest simulated food levels not being sufficient for turtles to attain sexual maturity. DEB state variables (Reserve energy, Structural volume, Maturity, Reproductive buffer) are depicted in row 2, whereas observable traits (Physical length, Weight-length relationship, Fecundity) are provided in row 3. Model parameters as in Table A.2.

Table A.3
Simulations for growth and reproduction of NWA leatherback turtles at a range of (constant) food availabilities, at temperature T = 21.15 °C; simulations ran for 35 years.

mdfy (%)	f	ap (yr)	Lp (cm SCL)	Li (cm SCL)	Wi (kg)	Ri (egg/ season)	cumF (eggs)
−50	0.818	NaN	NaN	121.49	362.5	0	0
−45	0.832	NaN	NaN	123.53	386.0	0	0
−40	0.844	NaN	NaN	125.29	407.0	0	0
−35	0.854	NaN	NaN	126.81	426.0	0	0
−30	0.863	NaN	NaN	128.15	443.2	0	0
−25	0.871	NaN	NaN	129.33	458.8	0	0
−20	0.878	NaN	NaN	130.38	473.0	0	0
−15	0.884	23.96	131.15	131.32	488.2	31	86
−10	0.890	18.50	131.37	132.17	508.6	154	729
−5	0.895	16.62	131.56	132.94	527.3	266	1452
0	0.900	15.51	131.73	133.64	544.6	370	2171
+10	0.908	14.17	132.02	134.86	575.4	554	3532
+20	0.915	13.36	132.26	135.90	602.1	713	4760
+30	0.921	12.80	132.46	136.79	625.4	851	5860
+40	0.926	12.38	132.63	137.57	645.9	973	6845
+50	0.931	12.06	132.78	138.24	664.1	1080	7728
+60	0.935	11.80	132.91	138.84	680.4	1176	8523
+70	0.939	11.59	133.02	139.37	695.0	1262	9242
+80	0.942	11.41	133.12	139.85	708.2	1340	9894
+90	0.945	11.26	133.21	140.28	720.2	1410	10 488
+100	0.947	11.13	133.29	140.67	731.1	1474	11 032

Columns: 'mdfy (%)'- factor by which the initial food availability was modified; 'f' - resulting scaled functional response for food availability; 'ap (yr)' - predicted age at puberty in years; 'Lp (cm SCL)' - predicted length at puberty in cm of straight carapace length; 'Li (cm SCL)' - predicted ultimate length in cm of straight carapace length; 'Wi (kg)' - predicted ultimate weight in kilograms; 'Ri (egg/season)' - predicted seasonal reproductive output by one nesting female at our estimate of maximum size, in number of eggs; 'cumF (eggs)' - predictive cumulative lifetime reproductive output in number of eggs. Remigration interval is simulated as 2.5 years.

