

# Comparative physiological energetics of Mediterranean and North Atlantic loggerhead turtles

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## Abstract

Population of loggerhead turtles nesting in the Mediterranean Sea has probably evolved from the North Atlantic (NA) population, but is geographically and genetically distinct. We aggregated previously published and new unpublished data, and took two approaches to comparing these populations: an empirical one based on statistical analyses of morphological data, and a physiological one based on a Dynamic Energy Budget (DEB) model. We then analyzed causes of faster growth and maturation, but smaller size at puberty and ultimate size of the Mediterranean (MED) loggerhead turtles relative to their NA conspecifics. The empirical analysis showed that MED eggs, hatchlings, and nesting adults were consistently smaller in terms of length and mass. The physiological approach suggested physiological adaptations of the MED population to higher salinity and scarcer food availability. In particular, these adaptations included an increase in somatic maintenance needs, and a decrease in energy investment to reach and maintain sexual maturity. Our study therefore offers a mechanistic underpinning of previously observed but unexplained life-history traits, and showcases an application of DEB theory as a tool for comparative analysis of two distinct populations of the same species.

### *Keywords:*

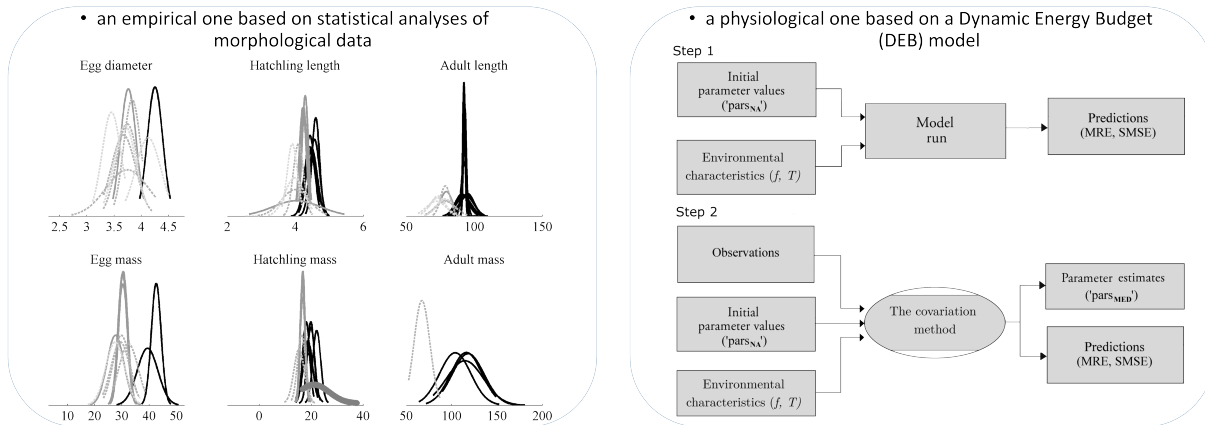
Marine turtles, Mechanistic modeling, Somatic maintenance, Sexual maturity, Environmental adaptation, *Caretta caretta*, Life-history traits, Energy budget

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## Graphical abstract:

We compared life history traits and energy budgets of Mediterranean and North Atlantic loggerhead turtles, using two approaches:



## 1. Introduction

Loggerhead turtles inhabiting the Mediterranean Sea have probably evolved from the North Atlantic loggerhead turtles more than 10 000 years ago [1]. They are considered the same species even though they genetically differ [2, 3], and interbreed only to a limited extent when sharing the same feeding grounds [4]. The individuals from the two populations are morphologically similar, but Mediterranean (MED) loggerhead turtles are smaller than their North Atlantic (NA) relatives [1, 5, 6]. Nesting MED females are possibly also younger than the NA ones [3, 6, 7], with shorter remigration intervals and fewer clutches per season [8, 9, 10], but often more eggs per clutch [1, 5, 11].

The observed variabilities in size and reproductive output could be caused by a number of generally recognized factors, notably:

- (i) higher food abundance – a characteristic of the North Atlantic – results in faster growth rates and larger sizes (e.g., 12, 13, 14), while energy limited environments such as the Mediterranean reward earlier maturation at smaller sizes [5, 15];
- (ii) stable conditions – a characteristic of the Mediterranean Sea – support a longer reproductive season and higher population densities, resulting in smaller individuals due to less resources per individual (16, p. 297);
- (iii) genetic differences cause different growth and maturation potentials [17];
- (iv) some ecological pressures (e.g., trans-oceanic migrations) favor larger sizes, while other pressures (e.g., higher adult predation) favor earlier reproduction at smaller size [5];

21 (v) adaptations in feeding behavior may result in different ecological niches [13].

22 Investigating complex interactions resulting from the aforementioned environmental and  
23 physiological factors is complicated by the large number of possible combinations, and is  
24 further hindered by a long life-cycle of loggerhead turtles encompassing several decades and  
25 multiple habitat types. Therefore, a systemic approach combining empirical data and com-  
26 putational analysis may help.

27 We undertook such an approach using previously published and unpublished data. We  
28 organized our analyses in two stages. First, we performed statistical analyses based on em-  
29 pirical data on morphology of individuals from the two populations. Second, we developed  
30 a mechanistic physiological Dynamic Energy Budget (DEB) [16, 18] model specific to the  
31 Mediterranean population, and compared it to an analogous DEB model for NA logger-  
32 head turtles that had been described previously [19]. This is currently the only example  
33 of population-specific parameter sets in the Add-my-pet project [20, 21] and likely the first  
34 application of DEB models to compare two distinct populations of the same species using  
35 population-specific parameter values. The environmental characteristics of the two sea basins  
36 were taken into account for the comparison. By explicitly modeling the environmental fac-  
37 tors, we could better understand the environmental effects and possible causes of the observed  
38 differences between the populations.

39 In the following sections, we briefly present the main characteristics of the environment,  
40 and the main life history traits of loggerhead turtles. The emphasis is on the Mediterranean  
41 Sea and MED loggerhead turtles (for the NA loggerhead population, please see Marn et al.  
42 [19]). We describe the collected data and our two-step approach in the methodology section,  
43 and organize the results to maintain the distinction between the two modes of analysis.  
44 Discussion sets the results in a wider context of the possible environmental and evolutionary  
45 pressures and adaptations.

#### 46 *1.1. Environmental conditions*

47 Compared to the North Atlantic, the Mediterranean Sea is a relatively small basin –  
48 2.5 million km<sup>2</sup> [1, 22] vs. 106.5 million km<sup>2</sup>, (NOAA-facts) – and its only communication  
49 with other sea basins is with the Atlantic Ocean via the narrow Strait of Gibraltar. The  
50 main characteristics of the Mediterranean Sea are (adapted from [1, 22, 23, 24]): (i) High  
51 level of evaporation resulting in salinity difference and water deficit; (ii) Existence of two  
52 main basins, the western and the eastern, connected by a shallow Sicily Channel and the  
53 narrow Messina Strait, with the eastern basin more saline and warmer than the western  
54 basin; (iii) Generally oligotrophic conditions resulting in the Mediterranean being one of the  
55 less productive seas; and (iv) Very large biodiversity.

56 All sea turtles in the Mediterranean are listed on the IUCN Red List of Threatened  
57 Species and are protected by (inter)national conventions and laws [25, 26]. *Caretta caretta*  
58 (loggerhead turtle) is currently the most abundant sea turtle species in the Mediterranean  
59 and is one of the two sea turtle species nesting there [1, 11, 27]. MED loggerhead turtles  
60 mate and nest primarily in the east Mediterranean, with major nesting sites and rookeries  
61 in Greece, Cyprus, and Turkey [1]. Immature NA loggerhead turtles are encountered in the  
62 western Mediterranean basin [3, 4, 28]. Compared to the salinity of the North Atlantic (35-  
63 36 ppt, [29, 30]), salinity of the eastern Mediterranean Sea is higher (38-39 ppt, [24]), leading  
64 to a hypothesis about a "salinity barrier" experienced by NA turtles [2].

### 65 1.2. *Loggerhead turtle life cycle*

66 Generally the life cycle of MED loggerhead turtles is very similar to that of their NA  
67 conspecifics, but some notable differences exist. Namely, MED turtles reproduce at smaller  
68 sizes, especially those nesting in Libya, Tunisia, and Turkey, and they grow to a smaller  
69 size (1, 31, 32, Appendix I in Tiwari and Bjorndal [5]). Age at sexual maturity is variable,  
70 with estimates between 14 to 28 years for MED turtles [3, 6, 7], and similar or higher (>35  
71 years old) estimates for NA turtles [6, 33, 34]. Individuals of both MED and NA populations  
72 nest every 2–3 years, laying between 1 and 5 clutches per nesting season, but Mediterranean  
73 females lay on average fewer clutches into which they often deposit more eggs [1, 5, 9, 11, 35].

74 Incubation lasts 50–60 days with the duration of incubation being inversely proportional  
75 to the incubation temperature [36, 37, 38, 39]. Hatchling size varies between different nests  
76 within a population, which has generally been attributed to incubating conditions such as  
77 humidity, salinity, and temperature of the sand (Stokes et al. [37], Gutzke et al. [40], Packard  
78 and Packard [41], Reece et al. [42], Glen et al. [43], Bower et al. [44], but see Reid et al.  
79 [38], Reece et al. [42], Ji and Brana [45], Patino-Martinez et al. [46]). On average, MED  
80 hatchlings are smaller than the NA hatchlings [1, 37].

81 MED loggerhead turtles seem to grow and mature faster than NA loggerhead turtles feed-  
82 ing in the Mediterranean Sea [3], suggesting a certain physiological adaptation of the former.  
83 Size dimorphism between populations from the two basins was noticed in other species of sea  
84 turtles, as well as fish [13, 43, 47]. However, it is unclear whether the difference in size and, in  
85 the case of loggerhead turtles, reproductive output is also a difference in the general condition  
86 of the animal, and what are the likely physiological adaptations of loggerhead turtles to the  
87 environmental conditions of the Mediterranean Sea (see also discussion online [48]).

## 88 2. Methods

### 89 2.1. The empirical approach – Statistical analyses of size and condition

90 We comprehensively searched the literature for reports on the size of loggerhead eggs,  
91 hatching turtles, and nesting turtles, both for Mediterranean (MED) and North Atlantic (NA)  
92 populations. Size of an individual can be specified reasonably well by measurements of length  
93 and mass. However, most informative comparisons based on size include the information on  
94 age. For animals encountered in the wild, age is often unknown. To bypass the unknown  
95 age, we focused on discernible life history events in order to include as much data as possible  
96 into the analysis. Two such events are hatching and nesting. We prioritized first nesting  
97 to sexual maturation, because the exact moment of sexual maturity is hard to define and  
98 observe [19, 49]. We also took into account the average egg diameter and mass, because  
99 variations in egg size may explain a large part of the size variation in hatchlings [5, 43, 45, 50].

100 We first analyzed individual samples describing eggs, hatchlings, and nesting females. All  
101 data and sources are summarized in Section 2.2.1 and Appendix A. We prioritized straight  
102 carapace length (SCL) to other turtle length measurements, and we used wet weight to  
103 characterize body mass. When raw data were available, we tested datasets for normality  
104 using Lilliefors test. When only descriptive statistics were provided, such as sample size,  
105 mean and standard deviation, or mean and range of the dataset, we assumed a normal  
106 distribution. In several cases, we calculated the standard deviation of the sample using  
107 reported mean, range, and sample size following Hozo et al. [51]. We analyzed means and  
108 standard deviations of length and mass in each life-stage using Welch’s ANOVA F-test [52]  
109 and visually by plotting probability density plots.

110 We subsequently used pairwise Welch’s t-test of unequal variances to compare each MED  
111 sample to each of the NA samples of the same type, such that, e.g., each MED hatchling  
112 length sample was tested against each of the NA hatchling length samples. We expected  
113 NA loggerhead turtles to be larger than the MED ones, thus performing a one-sided test.  
114 To minimize the chance of false positives, we applied the Bonferroni correction ([http://  
115 mathworld.wolfram.com/BonferroniCorrection.html](http://mathworld.wolfram.com/BonferroniCorrection.html)).

116 Finally, we calculated Fulton’s condition index,  $K$ , as the ratio of the mass and length  
117 cubed in  $\text{g}/\text{cm}^3$  [53] as:

$$K = W/L^3. \quad (1)$$

118 Fulton’s condition index is often used as an indication of the physiological condition of the  
119 animal: a larger  $K$  means that the animal is better fed, i.e., has more energy available for  
120 various processes. Although originally developed for fish,  $K$  has already been applied to  
121 many species of vertebrates, including sea turtles (see Stevenson and Woods Jr [54] for an

122 overview), and has the advantage of not assuming a “standard” or “healthy” value that, e.g.,  
123 relative mass indices assume [54].

124 To obtain the mean values of  $K$ , we pooled all samples that pertain to the same size  
125 measurement of the same life-stage and the same population. Each pooled sample was  
126 described by a mean of means (Welch’s mean computed by taking into account the size and  
127 standard deviation of the sample [52]), and by pooled standard deviation [55]. We calculated  
128 the “condition index” of the egg, akin to Fulton’s condition index, as the ratio of egg mass  
129 (in g) to cubed egg diameter (in  $\text{cm}^3$ ). We performed all analyses in Matlab R2015a.

## 130 2.2. The physiological approach – a mechanistic Dynamic Energy Budget (DEB) model

131 Life-history traits of loggerhead turtles are described well by the standard DEB model [19].  
132 Accordingly, we characterized an individual MED turtle with three state variables: structural  
133 length ( $L$ ), reserve energy ( $E$ ), and maturity level ( $E_H$ ). Changes in these three state vari-  
134 ables are due to ingestion and assimilation of energy, which is subsequently used for mainte-  
135 nance, growth, maturation, and reproduction. A detailed specification of the standard DEB  
136 model is given in Appendix B.

137 We converted the state variable of the standard DEB model into measurable quantities  
138 (e.g., body length and mass) by means of conversion parameters. For example, we obtained  
139 straight (SCL) and curved (CCL) carapace lengths from structural length using two shape  
140 parameters,  $\delta_{\text{SCL}}$  and  $\delta_{\text{CCL}}$ , such that:

$$L_{\text{SCL}} = L/\delta_{\text{SCL}}, L_{\text{CCL}} = L/\delta_{\text{CCL}}. \quad (2)$$

141 By keeping the two shape parameters constant, we implicitly assumed isomorphic growth,  
142 thus ignoring a minor change in shape between hatchlings and late juveniles [56].

143 Converting the state variables to body mass,  $W$ , required including the contributions of  
144 both structure and reserve. The former contribution is by definition  $\rho L^3$ , with the density of  
145 structure being approximated by  $\rho = 1 \text{ g cm}^{-3}$ . The latter contribution is also proportional  
146 to  $\rho L^3$ , but only after correcting for the reserve capacity and composition via dimensionless  
147 parameter  $\omega$ , and the state of reserve via food availability  $f$ :

$$W = \rho L^3(1 + f\omega). \quad (3)$$

148 Quantity  $f$ , also called the scaled functional response, accounts for food availability on a  
149 scale of 0 for no food to 1 for abundant food (see Kooijman [16] for details and Marn et al.  
150 [14]).

151 *2.2.1. Constructing a DEB model for Mediterranean loggerhead turtles*

152 Parameters of every DEB model are specific to each individual. Generally, we assume  
153 that similarities between individuals of the same species are greater than those between indi-  
154 viduals of different species. This assumption makes it possible to use data from individuals  
155 of one species to estimate parameters representative of the whole species [16, 21, 57]. Here,  
156 however, we extended this assumption to population-level similarities, i.e., we assumed that  
157 similarities between individuals within a population are greater than those between individ-  
158 uals belonging to different populations, and that parameters representative of the population  
159 could be obtained.

160 First, we tested whether a single set of parameters (Marn et al. [19], an updated set in  
161 Table 2) can describe both populations. This parameter set will be henceforth referred to as  
162 ' $pars_{NA}$ '. We simulated environmental conditions (temperature and scaled food availability)  
163 of the Mediterranean Sea, therefore testing whether environment alone can account for the  
164 observed differences between the two populations (Fig. B.13).

165 Second, we assumed that some parameters might differ between the two populations,  
166 and then estimated these parameters using only data for the Mediterranean population and  
167 ' $pars_{NA}$ ' as initial values. Out of the 15 core parameters of the standard DEB model (in-  
168 cludes the extra maturity level for hatching), we allowed eight parameters to differ between  
169 populations and used a species-specific value or a default value for the remaining parameters  
170 (see Table 2). The resulting parameter set will be henceforth referred to as ' $pars_{MED}$ '.

171 We quantified the goodness of fit between each model prediction and the corresponding  
172 data set or data point with relative error (RE) and symmetric squared error (SSE). Calculating the mean of all RE and the mean of all SSE gave two measurements for an overall  
173 goodness of fit (MRE and SMSE, respectively) [58, this issue]. We assessed the performance  
174 of the two parameter sets by comparing the corresponding MRE and SMSE values. In addition,  
175 we compared RE values obtained by ' $pars_{NA}$ ' to RE values obtained by ' $pars_{MED}$ ' using  
176 the Wilcoxon signed rank test (`signrank` in Matlab) and sign test, which have been rec-  
177 ommended for comparisons of two classifiers over multiple data sets [59]. We approximated  
178 uncertainty of parameter values by combining the information on data availability (COM-  
179 PLETE level, [57]) and data agreement (MRE, SMSE), following the approach presented in  
180 Pauly and Zeller [60].

182 We hypothesized that if model predictions based on ' $pars_{MED}$ ' fit the data better than  
183 those based on ' $pars_{NA}$ ' after accounting for environmental differences, then we would be  
184 able to infer which physiological characteristics cause the two populations to differ. Put  
185 alternatively, we would better understand how evolution adapted MED loggerhead turtles

186 to life in the Mediterranean Sea. We wrote and executed all code in Matlab R2015a, using  
187 the current release of the DEBtool package ([61], downloaded 09-April-2018) for parameter  
188 estimation [58, this issue] and model predictions.

189 *Gathering data.* The process of parameter estimation uses several types of data [57, 58, 62,  
190 this issue]: *data-points* such as age and size at hatching and puberty, maximum reproduction  
191 etc.; and *data-pairs* such as length-at-age, mass-at-length, etc. We obtained the necessary  
192 data by performing a comprehensive literature search and securing previously unpublished  
193 data from a rearing program in Marineland. The latter data pertained to adults captured  
194 in the Mediterranean Sea and their offspring. Generally, we prioritized straight carapace  
195 length (SCL) [63]. We did use curved carapace length (CCL) to estimate length at puberty  
196 and ultimate length, because only CCL had been reported in most published literature on  
197 Mediterranean loggerhead turtles. Some data required additional assumptions (stated below);  
198 all data is presented in Table 3, and Figs. 3–6.

199 Birth from the perspective of physiological energetics denotes the transition from the  
200 embryo stage, in which there is no feeding nor reproduction, to the juvenile stage, in which  
201 feeding occurs. In the case of loggerhead turtles, hatching as the moment of leaving the egg,  
202 emergence as the moment of leaving the nest, and birth as the onset of feeding take place  
203 several days apart. We assumed that the duration of the period between hatching and birth  
204 depends on temperature, but is the same for both populations.

205 We considered sexual maturity or puberty, defined as the onset of energy allocation to  
206 reproduction, as equivalent to the event of first nesting (as in Marn et al. [19]). Only *estimates*  
207 were available for the age at puberty because the onset of energy allocation to reproduction  
208 generally cannot be observed directly. Estimates are reported as a range and mostly depend  
209 on the length defined as the “length at puberty” and on the method used for estimation  
210 [3, 6, 7, 64]. The value used as the “observed value” (18 years) was therefore quite uncertain  
211 and was consequently given lower weight in the parameter estimation procedure (see also  
212 Lika et al. [57], Marques et al. [58, this issue]). We calculated size (length and wet weight)  
213 at puberty as the average of the low end of the reported ranges.

214 To calculate the reproductive output (clutch size) of a female of a certain size, we modeled  
215 the investment into reproduction as a continuous process and then used a simplified linear re-  
216 lationship by which females produce two clutches per nesting season every two years (average  
217 values from Broderick et al. [35]). We calculated the maximum reproductive output using  
218 the high end of the reported median values (2.2 clutches per nesting season with nesting 2  
219 years apart).

220 We assumed the maximum life span and the maximum length under *ad libitum* food to be



221 relatively consistent within a species and, due to a lack of data for MED loggerhead turtles,  
222 we used the same values as for the NA population: 65 yr [65, 66] and 130 cm SCL [67]. We  
223 calculated the ultimate size as the average of the high end of the reported values. We then  
224 used the ratio between the average ultimate length and maximum length as the initial value  
225 for scaled food availability ( $f = 0.67$ ) during parameter estimation.

226 All of the aforementioned data-*points* described the MED loggerhead turtles living and  
227 nesting in the wild. Datasets of data-*pairs* only partially pertained to the wild MED turtles:  
228 temperature vs. incubation duration, growth in length, and carapace length vs. clutch size.  
229 We secured additional growth data (mass and carapace length vs. time) from a rearing  
230 facility located in the Mediterranean. Data from the rearing facility comprised four years of  
231 measurements of two loggerhead turtles that hatched in 2010, and three years of measurement  
232 of several loggerhead turtles that hatched in 2011. An important feature of these data was  
233 that the exact age of measured individuals and environmental conditions in terms of food  
234 and temperature had been known.

235 Following the approach for the NA population [19], we characterized the environmental  
236 conditions experienced by wild loggerhead turtles by an average sea surface temperature and  
237 average food availability. Specifically, we set  $T_{\text{MED}} = 21^{\circ}\text{C}$  [24] because this is the average  
238 seawater temperature in the eastern Mediterranean basin where MED loggerhead turtles are  
239 mostly concentrated [1]. For food availability, we initially set  $f = 0.67$  based on the ratio  
240 between ultimate and maximum lengths, but later we treated this quantity as a parameter to  
241 be estimated simultaneously with other parameters. We characterized the rearing facilities  
242 with recorded temperature ( $T = 22 - 26^{\circ}\text{C}$ ) and *ad libitum* food ( $f = 1$ ). Because we could  
243 include into the model different temperatures and food availabilities for wild and captive  
244 individuals, it was possible to simultaneously use data from the wild and from captivity.

### 245 3. Results

#### 246 3.1. Size and condition of Mediterranean and North Atlantic loggerhead turtles

247 Statistical analyses point to a distinct physiology between the two studied populations  
248 (Fig. 1, Table 1). On average, MED eggs are 14% shorter and 45% lighter than NA eggs, MED  
249 hatchlings are 11% shorter and 23% lighter than NA hatchlings, and nesting MED females are  
250 19% shorter and 64% lighter than nesting NA females. Surprisingly, despite these differences  
251 in size and mass between the two populations, condition remains similar when comparing the  
252 same life events (Table 1). Such similarity, taken together with the decrease of the condition  
253 index with age (Table 1), suggests that condition may be a geographically invariant indicator  
254 of the ontogenetic state of loggerhead turtles. We could only obtain point estimates for the

255 condition indices in Table 1, which is why we refrained from using them in any additional  
 256 statistical analyses or to make any definite conclusions. However, we did have independent  
 257 data to estimate the 95% confidence intervals for the condition indices of NA hatchlings and  
 258 adults (Fig. 2). The obtained values are in broad agreement with the results in Table 1.

Table 1: Population-level means (and standard deviations) of egg diameter and wet weight, SCL and wet weight at hatching, and SCL and wet weight at nesting. Fulton’s condition index,  $K$ , is given for comparison (Eq. (1)). The condition index is similar if the same life events of the two populations are compared, but seems to decrease through ontogeny. See Methods and Tables A.4–A.6 in Appendix A for more details.

Life stage	Measurement	North Atlantic	Mediterranean
Egg size	Diameter (cm)	4.25 (SD 0.14)	3.71 (SD 0.224)
	Wet weight (g)	41.98 (SD 3.00)	28.90 (SD 3.241)
	$K$	0.5469	0.5659
Hatching	Length SCL (cm)	4.51 (SD 0.1456)	4.05 (SD 0.376)
	Wet weight (g)	19.26 (SD 1.642)	15.60 (SD 1.933)
	$K$	0.2100	0.2348
Nesting	Length SCL (cm)	92.84 (SD 4.539)	78.03 (SD 5.138)
			78.77 (SD 4.521) <sup>†</sup>
	Wet weight (kg)	110.18 (SD 18.054)	67.26 (SD 8.62) <sup>†</sup>
	$K$	0.1377	0.1376 <sup>†</sup>

Condition of two adult females in the Marineland (France) reproductive program is  $K = 0.1959$  and  $K = 0.2525$ .

† Values based on data pertaining to the turtles nesting in Greece and Cyprus only, which are slightly larger than those nesting in, e.g., Turkey and Libya. Marked values were used to calculate the condition index of nesting Mediterranean loggerhead turtles, because Wet weight data was available just from Greece and Cyprus.

259 Further statistical analyses are outlined in Appendix A (Figs. A.9–A.11) with the main  
 260 result being a larger size of NA turtles relative to MED turtles almost irrespective of the  
 261 compared locations. However, given the limitations in data quality and a lack of mechanistic  
 262 underpinning for the obtained results, we proceed to examine the observed size differences  
 263 between MED and NA loggerhead turtles by means of a modeling approach.

### 264 3.2. Mechanistic DEB-based modeling of the Mediterranean population

265 Our approach yielded two sets of model predictions that we compared to the data. First  
 266 were the predictions obtained by assuming that the same parameter values pertained to  
 267 both NA and MED populations ( $'pars_{NA}'$  in Table 2 excluding the value of scaled functional  
 268 response,  $f$ ), meaning that the differences between the two populations originated solely from  
 269 the different environmental conditions. Second were the predictions obtained by estimating  
 270 the parameter values for MED population ( $'pars_{MED}'$  in Table 2), and then accounting for  
 271 the different environmental conditions. The relative errors for predictions obtained with

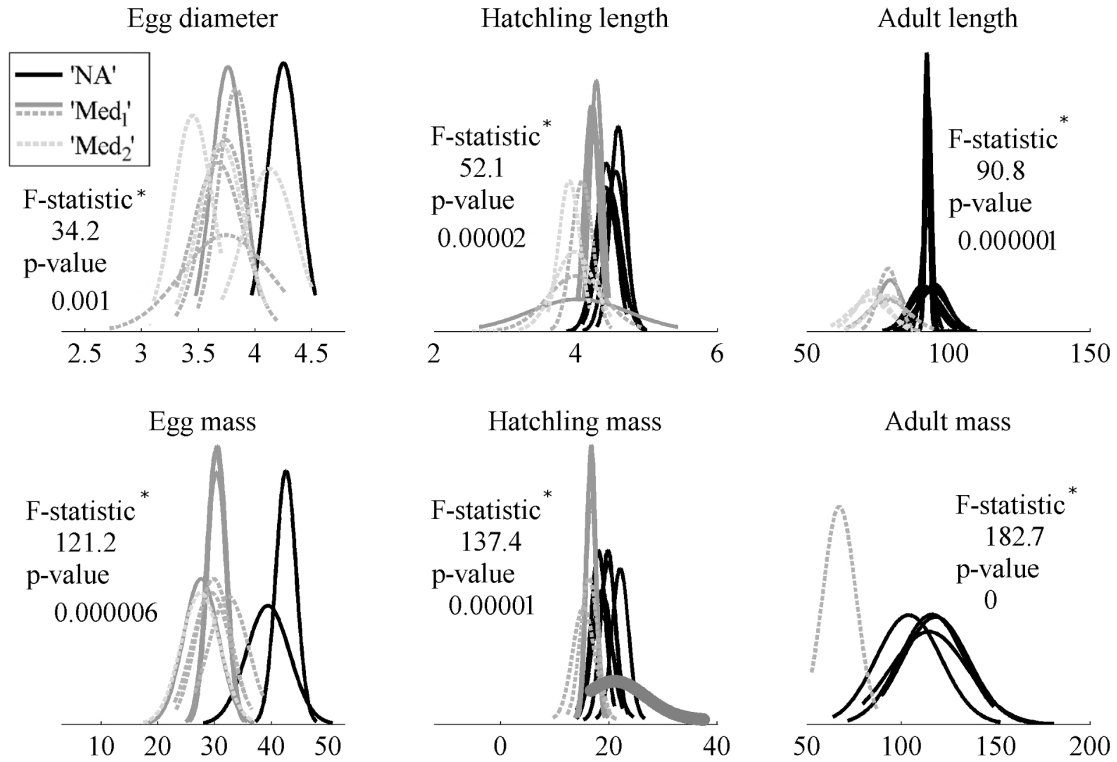


Figure 1: **Theorized size distributions of loggerhead turtles and the results of the Welch ANOVA test.** The ANOVA in all cases rejects the hypothesis that all samples come from the same distribution. A visual inspection of size distributions suggests that NA turtles are larger than MED ('Med<sub>1</sub>'–Greece and Cyprus; 'Med<sub>2</sub>'–Turkey and Libya) irrespective of the life stage. Normal size distributions were assumed and plotted using means and standard deviations from Tables A.4–A.6. Where a value for the standard deviation was unavailable, we made an estimate following Hozo et al. [51]. Thick gray curve in the panel for hatchling mass represents the data from the reproduction program, which were analyzed separately. Distributions were plotted either over the reported data range (when available), or over a range defined as three standard deviations from the mean. For more details, see Figures A.9 and A.10 in Appendix A.