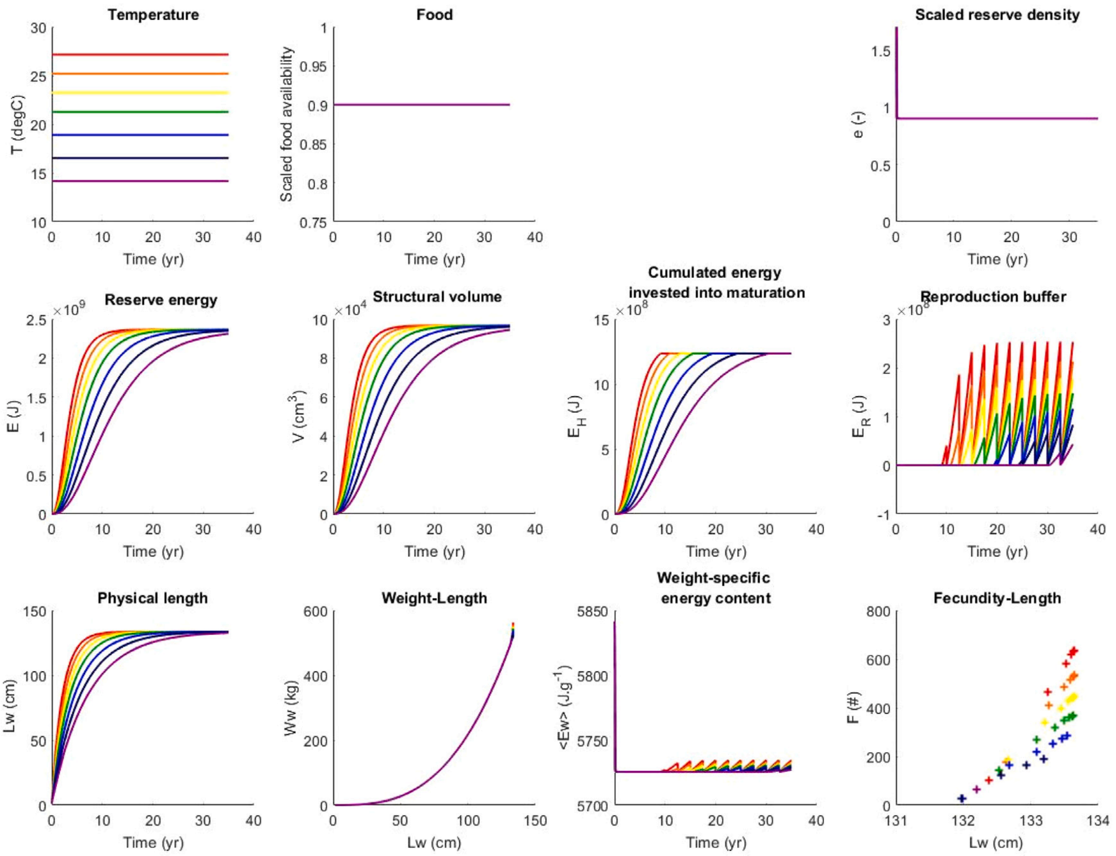

Fig. A.4. Simulations for growth and reproduction of NWA leatherback turtles for several temperatures (T = 14–28 °C) under constant food availability resulting in scaled functional response of $f = 0.9$. Simulation run for 35 years. Temperature has an effect on rates (growth, maturation, and reproduction rate), but no effect on ultimate size. DEB state variables (Reserve energy, Structural volume, Maturity, Reproductive buffer) are depicted in row 2, whereas observable traits (Physical length, Weight-length relationship, Fecundity) are provided in row 3. Model parameters as in Table A.2.

MDS clusters species in multidimensional space. We present in the manuscript 'only' a two-dimensional plot (Fig. 3), but the eigenvalues in the bottom right corner of the figure indicate that the first dimension is the most relevant one: second and third eigenvalue are already much smaller than the first and the second one. Therefore, the 2D-graph is a good indication of the species' position relative to each other; for an interactive image that can be rotated see Supplementary Material. As a general pattern, we can observe that sea turtles (Cheloniodiea + Dermochelydae) cluster together relative to the x-axis (representing the first eigenvector) and relative to the y-axis (representing the second eigenvector), whereas most of the tortoises (Testudinidae) cluster together relative to the y-axis. When correlating the traits with the first eigenvector, the weight at birth, ultimate weight and age at puberty have the highest correlation (W_w^b +0.64, W_w^i +0.53, and a_p +0.53) with the first eigenvector, followed by the maximum reserve density ($[E_m]$ −0.51), maximum lifespan (a_m +0.46) and somatic maintenance rate ($[\dot{p}_M]$ −0.40) correlating with the second eigenvector. This points to the main traits characterizing the analyzed groups, and is consistent with the results of MDS performed on reptiles as a group, where the strongest correlations with the first two eigenvectors were for a_m, a_p, s_H^{bp}, $[E_m]$, $[\dot{p}_M]$, and $\{\dot{p}_{Am}\}$ (Marn and Kooijman, 2022).

A.4. Parameter sensitivity analysis

Several primary parameters (κ, $\dot{v}$, $[\dot{p}_M]$, $\{\dot{p}_{Am}\}$, E_H^p) and one auxiliary parameter (del_{Ma}) were selected to check the sensitivity of selected life-history traits to relative changes in these parameters; see Table 4 for the description and estimated value of all parameters. A change in parameter value was simulated as a change of +/−5% of the default value. A relative change in a given life history trait (LHT) was then calculated as: $(LHT_{new}$ - $LHT_{default})/LHT_{default}$.

Results implied a relatively high sensitivity of age at puberty to most of the tested parameters, with predicted values for age at puberty ranging between 60% higher to 40% lower relative to the value predicted with the default (estimated) parameter set (Fig. A.5). This could reflect that a high variability observed in this trait (also generally for sea turtles) was stemming from a naturally present variation in one or more parameters. Weight at puberty also showed a relatively high sensitivity (+40% to −20%) to parameter perturbation, particularly when the maximum assimilation rate ($\{\dot{p}_{Am}\}$) was varied. Maximum seasonal reproductive output was quite sensitive to all tested parameters, especially the allocation to soma (κ) and $\{\dot{p}_{Am}\}$, but exhibited no sensitivity to the mobilization rate ($\dot{v}$). The remaining two explored traits (length at puberty and ultimate size) showed only a relatively small sensitivity (+/−4%) to the tested parameters, with the largest source of sensitivity of both traits being the shape coefficient (del_{Ma}), and for ultimate size the $\{\dot{p}_{Am}\}$.

Appendix B. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107781.

Data availability

All code and results for the physiological model are available at: Add-my-Pet website (https://www.bio.vu.nl/thb/deb/deblab/add_my_

Table A.4
Simulations for growth and reproduction of NWA leatherback turtles at several (constant) temperatures (T = 14–28 °C), at scaled food availability corresponding to $f = 0.9$; simulations ran for 35 years.