272 *'pars<sub>NA</sub>'* and *'pars<sub>MED</sub>'* differ significantly (Wilcoxon sign rank test,  $F = 166$ ,  $z$ -value = -2,  
 273  $p=0.004$ ). Predictions with the *'pars<sub>MED</sub>'* parameter set perform better in terms of the sign  
 274 test, wherein 19 (57.58%) data sets have a significantly smaller relative error with *'pars<sub>MED</sub>'*  
 275 than *'pars<sub>NA</sub>'*. The *'pars<sub>MED</sub>'* parameter set also yields smaller MRE and SMSE values of  
 276 0.138 and 0.222 relative to 0.194 and 0.349 for *'pars<sub>NA</sub>'*. Keeping in mind that the life history  
 277 traits observed in nature are better defined in terms of ranges than unique critical values, we  
 278 focus on qualitative rather than numerical analysis of the differences between populations.

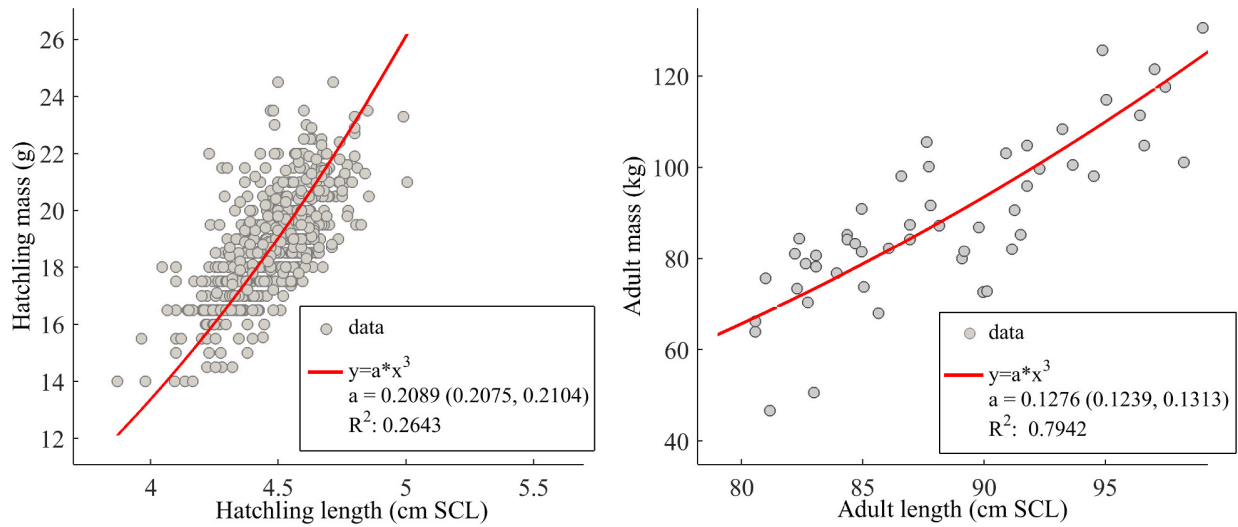


Figure 2: **Estimating the condition indices of NA loggerhead turtles with independent data.** By fitting model  $y = ax^3$ , where  $x$ -axis is length, and  $y$ -axis is mass, parameter  $a$  becomes an estimate of the condition index (95% confidence intervals in parentheses). The  $R^2$  is satisfactory for the adult data, but low for the hatching data. The low  $R^2$  could signify a large inter-individual variation, but could also be an artifact of the measurement error as the ranges of measured weights and lengths are small (10 g and 1 cm, respectively). Data sources: size at hatching partially published in Stokes et al. [37]; size at nesting from Wabnitz and Pauly [68] selected such that length is larger than the smallest reported length of nesting turtles [69, 70].

Table 2: Parameters for the North Atlantic ('pars<sub>NA</sub>', AmP *Caretta caretta* [dataset] 2018) and the Mediterranean ('pars<sub>MED</sub>') loggerhead turtle at reference temperature  $T_{ref} = 273$  K. Primary parameters (directly linked to processes), auxiliary parameters (linking measured and observed quantities), and compound parameters (functions of two or more primary parameters, [16]) are separated with horizontal lines. Parameters estimated using the covariation method [57, 58, this issue] are marked with the † symbol. Parameters marked with a **bold** font are later discussed in more detail. Primary and auxiliary parameters for which the default values were used are listed below the table. More details about parameter values of loggerhead turtles can be found in Marn et al. [19], N/A [20].

Parameter	Symbol	'pars <sub>NA</sub> '	'pars <sub>MED</sub> '	Unit
<b>Maximum specific assimilation rate</b>	$\{\dot{p}_{Am}\}$	<b>747.3</b> †	<b>895</b> †	J d <sup>-1</sup> cm <sup>-2</sup>
Energy conductance	$\dot{v}$	0.0681†	0.0721†	cm d <sup>-1</sup>
Allocation fraction to soma	$\kappa$	0.729†	0.733†	-
<b>Volume-specific somatic maintenance</b>	$[\dot{p}_M]$	<b>11.20</b> †	<b>13.5</b> †	J d <sup>-1</sup> cm <sup>-3</sup>
Specific cost for structure <sup>a</sup>	$[E_G]$	7322	7322	J cm <sup>-3</sup>
Maturity maintenance rate coefficient	$\dot{k}_J$	0.00112†	0.00152†	d <sup>-1</sup>
Maturity at hatching <sup>b</sup>	$E_H^h$	21 080†	22 320†	J
Maturity at birth <sup>b</sup>	$E_H^b$	25 350†	22 320†	J
<b>Maturity at puberty</b>	$E_H^p$	<b>98 750</b> †	<b>58 580</b> †	kJ
Weibull aging acceleration	$\dot{h}_a$	1.112e-10†	1.532e-10†	d <sup>-2</sup>
Scaled functional response	$f$	0.81†	0.67†	-
Arrhenius temperature <sup>a</sup>	$T_A$	7200	7200	K
Shape coefficient	$\delta_{SCL}$	0.3915†	0.3915	-
Shape coefficient <sup>c</sup>	$\delta_{CCL}$	0.3117† (0.3645)	0.3645†	-
Density of structure and reserve <sup>a</sup>	$d_V = d_E$	0.28	0.28	-
Zoom factor <sup>d</sup>	$z$	48.61†	48.61†	-
<b>Maximum reserve density</b>	$[E_m]$	<b>10 980</b>	<b>12 410</b>	J cm <sup>-3</sup>
Contribution of reserve to biomass	$\omega$	1.70	1.93	-
Maintenance ratio <sup>e</sup>	$k$	0.73	0.83	-

Other primary parameters (default values from N/A [20] used): Maximum searching rate,  $\{\dot{F}_m\} = 6.51 \text{ d}^{-1} \text{ cm}^{-2}$ ; Digestion efficiency (of food to reserve),  $\kappa_X = 0.8$ ; Defaecation efficiency (of food to faeces),  $\kappa_P = 0.1$ ; Reproduction efficiency,  $\kappa_R = 0.95$ ; Gompertz stress coefficient,  $s_G = 0.0001$ , Surface-area specific somatic maintenance,  $\{p_T\} = 0 \text{ J/d cm}^{-2}$ .

<sup>a</sup> Species-specific values:  $[E_G]$  such that it results in 80% growth efficiency [16, 20],  $d_V$  from Kraemer and Bennett [72];  $T_A$  estimated independently from data [1, 16, 37].

<sup>b</sup> A delay in onset of embryonic growth ( $t_0$ , [73, this issue]) was estimated as 12.79 d for NA and 8.89 d for MED population at  $T_{ref} = 273$  K.

<sup>c</sup> CCL shape coefficients convert different types of carapace length: for the MED population the curved carapace length has been reported, whereas for the NA population the type of length measurement has not been reported. For the results presented here, we used  $\delta_{CCL} = 0.3645$  in all model runs.

<sup>d</sup> We constrained parameter  $z$  of the MED population to the same or smaller values than that of NA population to reflect that MED individuals do not become larger than NA individuals.

<sup>e</sup>  $k = \dot{k}_J[E_G]/[\dot{p}_M]$ ; values larger than one are unrealistic because they imply individuals undergo metabolic switches at larger sizes when food is restricted. The only two sea turtles species in the AmP collection with values of  $\dot{k}_J$  at the default value (AmP *Derموchelys coriacea* [dataset] 2015 and AmP *Lepidochelys kempii* [dataset] 2015) have a value of  $k$  around 0.75.

279 **Predictions using 'pars<sub>NA</sub>' parameter set.** Parameter set 'pars<sub>NA</sub>' obtained originally  
 280 for NA loggerhead turtles does not match the data on MED loggerhead turtles well (3rd  
 281 column of Table 3 and dashed lines in Fig. 3–6). The most important mismatches between  
 282 data and predictions are (i) the failure to capture observed smaller sizes at puberty of MED  
 283 individuals, and (ii) a very low prediction of the maximum reproductive output (Table 3,  
 284 Fig. 6.b). The model also predicts that captive reared individuals grow slower than observed  
 285 (Fig. 4).

Table 3: Comparison between observations and model predictions using two sets of parameters. Here, we set  $T = 21^\circ\text{C}$  [24] and  $f = 0.67$  in conjunction with both parameter sets, which are the environmental conditions prevailing in the Mediterranean. Overall goodness of fit is expressed as mean relative error (MRE) and symmetrical mean squared error (SMSE). All parameters are listed in Table 2. For more details see Section 2.2.

Data	Ob- served	Predicted (‘pars <sub>NA</sub> ’)	Predicted (‘pars <sub>MED</sub> ’)	Observed, range	Unit	Data source
age at hatching	<b>49.08</b>	51.06	<b>49.58</b>	45.8-55.8	d	1
age at birth	<b>55.18</b>	66.13	<b>58.07</b>	2-3 d after emergence	d	2,3
SCL at birth	<b>4.04</b>	5.36	<b>5.17</b>	2.5-4.9	cm	1, 4
wet weight at birth	<b>15.59</b>	19.59	<b>18.97</b>	9.4-21.5	g	4
age at puberty	<b>18</b>	21.7	<b>12.41</b>	14-28	yrs	5,6
SCL at puberty	<b>62.5</b>	77.07	<b>67.8</b>	55-69	cm	4,7,8
CCL at puberty	<b>69.00</b>	82.46	<b>72.8</b>	60-78	cm	4
wet weight at puberty	<b>52.00</b>	58.07	<b>42.71</b>	52.5	kg	7
life span	<b>67.00</b>	75.5	<b>67</b>	65+	yrs	9
ultimate SCL	<b>87.00</b>	83.32	<b>82.85</b>	77-91	cm	4,7,8
ultimate CCL	<b>91.00</b>	89.14	<b>88.96</b>	85-99	cm	4
ultimate wet weight	<b>87.00</b>	73.35	<b>77.79</b>	87	kg	7
initial energy content of the egg	<b>170.00</b>	164.5	<b>156.6</b>	165-260	kJ	10
maximum repro- duction rate †	<b>0.4822</b>	0.2022	<b>0.5158</b>	0.3452- 0.8630	d <sup>-1</sup>	4,7,8,11
MRE	-	0.194	0.138	[0 ∞)		
SMSE	-	0.349	0.222	[0 1]		

† Expressed as the number of eggs per day by taking into account the 2.2 nests (clutches) per nesting season, 160 eggs per clutch, and remigration interval of 2 years:  $R_i = 2.2 \times 160 / (2 \times 365) \text{d}^{-1}$ .

**Data sources:** {1} Reid et al. [38], {2} Godfrey and Mrosovsky [76], {3} data partially published in Stokes et al. [37], {4} Margaritoulis et al. [1], {5} Casale et al. [7], {6} Piovano et al. [3], {7} Groombridge [11], {8} Tiwari and Bjorndal [5], {9} FAQ <https://gstc.jekyllisland.com/>, Accessed: 18-Nov-2015, {10} Hays and Speakman [8], {11} [35]

286 **Predictions using 'pars<sub>MED</sub>' parameter set.** The parameter set estimated for MED  
 287 loggerhead turtles (Table 2) generates close-to-the-observed size at puberty, reasonable re-

288 productive output, and fast growth of captive reared individuals at different temperatures  
 289 (4th column of Table 3 and solid lines in Figs. 3–6). Most of the predictions for life history  
 290 traits are within or close to values reported for MED loggerhead turtles (Table 3).

291 Furthermore, age at hatching and birth is predicted well (Table 3), as is the slope of  
 292 incubation duration as a function of temperature, although the accompanying intercept is  
 293 somewhat underpredicted (Fig. 3). The predicted SCL and wet weight at birth are larger  
 294 than observed, whereas the predicted wet weight and age at puberty are lower than observed  
 295 (Table 3).

296 The model also matches growth and the length-to-weight relationship for captive-reared  
 297 juveniles, and faster growth at higher temperatures (Figs. 4 and 5). In reality, very similar  
 298 conditions sometimes lead to markedly different growth patterns (e.g., see Fig. 4, top right  
 299 and bottom left panels), which contributes substantially to the overall mean relative error.

300 Modeled growth of wild MED turtles matches the data up to approximately 25 cm CCL  
 301 and after 70 cm CCL, but there is a mis-match in-between (Fig. 6, left panel). Clutch size as  
 302 a function of carapace length (Fig. 6) suggests a more complex relationship than the assumed  
 303 two clutches every two years. The predictions for clutch size are realistic (90-160 eggs per  
 304 clutch), but initial energy in an egg is a bit lower than Hays and Speakman [8] assumed for  
 305 MED loggerhead turtles (Table 3).

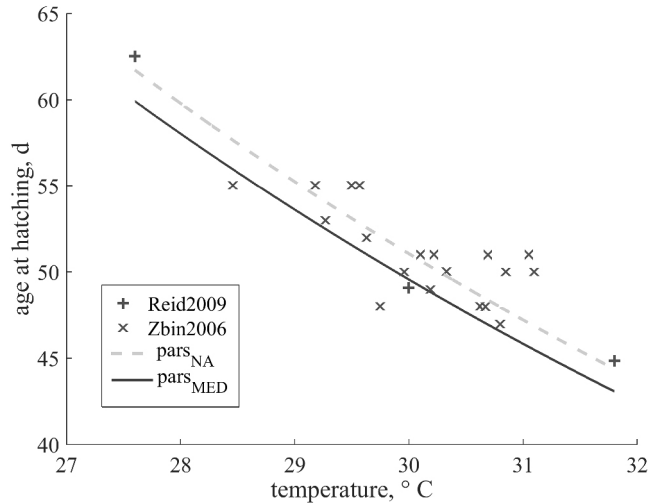


Figure 3: **Incubation duration as a function of incubation temperature of wild MED loggerhead turtles** - data and model predictions. Legend denotes the parameter set used to obtain model predictions (Table 2, see text for more details). The scaled functional response was estimated to be 0.703 for the MED population. Data from Reid et al. [38].

306 **Model parameters.** All nine estimated primary parameters ( $\{\dot{p}_{Am}\}, \kappa, [\dot{p}_M], \dot{v}, E_H^h, E_H^b,$   
 307  $E_H^p, k_J,$  and  $h_a$ ) differ in value between populations (Table 2). With a relatively high level of

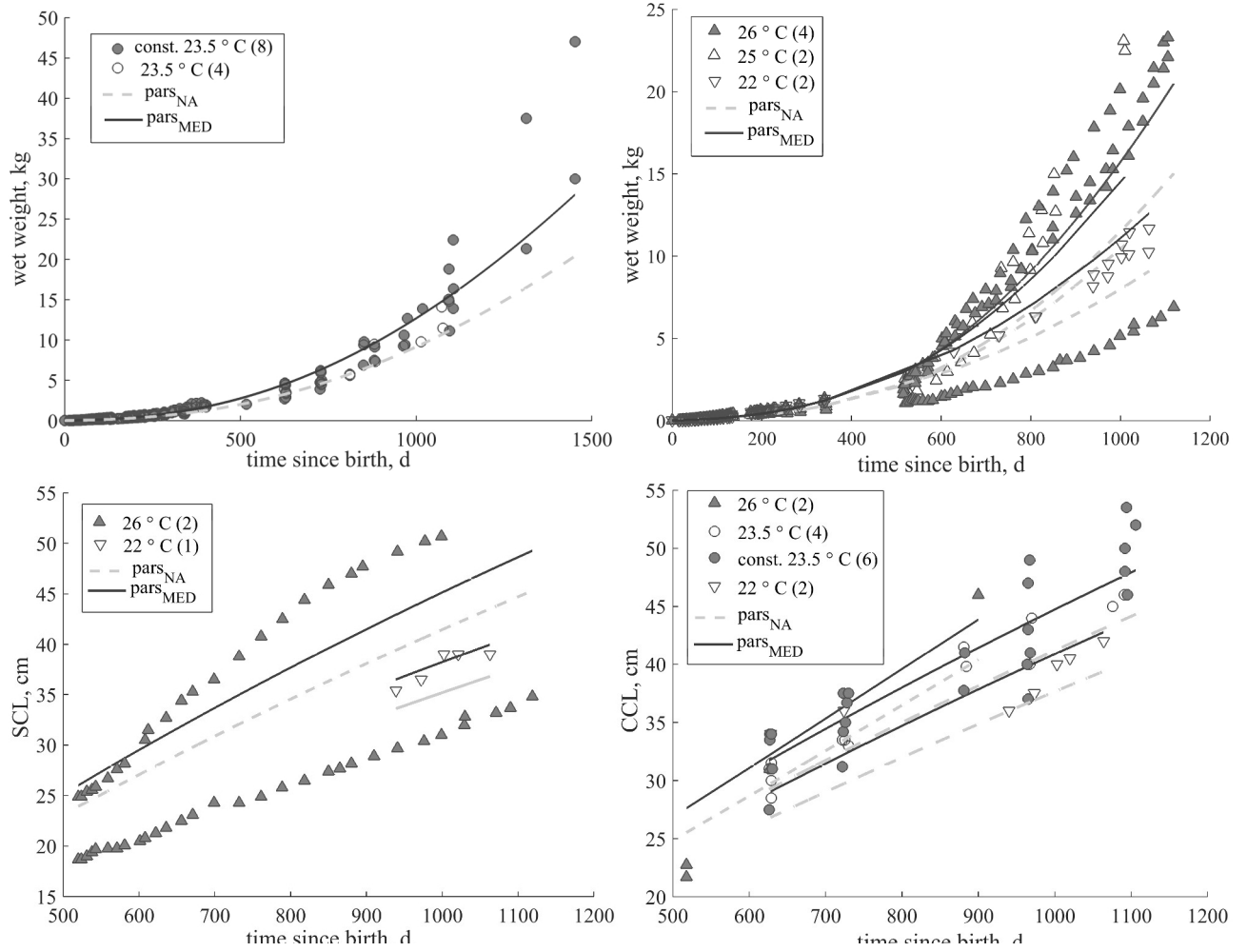


Figure 4: **Growth of captive reared hatchlings.** The top two panels show the predicted growth in wet weight, while the bottom two panels show the predicted increase in carapace length with age. Different symbols indicate different temperatures at which data was collected, and numbers in brackets refer to the number of individuals kept at a specific temperature regime (see legend). Parameter set used to obtain a specific set of model predictions (excluding  $f$ ) is denoted in the legend (values in Table 2, see text for more details). Temperature was explicitly included in model simulations and resulted in steeper growth curves predicted for higher temperatures. Food was assumed *ad libitum* ( $f = 1$ ). Previously unpublished data from Marineland rearing facility.

308 completeness  $\approx 3$  and a satisfying goodness of fit in the context of the AmP collection [21],  
 309 we judge the level of uncertainty of parameter values to be  $\approx 10\text{--}20\%$  (Table 2 in Pauly and  
 310 Zeller [60]). Differences exceeding this threshold are present in three primary parameters:  
 311 specific assimilation rate ( $\{\dot{p}_{Am}\}$ ), specific somatic maintenance rate ( $[\dot{p}_M]$ ), and maturity  
 312 level at puberty ( $E_H^p$ ) (Table 2).

313 Specific assimilation rate ( $\{\dot{p}_{Am}\}$ ) and specific somatic maintenance rate ( $[\dot{p}_M]$ ) are 20%  
 314 higher for MED loggerhead turtles than for their NA relatives. The surface-area specific



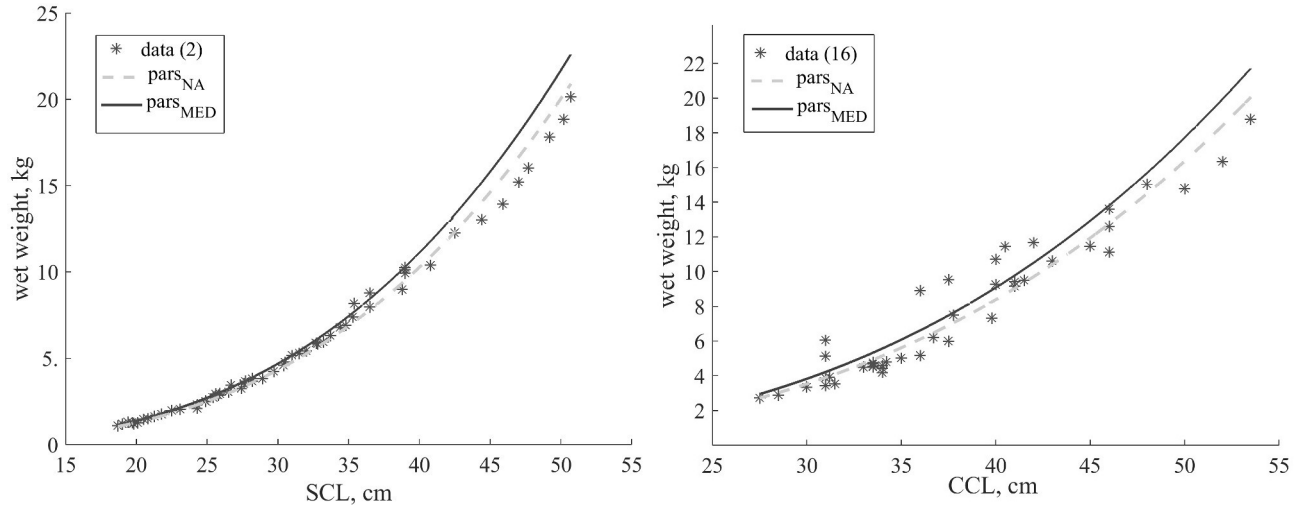


Figure 5: **Wet weight as a function of length for captive reared hatchlings.** Numbers in brackets refer to the number of individuals in the dataset (see legend); predictions are independent of temperature. Parameter set used to obtain a specific set of model predictions (excluding  $f$ ) is denoted in the legend (values in Table 2). Food was assumed *ad libitum* ( $f = 1$ ). Previously unpublished data from Marineland rearing facility.

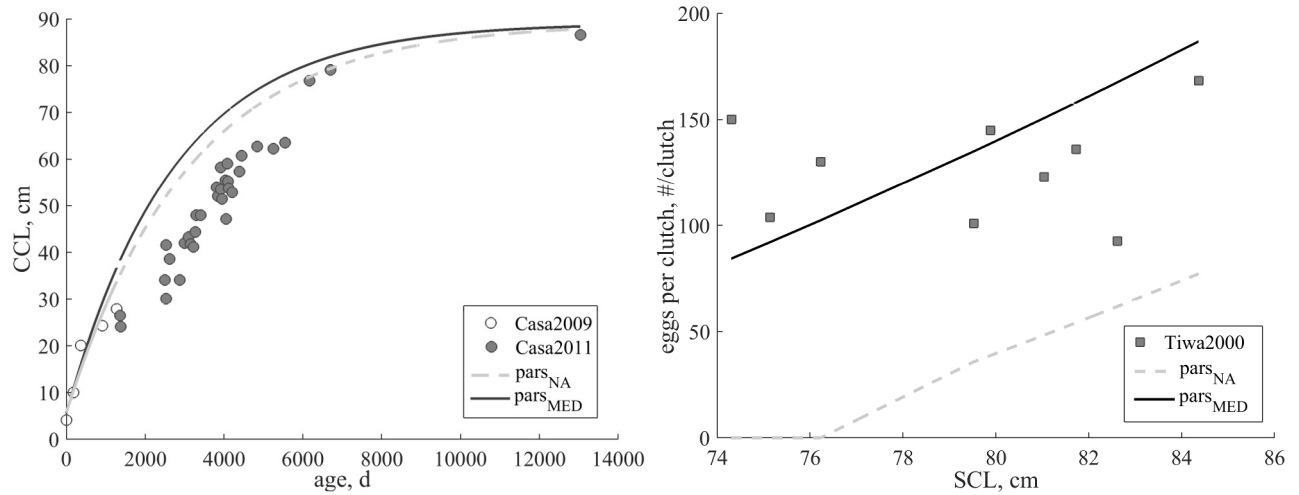


Figure 6: **Growth in length** (left panel, data from Casale et al. [7, 77]), and **clutch size as a function of carapace length** (right panel, data from [5]) **of wild MED loggerhead turtles:** data and model predictions. Growth is overpredicted between sizes of approximately 25 and 65 cm CCL. The linear relationship between carapace length and clutch size (assuming an average number of 2 clutches per nesting season every 2 years) does also not completely match the data. Predictions were obtained for the MED environment assuming the (constant) estimated  $f_{MED}$  (Table 2) and  $T = 21^\circ\text{C}$ ; mis-match with the data suggests a more variable environment and/or additional factors which were not included in the calculations. Parameter are listed in Table 2; see text for more details.

315 assimilation rate is a primary parameter calculated as  $L_m^{ref} z[\dot{p}_M]/\kappa$ , where  $L_m^{ref}$  is a reference

316 structural length of 1 cm. The zoom factor,  $z$ , is tightly linked to the maximum length an  
 317 animal can reach. Since NA individuals are typically larger than MED individuals [6], the  
 318 zoom factor  $z$  was estimated with the constraint that it cannot be larger for the MED than  
 319 the NA population. When compared to the ' $pars_{NA}$ ' set,  $z$  is the same and allocation to soma  
 320  $\kappa$  is similar, but somatic maintenance rate [ $\dot{p}_M$ ] is higher in the ' $pars_{MED}$ ' set. Consequently,  
 321 the parameters imply that MED loggerhead turtles can assimilate 20% more energy per unit  
 322 of structural surface area per day than NA loggerheads can ( $\{\dot{p}_{Am}\}=895 \text{ J cm}^{-2} \text{ d}^{-1}$  compared  
 323 to  $747 \text{ J cm}^{-2} \text{ d}^{-1}$ ), but need to pay 20% more maintenance per unit of structural volume per  
 324 day ( $[\dot{p}_M]=13.5 \text{ J d}^{-1} \text{ cm}^3$  compared to  $11.20 \text{ J d}^{-1} \text{ cm}^3$ ).