T (°C)	ap (yr)	Lp (cm SCL)	Li (cm SCL)	Wi (kg)	Ri (egg/season)	cumF (eggs)
14.00	30.46	131.73	132.62	514.9	64	64
14.71	28.43	131.73	132.92	520.6	113	164
15.43	26.55	131.73	133.15	525.2	148	293
16.14	24.79	131.73	133.31	529.0	181	450
16.85	23.16	131.73	133.42	532.1	211	631
17.56	21.65	131.73	133.50	534.8	239	836
18.28	20.24	131.73	133.56	537.1	267	1062
18.99	18.93	131.73	133.59	539.1	293	1309
19.70	17.71	131.73	133.62	541.0	318	1576
20.42	16.57	131.73	133.63	542.8	344	1864
21.13	15.51	131.73	133.64	544.6	370	2171
21.82	14.56	131.73	133.64	546.4	396	2487
22.50	13.67	131.73	133.64	548.2	423	2823
23.19	12.84	131.73	133.64	550.1	451	3179
23.88	12.06	131.73	133.65	552.1	480	3557
24.56	11.34	131.73	133.65	554.2	511	3957
25.25	10.66	131.73	133.65	556.5	544	4381
25.94	10.02	131.73	133.65	558.9	578	4830
26.63	9.42	131.73	133.65	561.4	615	5305
27.31	8.87	131.73	133.65	564.0	654	5808
28.00	8.34	131.73	133.65	566.8	695	6340

Columns: 'mdfy (%)'- factor by which the initial food availability was modified; 'f' - resulting scaled functional response for food availability; 'ap (yr)' - predicted age at puberty in years; 'Lp (cm SCL)' - predicted length at puberty in cm of straight carapace length; 'Li (cm SCL)' - predicted ultimate length in cm of straight carapace length; 'Wi (kg)' - predicted ultimate weight in kilograms; 'Ri (egg/season)' - predicted seasonal reproductive output in number of eggs; 'cumF (eggs)' - predictive cumulative lifetime reproductive output by one nesting female at our estimate of maximum size, in number of eggs. Remigration interval (defining how much time a turtle had between seasons to accumulate energy for eggs) is simulated as 2.5 years.

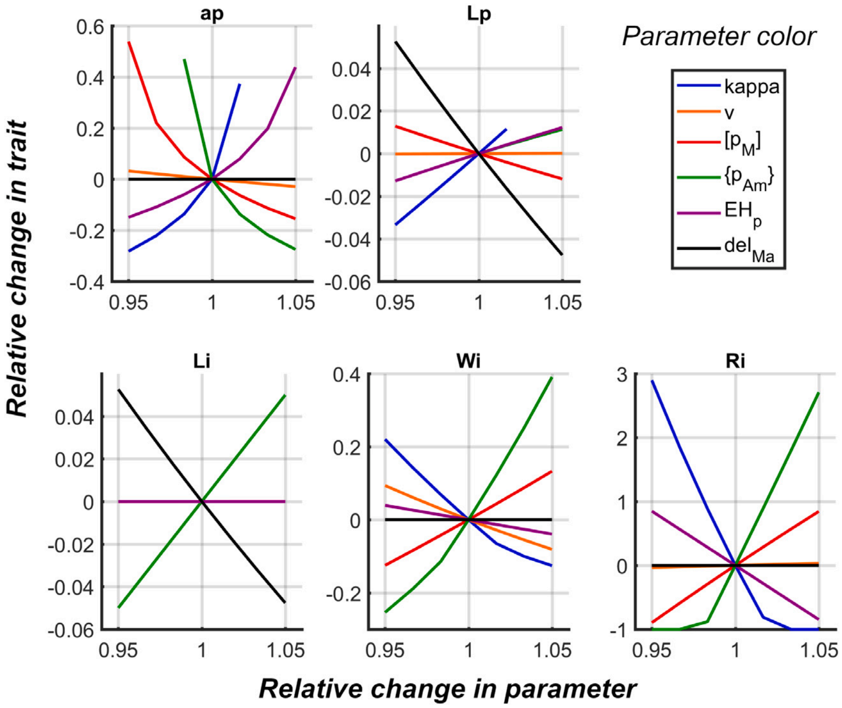

Fig. A.5. Sensitivity analysis performed for several primary parameters (κ, $\dot{v}$, $[\dot{p}_M]$, $\{\dot{p}_{Am}\}$, E_H^p) and one auxiliary parameter (del_{Ma}) in five life history traits: age at puberty **ap**, length at puberty **Lp**, ultimate length **Li**, ultimate weight **Wi**, and seasonal reproduction at ultimate size **Ri**. Relative change in trait is calculated as (new value - default value)/default value.

pet/species_list.html), entry *Dermochelys coriacea*, Version 2025/05/09. Results of the MDS are available as an interactive figure in Supplementary Material.

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