325 Maturity levels (hatching  $E_H^h$ , birth  $E_H^b$ , and puberty  $E_H^p$ ) all have lower values for the  
 326 MED population, with the biggest difference of 40% for  $E_H^p$  (58 580 kJ in ' $pars_{MED}$ ' compared  
 327 to 98 750 kJ in ' $pars_{NA}$ '). Maintaining each unit of maturity is slightly more energy-expensive  
 328 for MED turtles than for NA turtles ( $k_J=0.0015 \text{ J d}^{-1}$  compared to  $0.0011 \text{ J d}^{-1}$ ).

329 The three primary parameters with inter-population differences exceeding the 20% thresh-  
 330 old are linked to three processes: assimilation, maintenance, and maturation (reproduction).  
 331 Energy budget of MED turtles changes through ontogeny, and so does the daily energy allo-  
 332 cation between main physiological processes (Fig. 7). The energy allocation exhibits a similar  
 333 pattern between the two populations, with the similar proportions of daily assimilation allo-  
 334 cated to maintenance and development (in juveniles), or reproduction (in adults) (numbers  
 335 above the bars in the lower panel of Fig. 7). However, the absolute amounts of energy assimi-  
 336 lated and invested daily into specific processes differ. For example, because MED loggerheads  
 337 grow to a smaller size, a fully grown MED female daily needs to invest  $\approx 270 \text{ kJ}$  less energy  
 338 into somatic and maturity maintenance than a fully grown NA female. Even though the  
 339 MED female also *assimilates* less energy ( $\approx 340 \text{ kJ.d}^{-1}$  less than the NA female), she can still  
 340 invest 12% of her assimilation flux into reproduction, which is comparable to 16% invested  
 341 by the NA female (lower panel in Fig. 7).

342 MED loggerhead turtles have slightly larger energy conductance ( $\dot{v}=0.0721 \text{ cm d}^{-1}$  in  
 343 ' $pars_{MED}$ ' compared to  $0.0681 \text{ cm d}^{-1}$  in ' $pars_{NA}$ '). Their maximum reserve density ( $[E_m] =$   
 344  $\{\dot{p}_{Am}\}/\dot{v}$ ) is however larger ( $12.4 \text{ kJ cm}^{-3}$  in ' $pars_{MED}$ ' compared to  $11 \text{ kJ cm}^{-3}$  in ' $pars_{NA}$ '),  
 345 resulting in a larger contribution of reserve to biomass ( $\omega=1.93$  in ' $pars_{MED}$ ' compared to  $1.70$   
 346 in ' $pars_{NA}$ ', Table 2). These results are interesting in the context of similar condition indices  
 347 (Table 1) regardless of the lower food availability in the Mediterranean Sea (see Discussion).

348 Initially, based on the ratio between maximum and ultimate lengths, we set scaled food  
 349 availability to  $f = 0.67$ . By modeling all life history points (Table 3) and multiple datasets,  
 350 such as reproduction and growth (Fig. 6) of wild individuals we found that  $f = 0.67$  represents  
 351 the feeding conditions in the Mediterranean very well. However, because similar condition

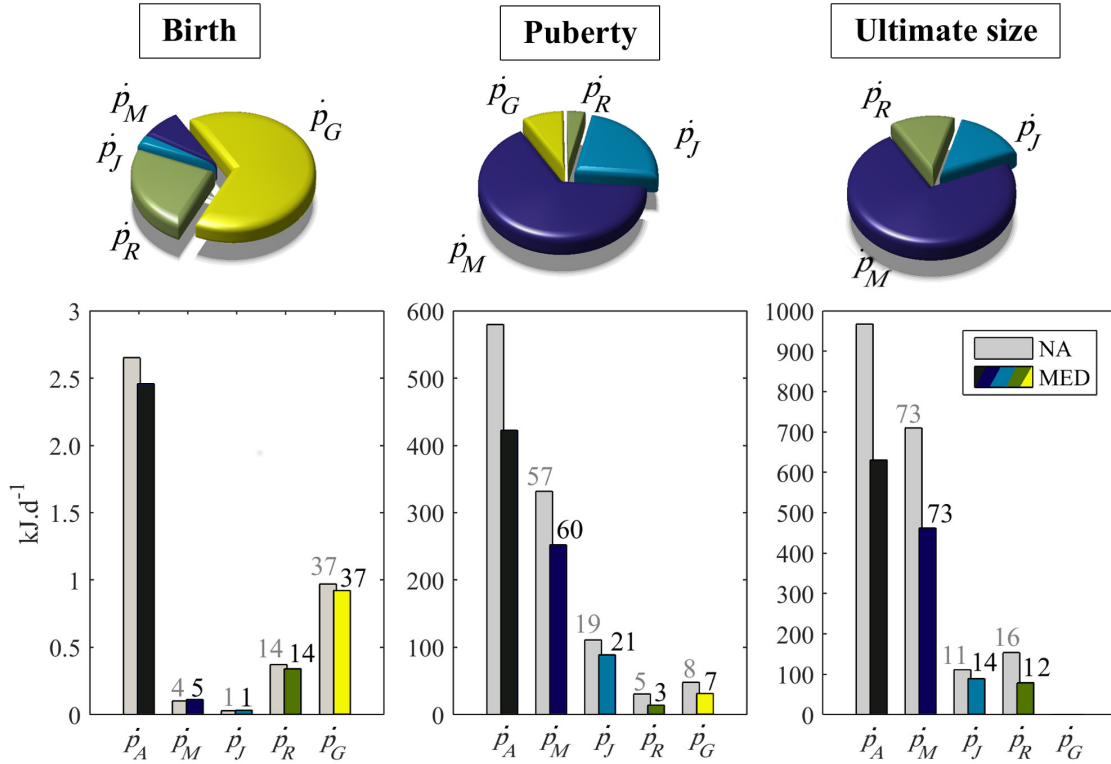


Figure 7: A visualization of the MED loggerhead turtle’s energy budget at birth, puberty, and ultimate size:  $\dot{p}_A$  - assimilation flux,  $\dot{p}_G$  - growth flux,  $\dot{p}_R$  - maturation/reproduction flux,  $\dot{p}_M$  - somatic maintenance, and  $\dot{p}_J$  - maturity maintenance, presented as fractions of the mobilization flux (pie charts) and as absolute values in kilojoules (histograms). Numbers above the histogram bars are proportions of the assimilation flux invested into a specific process, with NA values denoted in gray and MED values in black. Values do not necessarily add to a 100% - energy that is assimilated but not mobilized stays in the reserve. Legend: MED - Mediterranean loggerhead turtle (parameters  $pars_{MED}, f = 0.67$ ), NA - North Atlantic loggerhead turtle (parameters  $pars_{NA}, f = 0.81$ ). Parameters values are listed in Table 2.

352 indices of NA and MED individuals (Table 1) hint at a similar scaled food availability, we  
 353 repeated the parameter estimation starting with the value of  $f = 0.81$  (from ' $pars_{NA}$ ') to  
 354 ensure robustness with respect to the starting choice of  $f$ . The estimation routine, which  
 355 could now freely vary the value of  $f$ , returned  $f = 0.67$ , thus confirming the validity of our  
 356 original setting.

#### 357 4. Discussion

358 Environmental conditions can affect physiological characteristics of organisms. For ex-  
 359 ample, reducing food availability directly reduces ultimate size, and changes in temperature  
 360 directly affect the growth rate [12, 14, 78]. The environmental effects can also be indirect.  
 361 Even subtle differences in environments can affect individuals on the biomolecular level and

362 affect energy utilization patterns. We have found evidence of both direct and indirect effects  
363 in this study.

364 We analyzed loggerhead turtles from the Mediterranean (MED) population, and compared  
365 them to loggerhead turtles from the North Atlantic (NA) population. By simultaneously an-  
366 alyzing morphology, physiological (condition) index, and the energy budget-related processes  
367 of turtles inhabiting areas with different environmental conditions, we explored how environ-  
368 mental conditions, physiological characteristics, and the interaction of the two might result  
369 in size dimorphism and different growth and reproduction reported previously [3, 5, 6].

#### 370 *4.1. Analyses of size and condition indices*

371 Empirical analyses show that the size dimorphism is present during the whole loggerhead  
372 turtle life cycle, with MED turtles being smaller than NA loggerhead turtles. Captive-reared  
373 hatchlings are heavier than the wild hatchlings of both populations (Figure A.9, panel b),  
374 which is consistent with the maternal effect as implemented in the standard DEB model;  
375 better fed mothers produce larger offspring [73, 79, this issue]. Size dimorphism is most  
376 pronounced at nesting; size difference between nesting females is consistent with a previous  
377 study [5, 6]. Because food availability is lower in the Mediterranean Sea than in the North  
378 Atlantic, [23, 80, 81], the dimorphism could qualitatively be explained by this difference  
379 [14, 16]. But is it enough?

380 The differences in food availability may not be the only reason for size dimorphism. We  
381 would intuitively expect an organism exposed to less food in the environment to have a lower  
382 condition index. The two populations, however, have similar condition indices regardless of  
383 the lower food availability in the Mediterranean Sea. To see whether our model provides  
384 an explanation for this pattern, we refer back to Eqs. (2) and (3) to obtain a first-order  
385 theoretical approximation for the condition index,  $K = \delta^3 \rho (1 + f\omega)$ . Assuming the same  
386 shape factor,  $\delta$ , and density of structure,  $\rho$ , for turtles from both populations (as we did  
387 throughout this study) shows that the ratio of condition indices is

$$\frac{K_{\text{NA}}}{K_{\text{MED}}} = \frac{1 + \omega_{\text{NA}} f_{\text{NA}}}{1 + \omega_{\text{MED}} f_{\text{MED}}}. \quad (4)$$

388 NA loggerhead turtles experience better feeding conditions,  $f_{\text{NA}} = 0.81$  compared to  $f_{\text{MED}} =$   
389  $0.67$ . In contrast, MED loggerhead turtles have a higher maximum reserve density, leading  
390 to  $\omega_{\text{NA}} = 1.70$  compared to  $\omega_{\text{MED}} = 1.93$  (Table 2). Inserting these values into Eq. (4) gives  
391  $K_{\text{NA}}/K_{\text{MED}} = 1.0366$ , thus indicating that the conditions indices of the two populations should  
392 be very similar. More importantly, we see that the reserve capacity of MED loggerhead turtles  
393 compensates for lower food availability in the Mediterranean ( $[E_m]$ , Table 2). Increasing

394 the reserve capacity is, in fact, a reasonable adaptation to lower food availability because  
395 organisms with more reserves better withstand starvation periods, which in turn are more  
396 likely to occur in an environment with little food to begin with. Admittedly, Eq. (4) misses  
397 potentially important contributions to the condition index, such as the reproductive buffer  
398 or the total body water content, but these contributions are variable in time, and thus  
399 responsible for second-order effects for which more elaborate longitudinal measurements are  
400 necessary.

#### 401 *4.2. Environmental characteristics known to affect size and physiological performance*

402 *Incubating (nest) environment* can be very different between NA and MED nesting  
403 beaches, and may be responsible for some of the size difference in hatchlings. Based on  
404 results from intra-population studies, incubation at colder and moister sites generally yields  
405 heavier and larger hatchlings [37, 40, 41, 42, 43], but see [38, 42, 45, 46]. In contrast, high  
406 salinity in the incubating environment, mirroring the physiological effects of a dry incubat-  
407 ing environment, yields smaller hatchlings [44]. Nesting locations for each of the populations  
408 show great variability in the average incubation duration, hatchling size, and hatchling sex  
409 ratio [82], suggesting markedly different incubation conditions even within a single popu-  
410 lation. Making comparisons on the basis of population-specific abiotic factors is therefore  
411 extremely susceptible to source-based bias in the available data. With caution, nevertheless,  
412 some general patterns can be explored.

413 The average incubation temperatures of nests on MED beaches (Cyprus and Turkey, [83,  
414 84]) are higher than those on NA beaches (Georgia, [85]), the higher temperature in natural  
415 nests being often combined with a drier substrate [42]. Such a combination suggests that the  
416 smaller size of the MED hatchlings could be linked to warmer and drier nests. The correlation  
417 of temperature and humidity to size at hatching does, however, exhibit some inconsistencies  
418 (cf. Stokes et al. [37], Reece et al. [42], Glen et al. [43], Ji and Brana [45], Patino-Martinez  
419 et al. [46]). In addition to temperature and moisture affecting the hatchling morphology  
420 independently, a combination of the effects can be present [40], including indirect effects on  
421 size via incubation duration and embryonic yolk utilization [40, 45, 86].

422 Osmotic water absorption of eggs and embryos of freshwater snapping turtle is suscep-  
423 tible to salinity [44]. It is reasonable to assume that osmotic absorption of sea turtle eggs  
424 and embryos [46] is susceptible to similar phenomena. However, the effects of salinity on  
425 embryonic development and hatchling size have yet to be explored for loggerhead turtles.

426 *Higher food availability and warmer temperature* should both positively affect growth,  
427 reproduction, and size of loggerhead turtles [14]. We assumed the same temperature sensi-  
428 tivity within the thermal tolerance range (parameter  $T_A$ ) for individuals from both popula-

429 tions. The assumption was supported by the good fit of model predictions to data (Figs. 3  
430 and 4). Food availability was assumed higher in the North Atlantic. Within the same popu-  
431 lation, females that experience higher food availability are larger, reproduce more frequently  
432 [14, 87, 88], and produce larger hatchlings [88]. However, the egg size within a population is  
433 generally uniform [5] and does not differ significantly in (energy-providing) yolk content [89].  
434 Eggs of different populations do, however, differ in size with a positive correlation between  
435 yolk amount and egg size (e.g., [50]). Earlier onset of reproduction is linked to food availabil-  
436 ity in sibling species [90]. It therefore seems reasonable to assume that such environmental  
437 cues may cause distinct adaptations at the population level.

438 *Other pressures present in the environment*, such as predation and anthropogenic pres-  
439 sures, can result in evolutionary size selection. Smaller size and younger age at nesting, as  
440 identified in this study (see also Piovano et al. [3]), might be a result of the selection driven by  
441 anthropogenic pressures. Strong anthropogenic pressure (especially, commercial harvesting)  
442 is known to drive down the age and size at first breeding of fish and predators in the marine  
443 ecosystems [91, 92]. The main source of loggerhead turtle mortality in the Mediterranean is  
444 bycatch [11, 93], with other significant anthropogenic pressures such as shipping and mass  
445 tourism [94] also having a high probability of interaction and a negative impact on loggerhead  
446 turtles. Such pressures exert a strong evolutionary incentive for the MED population to breed  
447 at a younger age and, consequently, smaller size—particularly in a food-limited environment.

#### 448 4.3. Model predictions for MED loggerhead turtles

449 Given the relatively high level of data completeness [21], our model generates satisfac-  
450 tory fits, but it is still imperfect. The mis-matches between the model’s outputs and data  
451 are informative nonetheless, because they help identify limitations in data availability or  
452 oversimplifications used in the model formulation.

453 For example, the “observed” size at nesting, calculated from all available data, included a  
454 relatively high proportion of sea turtles nesting in Turkey and Libya, which are smaller than  
455 those nesting in Greece and Cyprus (Margaritoulis et al. [1], Groombridge [11] and Table A.6).  
456 In reality, the Greek subpopulation comprises the largest proportion of the Mediterranean  
457 population [1], meaning that the average length at puberty is likely to be larger, i.e., closer  
458 to the predicted value.

459 Age at puberty was predicted to be lower than the observed value, as in other sea turtle  
460 DEB models [19, 73, this issue]. It could be that sea turtles start allocating to reproduction  
461 several years prior to actual nesting, or that they experience a period of less favorable (than  
462 simulated) environmental conditions during their juvenile stage, which would prolong the  
463 time needed to reach puberty [14, 95]. A less favorable environment during the juvenile

464 stage would account also for slower-than-predicted growth of wild MED turtles in Fig. 6 (left  
465 panel).

466 A favorable prediction of the maximum reproduction rate (Table 3) and a somewhat less  
467 satisfactory prediction of the clutch size as a function of carapace length (Figure 6) imply  
468 that the modeled allocation to reproduction is correct, but the clutch size is determined by  
469 factors other than available energy alone. Data for total seasonal reproductive output rather  
470 than clutch size may be more appropriate for model validation, but are not available in part  
471 because of how logistics hinders data gathering [5, 9, 10].

472 In summary, our model successfully reproduces the main life-history traits and the size  
473 dimorphism of MED and NA loggerhead turtles, but only after calibrating both the envi-  
474 ronmental forcing and the model parameters. The need to separately calibrate the model  
475 parameters suggests that MED loggerhead turtles underwent evolutionary adaptations to the  
476 prevailing conditions in the Mediterranean Sea. Furthermore, the success of our modeling  
477 approach provides support for a wider implementation of predictive models in conservation  
478 efforts [96].

#### 479 4.4. *Can a North Atlantic turtle thrive in the Mediterranean Sea?*

480 Applying the same theoretical and practical framework as was done for the NA population  
481 [14, 19], we simulated the Mediterranean environment for a NA turtle, and the North Atlantic  
482 environment for a MED turtle. Simulated environments effectively differed only in the scaled  
483 food availability ( $f_{\text{MED}} = 0.67$  this study,  $f_{\text{NA}} = 0.81$  Marn et al. [19], AmP *Caretta caretta*  
484 [dataset] 2018). The turtles physiology differed due to parameter values (Table 2).

485 Predictions for the NA loggerhead turtle imply that this turtle would reach a smaller  
486 ultimate size than she would in the North Atlantic (83 cm compared to 105 cm SCL), i.e., the  
487 same ultimate size as is predicted for the MED turtle in the Mediterranean. Size at puberty  
488 is predicted to be similar as in the North Atlantic (77 cm SCL), however the needed time to  
489 reach puberty would be 9 years longer than in the North Atlantic (22 compared to 13 years)  
490 and the reproduction rate would be only about 26% of that observed in the North Atlantic  
491 (Marn et al. [19] and AmP *Caretta caretta* [dataset] 2018). The combination of much delayed  
492 onset of reproduction and a lower reproduction rate, would drastically reduce fitness of NA  
493 turtles. Assuming a lower sea temperature based on the information that the NA loggerhead  
494 turtles mostly forage in the western (cooler, 19° C Manca et al. [24]) Mediterranean basin  
495 [2, 3] would amplify the effect further. Hence, it is possible that, even without fidelity to  
496 their nesting beaches, the NA turtles visiting the Mediterranean Sea would not reproduce  
497 there due to energy limitation.

498 The Mediterranean turtle venturing into the Atlantic would have an advantage over the

499 NA loggerhead turtles. Because she needs to invest less energy into maturation to reach  
500 puberty than the NA turtle does (Table 2), she would mature several years earlier (pre-  
501 dicted age at puberty at  $f = 0.81$  is 9 years for the MED loggerhead turtle). Lower energy  
502 needed for maintaining the maturity level of puberty enables that more energy is allocated  
503 to reproduction: predicted ultimate size of 100 cm SCL matches the prediction for the NA  
504 turtle in the North Atlantic, and the reproduction rate at the ultimate size was predicted to  
505 be around 65% higher than the observed reproduction rate of NA individuals of the same  
506 size, and 43% higher than the reproduction rate predicted by the model for the NA turtle  
507 (Marn et al. [19], and AmP *Caretta caretta* [dataset] 2018). Increase in size is also predicted  
508 to be faster for the MED loggerhead turtle. Faster maturation and growth of MED turtles  
509 experiencing similar condition as NA turtles is in accordance with reports [3], however there  
510 are no available data on MED loggerhead turtles nesting in the North Atlantic that we could  
511 use to check whether such high reproduction output is reasonable. An advantage over NA  
512 turtles would be a strong incentive for MED turtles to go into North Atlantic. Perhaps they  
513 do (but encounters with them have not been frequent) or the fidelity to nesting beaches and  
514 direction of sea currents keep them in the Mediterranean Sea.

#### 515 4.5. Evolutionary implications of the parameter values

516 Our results are consistent with the idea that MED loggerhead turtles have evolved from  
517 NA ones. Namely, known genetic differences between the two populations [2, 3] are likely  
518 to be reflected in the different parameter values in the model, because genotype determines  
519 phenotype, and parameter values are a manifestation of the latter [97]. The simulations  
520 presented herein were indeed unable to reproduce the different life-history traits of MED  
521 and NA loggerhead turtles simply by modifying the environmental forcing of the model.  
522 To successfully model both populations it was necessary to modify several core parameter  
523 values (Tables 2). However, that the two populations are closely related is also seen from  
524 these parameter values because they differ much less between themselves than in interspecies  
525 comparisons (Fig. 8).

526 Changes in the parameter values obtained for MED loggerhead turtles relative to NA  
527 ones appear consistent with the prevailing environmental conditions in the Mediterranean  
528 Sea. For example, the surface area specific maximum assimilation rate ( $\{\dot{p}_{Am}\}$ ) controls  
529 the assimilation flux, but also affects energy storage capacity. A 20% higher  $\{\dot{p}_{Am}\}$  for  
530 MED loggerhead turtles, coupled with only a 6% higher value of the energy conductance ( $v$ ,  
531 Table 2), not only enables that more energy is assimilated per unit of surface area, but also  
532 results in maximum reserve density ( $[E_m] = \{\dot{p}_{Am}\}/v$ ) of MED turtles being larger by 13%.  
533 This enables MED loggerhead turtles to survive longer periods of food shortage, as expected



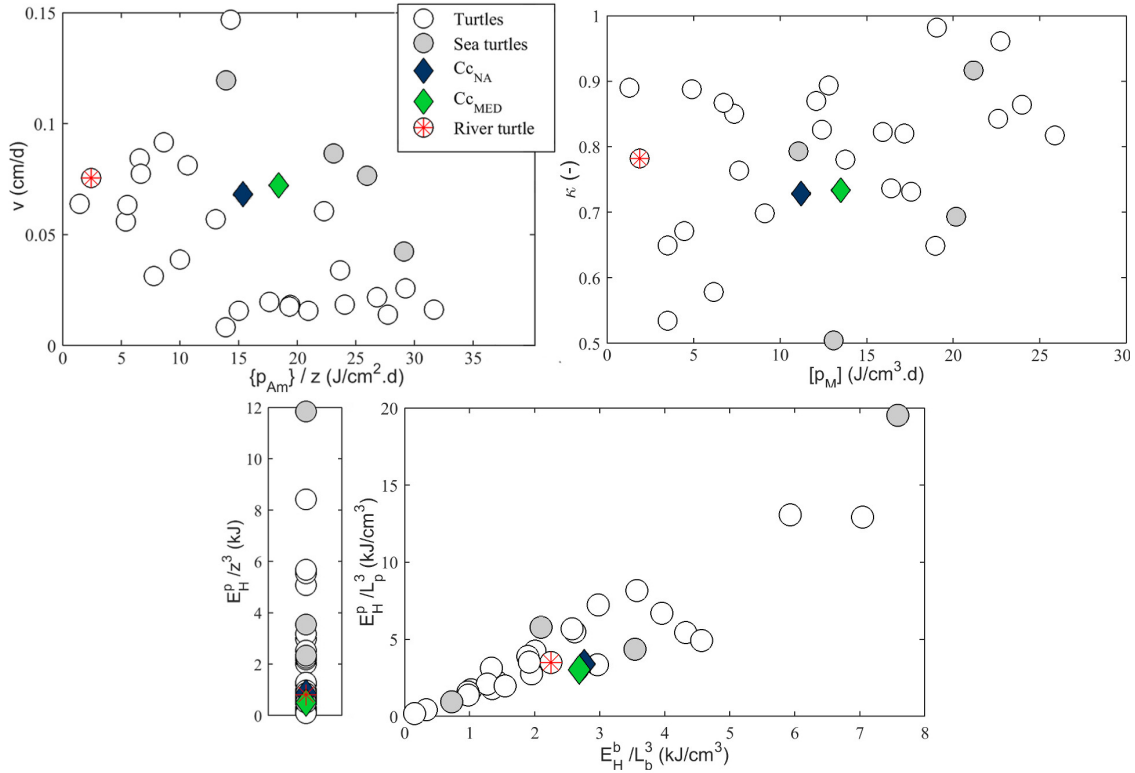


Figure 8: Values of several core parameters (maximum assimilation rate,  $\{\dot{p}_{Am}\}$ ; energy conductance,  $\dot{v}$ ; somatic maintenance rate,  $[p_M]$ ; allocation fraction to soma,  $\kappa$ ; maturity level at puberty,  $E_H^p$ ; and maturity densities  $E_H^*/L_*^3$ ) relative to other related species in the Add-my-pet collection [20]. Parameters that scale with size ( $\{\dot{p}_{Am}\}$  and  $E_H^p$ ) are divided by the zoom factor to enable comparisons between different-sized species [16]. The parameter values belonging to the same or closely related species are more similar than those of different species. Other sea turtle species (with AmP dataset references in parentheses) are: *Chelonia mydas* [dataset] 2017, *Lepidochelys kempii* [dataset] 2015, *Natator depressus* [dataset] 2017, and *Dermochelys coriacea* [dataset] 2015. The river turtle *Carettochelys insculpta* [dataset] 2017 (marked with a red asterisk) was included because of similar morphology (flippers).

534 in a food-deprived environment.

535 A higher value of volume-specific somatic maintenance for MED turtles may be linked to  
 536 the energetic costs of osmotic regulation related to the higher salinity of the Mediterranean.  
 537 Loggerhead turtles are excellent osmoregulators [101, 102, 103], but coping with the increased  
 538 salt load by a more intense secretion of the lachrymal salt glands can lead to dehydration  
 539 [104] and presumably carries an additional energetic cost reflected in the increased cost of  
 540 maintenance [105, 106]. While lower salinity does not seem to have adverse effects [107, 108],  
 541 areas of the Mediterranean with higher salinity may act as a “salinity barrier” *sensu* Carreras  
 542 et al. [2], thus restricting NA loggerhead turtles to areas with lower salinity [2, 28].

543 Maturity levels at birth and puberty ( $E_H^b$  and  $E_H^p$ , respectively) are metabolic switches  
 544 that mark transitions between embryo, juvenile, and adult stages independent of size or age

545 [16]. The difference between maturity at puberty is striking between the two populations of  
546 loggerhead turtles: MED loggerhead turtles need to invest 40% less energy than NA turtles  
547 to reach puberty, and they need to allocate around  $22\text{kJd}^{-1}$  less energy to maintain the  
548 maximum level of maturity (Fig. 7). Less investment into maturation and the corresponding  
549 lower maintenance is certainly favorable in low-food environments because—all else being  
550 equal—it leads to earlier sexual maturation and higher reproductive output at the same  
551 body size.

552 Faster growth and earlier maturation at a smaller size have three main energetic benefits:  
553 (i) less cumulative energy invested into growth, (ii) less cumulative energy spent on metabolic  
554 maintenance, and (iii) sexual maturation reachable at lower food levels [14]. This strategy  
555 is therefore beneficial in resource-poor environments with short periods of food availability  
556 as faster growth uses the (temporarily) available resources to rapidly increase in size, and  
557 smaller size at sexual maturity typically requires less energy to complete a reproduction cycle  
558 [15, 109].

559 Interestingly, the ratio of the maturity level and the predicted structural volume, i.e.,  
560 maturity density [110, 111, this issue] at a specific life stage transition is strikingly similar  
561 for both populations (Fig. 8). A correlation between maturity density at birth and maturity  
562 density at puberty seems to exist for all species of turtles (last panel in Fig. 8), and all  
563 animal taxa in the Add-my-pet collection [111, this issue]. Perhaps species-specific maturity  
564 densities rather than maturity levels drive metabolic switches (for more details see section  
565 1.1.4. of the online comments file, [112], pages 5-8).

566 The apparent success of our modeling approach to put the size dimorphism exhibited by  
567 the two studied populations in an evolutionary context points to a deeper connection between  
568 DEB theory and evolution. When individuals of a certain species move to expand the range  
569 of their species, they are likely to be less-than-optimally adapted to the new territory. In such  
570 circumstances, natural selection favors those adaptations that help sustain the presence in the  
571 new territory, implying that over an evolutionary time scale, even the parameters of a DEB  
572 model become dynamical variables. Future applications of DEB theory—e.g., in relation to  
573 conservation efforts [96]—should perhaps consider the kind of a modeling approach that can  
574 capture the dynamics of such variables. Jusup et al. [97] have made an early proposal in this  
575 direction, but the usefulness of their proposal is yet to be seen.

## 576 5. Conclusion

577 We demonstrate that the size dimorphism between the two studied populations of log-  
578 gerhead turtles cannot be explained solely by the difference in environmental conditions, but

579 requires a population-specific description. An implication is—also consistent with the genetic  
580 separation between the two populations [2, 3, 4]—that adaptations to the new environment  
581 drive the evolution of metabolic traits over sufficiently long time scales.

582 We find that three DEB primary parameters capture most of the differences in growth,  
583 maturation, and reproduction between North Atlantic (NA) and Mediterranean (MED) log-  
584 gerhead turtles:  $[\dot{p}_M]$ ,  $\{p_{Am}\}$ , and  $E_H^p$ . Higher somatic maintenance ( $[\dot{p}_M]$ ) and lower cumula-  
585 tive investment to maturity ( $E_H^p$ ) of the MED population are interpreted here as adaptations  
586 to environmental factors such as high salinity, which increases the energetic cost of salt gland  
587 activity, and low food availability, which favors sexual maturation at a smaller size. More  
588 specifically, we find that:

589 (i) MED loggerhead turtles grow and mature faster than their NA cousins when in the  
590 Mediterranean Sea due to a faster assimilation (i.e., larger  $\{p_{Am}\}$ ), but reach smaller ultimate  
591 size due to lower food availability (lower  $f$ ) and higher somatic maintenance (larger  $[\dot{p}_M]$ );

592 (ii) MED loggerhead turtles become sexually mature at a smaller size than their North  
593 Atlantic cousins due to a lower cumulative investment to maturation (lower  $E_H^p$ ). The ratio  
594 of the invested energy to the structural volume, dubbed maturity density, might indicate the  
595 corresponding maturity level for a metabolic switch when sizes at life events drastically differ  
596 between genetically distinct populations of a same species.

597 (iii) The smaller ultimate size of MED loggerhead turtles is a consequence of low food  
598 availability in the Mediterranean Sea, but the reproductive output is comparable to that of  
599 NA individuals because more energy is available for reproduction due to a lower maturity  
600 maintenance (proportional to  $E_H^p$ ).

601 (iv) A combination of lower food assimilation potential and higher costs of maturity  
602 maintenance in fully grown NA loggerhead adults offers a metabolic explanation for the  
603 observation that NA females do not nest in the Mediterranean.

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611 manuscript.

612 **Appendix A. Size data on North Atlantic (NA) and Mediterranean (MED) log-**  
613 **gerhead turtles, and additional results from statistical analyses**

614 All data used for the comparison is listed in Tables A.4 to A.6. The data was either  
615 available as a dataset, or reported as a mean with a range and/or standard deviation (SD).

616 For the MED population, substantially fewer datasets were available. The data for wild  
617 populations was mostly reported as a mean with a range and/or standard deviation. In  
618 addition, we used a previously unpublished dataset from a rearing and reproduction program  
619 in Marineland Antibes (France). The dataset contained measurements of weight at hatching  
620 and weekly weight increase up to the age of 2 years for 21 juveniles, and measurements of  
621 size and weight of two females reproducing in captivity. This data cannot be analyzed as a  
622 part of the wild MED population even though the adults were obtained (and reproduce) in  
623 the Mediterranean – the captive reared individuals experience considerably more favorable  
624 conditions than the turtles in the wild, and are therefore expected to have a better condition  
625 index and produce heavier hatchlings [16]. Consequently, the data from the reproduction  
626 program was analyzed separately.

627 For the analysis of the size at hatching, data reported at the moment of hatching (leaving  
628 the egg) was pooled together with the data reported for the moment of emergence (leaving  
629 the nest). This was justified as the length does not significantly change between hatching  
630 and emergence. The minor decrease in wet weight between hatching and emergence (due to  
631 dehydration, Bennett et al. [113]) was thus ignored. Length and/or wet weight are mostly  
632 reported at emergence for the field incubated nests (e.g. [37]), and at hatching for the  
633 laboratory incubated nests (e.g. [38]); pooling the data for analysis increased the sample size  
634 and aided the comparison.

635 By focusing on “size at nesting” rather than “size at puberty” we were able to use literature  
636 data for nesting turtles, which is mostly reported in such a way that data describing first-time  
637 nesters cannot be distinguished from that describing experienced nesters.

Table A.4: **Egg diameter and wet weight – overview of the data used in the analysis.** The range [minimum and maximum] and/or the standard deviation (SD) of the sample is given in the square brackets and parenthesis, respectively, and the number of data points in italicized font ( $N$ ) where the information was available. Data sources (ds) are indicated next to each data set.

Diameter (cm)				Mass (g)			
North Atlantic	ds	Mediterranean	ds	North Atlantic	ds	Mediterranean	ds
4.25 (0.14), <i>48</i>	1	3.76 (0.142), <i>23</i>	1	42.58 (1.78), <i>45</i>	2	27.6 (3.1), <i>23</i>	1
		3.74 (0.196) <sup>a</sup>		39.4 (3.8), <i>48</i>	1	32.4 (3.52) <sup>a</sup>	
		[3.29-3.96], <i>12</i>	3 <sup>1</sup>			[26.4-38.6], <i>12</i>	3 <sup>1</sup>
		3.8-3.86 <sup>b</sup> (0.133) <sup>a</sup>				26.9-31.9 <sup>b</sup> (3.42) <sup>a</sup>	
		[3.49-4.02], <i>13-26</i>	3 <sup>1</sup>			[22.8-36.5], <i>13-30</i>	3 <sup>1</sup>
		3.61-3.87 <sup>b</sup> (0.390) <sup>a</sup>				29.8 (3.10) <sup>a</sup> [23-35.4],	
		[2.7-4.26], <i>12-30</i>	3 <sup>2</sup>			<i>45</i>	3 <sup>3</sup>
		3.67 (0.223) <sup>a</sup>				27.5 (3.43) <sup>a</sup>	
		[3.3-4.19], <i>45</i>	3 <sup>2</sup>			[15.9-36.5], <i>173</i>	3 <sup>2</sup>
		3.45 (0.174) <sup>a</sup> [3.1-3.5],				30.48 (1.62), <i>10</i>	4
		<i>15</i>	3 <sup>3</sup>				
		3.7 (0.200) <sup>a</sup> [3.3-4.1],				30.21 (1.65), <i>10</i>	4
		<i>65</i>	3 <sup>3</sup>				
		4.04-4.21 <sup>b</sup> (0.232) <sup>a</sup>				30.31 (1.79), <i>10</i>	4
		[3.7-4.5], <i>5-8</i>	3 <sup>3</sup>				

<sup>a</sup> standard deviation calculated following Hozo et al. [51], no distribution assumed

<sup>b</sup> data for more than one season reported together; for our analysis we used a non-weighted mean of means and an average sample size

Data source key: {1} Tiwari and Bjorndal [5] (Greece and Florida), {2} Ackerman [50] (Florida),

{3} Margaritoulis et al. [1] and references therein – sample sites: <sup>1</sup>Cyprus; <sup>2</sup>Greece; <sup>3</sup>Turkey; {4} Reid et al. [38] (Greece)

Table A.5: **Hatchling length (SCL) and wet weight – overview of the data used in the analysis.** The range [minimum and maximum] and/or the standard deviation (SD) of the sample is given in the square brackets and parenthesis, respectively, and the number of data points in italicized font ( $N$ ) where the information was available. Data sources (ds) are indicated next to each data set. Data from the reproduction program is included as a separate group, with SCL at hatching unknown.

Length (cm)				Mass (g)			
North Atlantic	ds	Mediterranean	ds	North Atlantic	ds	Mediterranean	ds
4.48 (0.159) [4.13-5.0], <i>110</i>	1 <sup>1</sup>	4 (0.407) <sup>a</sup> [2.49-4.93], <i>2064</i>	3 <sup>1</sup>	22.08 (1.49) <i>41</i>	2	15.3 (2) <sup>a</sup> [9.4-21.4], <i>1482</i>	3 <sup>1</sup>
4.56 (0.141) [4.1-4.99], <i>129</i>	1 <sup>2</sup>	4.03-4.15 <sup>b</sup> (0.150) <sup>a</sup> [3.6-4.5], <i>180-325</i>	3 <sup>1</sup>	18.03 (1.33) [14-21], <i>110</i>	1 <sup>1</sup>	15.9-16.7 <sup>b</sup> (1.583) <sup>a</sup> [12-21.5], <i>180-325</i>	3 <sup>1</sup>
4.43 (0.134) [4.09-4.71], <i>114</i>	1 <sup>1</sup>	4.04 (0.7), <i>20</i>	3 <sup>2</sup>	19.87 (1.43), <i>129</i>	1 <sup>2</sup>	16.74 (0.82), <i>10</i>	4
4.45 (0.17) [3.96-4.76], <i>108</i>	1 <sup>1</sup>	3.98 (0.407) <sup>a</sup> [2.8-4.5], <i>302</i>	3 <sup>3</sup>	18.71 (2.18) [14-24.5], <i>114</i>	1 <sup>1</sup>	16.72 (1.02), <i>10</i>	4
4.42 (0.156) [3.87-4.7], <i>106</i>	1 <sup>1</sup>	3.91 (0.150) <sup>a</sup> [3.6-4.2], <i>37</i>	3 <sup>3</sup>	18.75 (1.743) [14-22], <i>108</i>	1 <sup>1</sup>	16.59 (0.9), <i>10</i>	4
4.6 (0.11) [4.3-4.9], <i>120</i>	5	4.29 (0.09), <i>10</i>	4	18.68 (1.743) [14-22.5], <i>106</i>	1 <sup>1</sup>		
		4.24 (0.1), <i>10</i>	4	19.8 (1.33) [15.3-22.4], <i>120</i>	5		
		4.22 (0.1), <i>10</i>	4				

<sup>a</sup> standard deviation calculated following Hozo et al. [51], no distribution assumed

<sup>b</sup> data for more than one season reported together; for our analysis we used a non-weighted mean of means and an average sample size

Data source key: {1} Data partially published in Stokes et al. [37] – sample sites: <sup>1</sup>Florida, <sup>2</sup>South Carolina; {2} Ackerman [50] (sample site: Florida); {3} Margaritoulis et al. [1] and references therein – sample sites: <sup>1</sup>Cyprus, <sup>2</sup>Greece, <sup>3</sup>Turkey; {4} Reid et al. [38] (Greece); {5} Reich et al. [114] (Florida); Additional data was available from the Marineland (Antibes, France) rearing facility : 21.02 (SD 5.8), range [16.7-37.5],  $N=21$  – data could not be approximated by a normal distribution and was analyzed separately.

Table A.6: **Adult length (SCL) and wet weight – overview of the data used in the analysis.** The range [minimum and maximum] and/or the standard deviation (SD) of the sample is given in the square brackets and parenthesis, respectively, and the number of data points in italicized font ( $N$ ) where the information was available. Data sources (ds) are indicated next to each data set.

Length (cm)				Mass (g)			
North Atlantic	ds	Mediterranean	ds	North Atlantic	ds	Mediterranean	ds
90.9 (4.9) [82-103], <i>84</i>	1	79.43 (4.4) [74.31-84.37], <i>14</i>	2	118.2 (17.5) [89.7-170.9], <i>47</i>	1	67.26 (8.625) <sup>a</sup> [52.5-87], <i>40</i>	3
92.3 (5.6) [81-110], <i>110</i>	1	76.8-80.1 <sup>b</sup> (6.799) <sup>a</sup> [63.5-87], <i>11-15</i>	4 <sup>1</sup>	116.3 (17.1) [71.7-148.9], <i>93</i>	1		
92.01 (5.34) [78.89-104.47], <i>102</i>	1*	78.6-79.1 <sup>b</sup> (7.250) <sup>a</sup> [66-95], <i>13-97</i>	4 <sup>1</sup>	114.7 (20.3) [79.6-180.7], <i>121</i>	1		
92.5 (2), [85-98], <i>13</i>	5 <sup>1</sup>	78.3-79.2 <sup>b</sup> (3.583) <sup>a</sup> [66-95], <i>195-343</i>	4 <sup>1</sup>	93.27 (22.64) [46.67-153.74], <i>56</i>	6*		
92.4 (0.8) [80.5-107], <i>52</i>	5 <sup>2</sup>	78.7 (6.273) <sup>a</sup> , [62.3-83.2], <i>9</i>	4 <sup>2</sup>				
93.1 (1) [83-105], <i>137</i> <sup>3</sup>	5	73.1 (5.925) <sup>a</sup> [60.2-83.9], <i>49</i>	4 <sup>3</sup>				
90.9 (5) [76.80-100.28], <i>51</i>	2	73.2 (5.375) <sup>a</sup> [66-87.5], <i>22</i>	4 <sup>3</sup>				
94.3 (5.5) [83.8-106.7], <i>41</i>	7	72 (7.250) <sup>a</sup> [58-87], <i>58</i>	4 <sup>3</sup>				
95.1 (4.8) [80.7-107.4], <i>84</i>	7						
94.73 (5.29) [80.72-107.34], <i>112</i>	7*						
89.59 (6.56) [80.56-105.04], <i>56</i>	6*						

<sup>a</sup> standard deviation calculated following Hozo et al. [51], normal distribution assumed

<sup>b</sup> data for more than one season reported together; for our analysis we used a non-weighted mean of means and an average sample size

Data source key: [1] Ehrhart and Yoder [69], \*digitalized from Figure 3 (sample site: Florida); [2] Tiwari and Bjorndal [5] (Greece and Florida); [3] Groombridge [11] (Greece); [4] Margaritoulis et al. [1] and references therein – sample sites:<sup>1</sup>Greece, <sup>2</sup>Lybia, <sup>3</sup>Turkey; [5] Stoneburner [31] (sample sites: <sup>1</sup>North Carolina, <sup>2</sup>Georgia, <sup>3</sup>Florida); [6] Wabnitz and Pauly [68], \*digitalized from Figure 1, only used samples from North Atlantic for loggerhead turtles longer than 80.5 cm SCL (sample sites: Virginia, Florida); [7] Byrd et al. [70], \*digitalized from Figure 3 (sample sites: South Carolina); Additional data was available from the Marineland (Antibes, France) rearing facility – individual values for two females: SCL = 70 cm and 80 cm, W = 86.6 kg and 100.3 kg – data was analyzed separately.

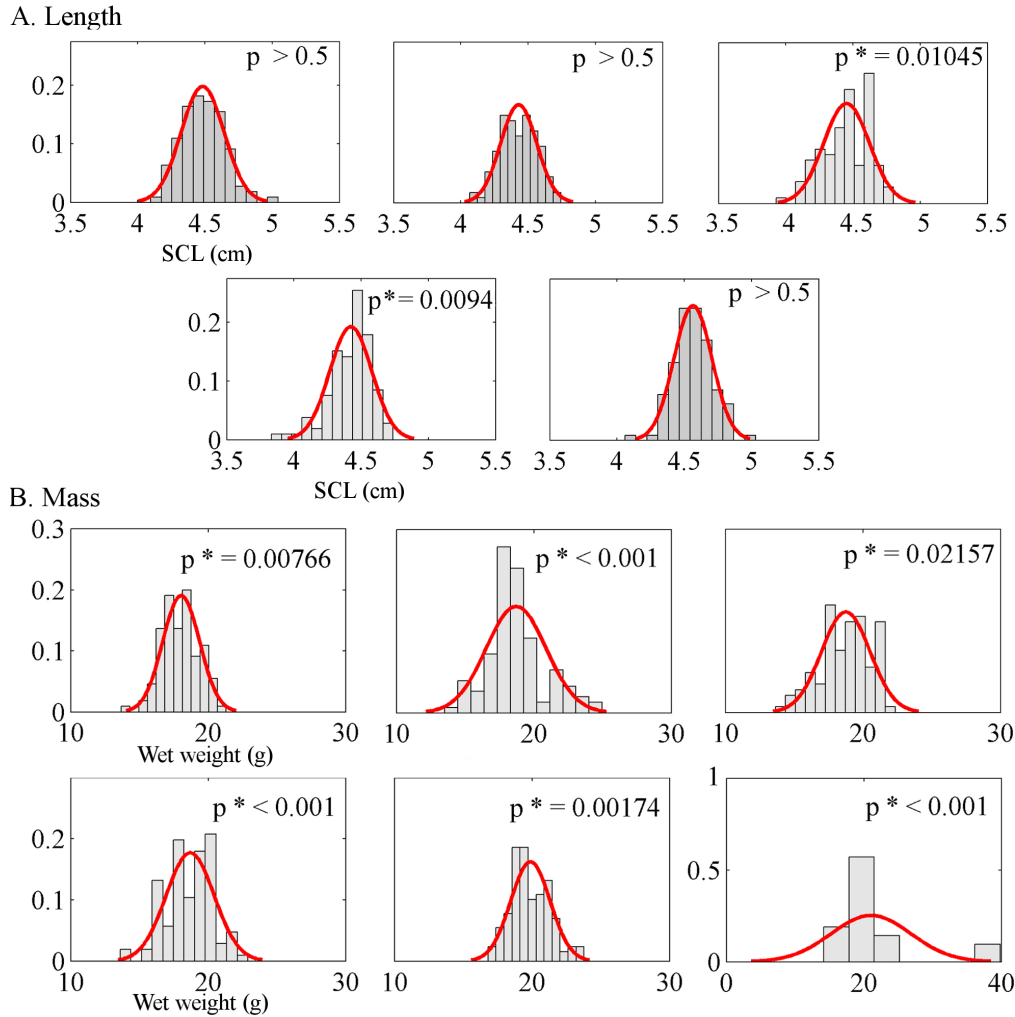


Figure A.9: **Hatchling size and results of the Lilliefors test for normality.** Histograms represent data and the solid line is the model of normal distribution based on the mean and standard deviation of the corresponding sample plotted across a range of three standard deviations from the mean. Even though some of the samples significantly differ from the normal distribution (indicated with a star next to the p-value), histograms of some datasets visually resemble a normal distribution. **Panel a.** Length. **Panel b.** Mass. All data for length and most data for mass are courtesy of L. Stokes (partially published in Stokes et al. [37]) and are from the NA population; data for mass include an additional previously unpublished dataset from Marineland (Antibes, France) rearing facility .

638 **Lilliefors test.** Test rejected the null hypothesis of that sizes at hatching are sampled  
 639 from a normal distribution (Lilliefors test,  $p < 0.05$ ) for two out of five length datasets and  
 640 all six tested mass datasets. However, histograms suggest that the discrepancies are driven  
 641 by just a few outliers that skew the distribution, which would otherwise resemble the normal  
 642 one (Figure A.9, panels a and b). We therefore chose to assume the normal distribution for  
 643 all datasets except those describing the captive reared hatchlings, for which the discrepancies  
 644 from the normal distribution were substantial. The size at nesting seems to follow the normal



645 distribution even more closely: the test could not reject the null hypothesis (Lilliefors test,  
646  $p > 0.05$ ) for none of the tested length datasets (see also Figure A.10).

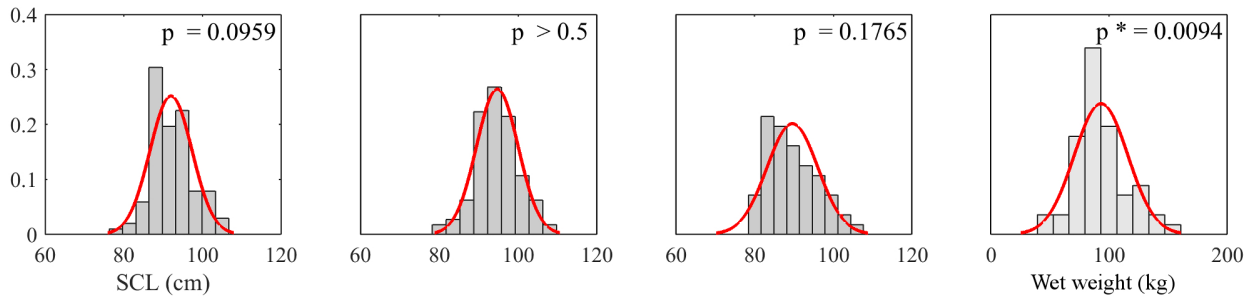


Figure A.10: **Adult size and results of the Lilliefors test.** Histograms represent data and the solid line is the model of normal distribution based on the mean and standard deviation of the corresponding sample plotted across a range of three standard deviations from the mean. The mass sample (last panel) significantly differs from the normal distribution (indicated with a star next to the p-value). Data sources: [68, 69, 70].

647 **Welch's F-test and unequal variances t-test.** The hypothesis that all samples de-  
648 scribing the same life stage came from the same statistical population was rejected (Welch's  
649 F-test  $p > 0.05$ , Figure 1), supporting the hypothesis that samples from the two popula-  
650 tions were different. Statistically even samples collected on neighboring beaches were not  
651 from the same population [37]. However, we grouped samples into NA and MED groups  
652 for the purpose of further analysis because: (i) visual analysis of probability density plots  
653 suggested a grouping of such type (Fig. 1); (ii) pairwise Welch's t-tests suggested that the  
654 size data assigned to the NA population were significantly larger than those assigned to the  
655 MED population in almost all cases (Fig. A.11); and (iii) grouping enabled inter-population  
656 comparison on a more general level.

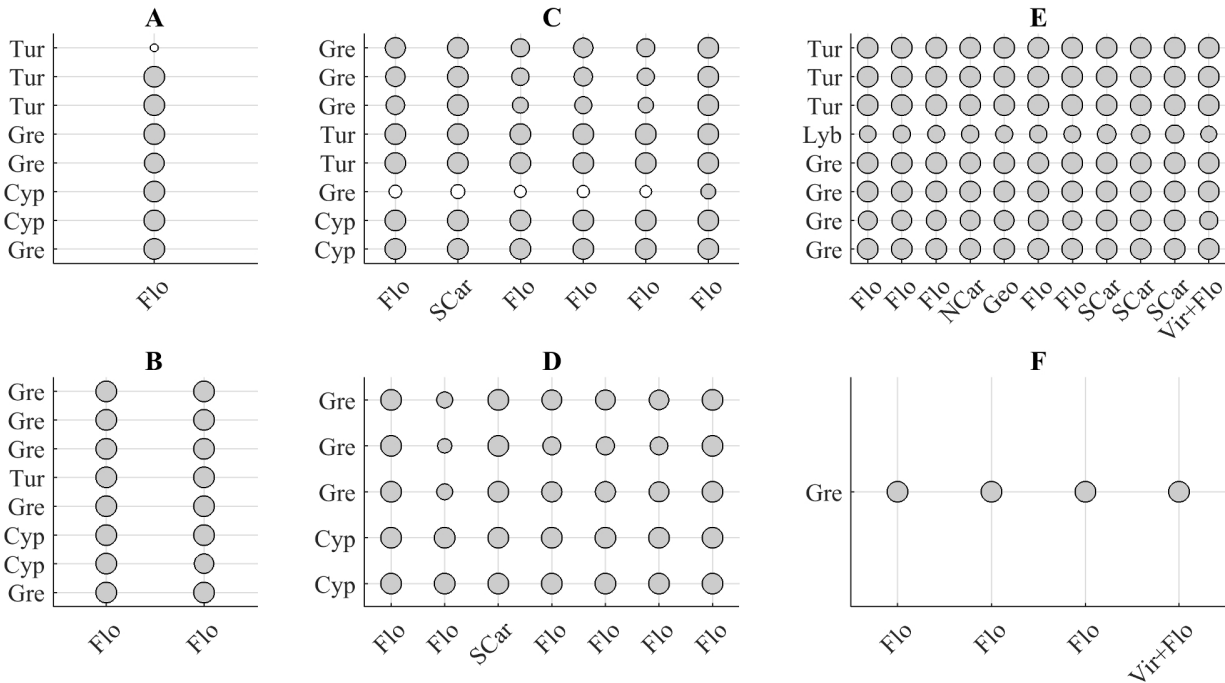


Figure A.11: Results of the pairwise Welch's t-test for sizes at the analyzed life events. Full circles denote the samples are significantly different ( $p < 0.05$ ) with the size of the circle proportional to statistical significance. **Egg** diameter (panel A) and mass (panel B); **Hatchling's** length (panel C) and mass (panel D) at hatching, and **adult female's** length (panel E) and mass (panel F) at nesting. Sampling location are indicated at the vertical axis for the MED population (Tur – Turkey, Gre – Greece, Cyp – Cyprus, Lyb – Lybia), and horizontal axis for the NA population (Flo – Florida, SCar – South Carolina, NCar – North Carolina, Vir – Virginia).

657 **Appendix B. Overview of the standard Dynamic Energy Budget (DEB) model**  
 658 **for loggerhead turtles**

659 The standard DEB model follows changes over time of three main state variables (marked  
 660 S1-S3 in Fig. B.12), and an auxiliary variable (R1 in Fig. B.12, present only in adults).  
 661 Temperature is included as an effect on all rates [16]. Food availability is included as the  
 662 scaled functional food response, i.e., a saturating function denoting the feeding rate as a  
 663 fraction of the maximum for an individual of the same size [16, 95].

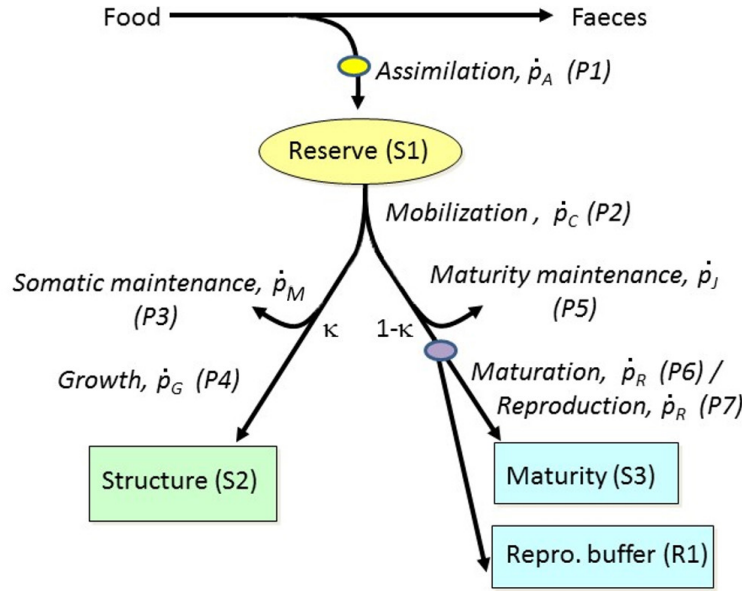


Figure B.12: **Schematic representation of the standard DEB model.** Dynamics of the state variables are determined by energy flows universally denoted  $\dot{p}_*$  (unit  $\text{Jd}^{-1}$ ). For dynamics of state variables see Table B.7, for process descriptions and equations Table B.8, and for parameters of the model Table 2. Food availability is quantified by the scaled functional response,  $f$  (i.e.,  $f = 1$  under unlimited food availability and  $f = 0$  when food is unavailable, see p. 32 of [16] for details.) Circles mark metabolic switches: birth (yellow circle) is the onset of feeding, whereas puberty (purple circle) is the onset of investment into reproduction. Mobilized reserve is partitioned according to the  $\kappa$ -rule: fixed fraction  $\kappa$  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).

Table B.7: **State variables of the standard DEB model.** S1-S3 in the "Notes" column refer to the corresponding compartment in Fig. B.12. For energy flows see Table B.8, for parameter descriptions and values Table 2.

State variable	Equation	Note
Reserve	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	S1
Structure	$\frac{dL}{dt} = \frac{1}{3L^2} \frac{\dot{p}_G}{[E_G]}$	S2
Maturity	$\frac{dE_H}{dt} = \dot{p}_R$ , if $E_H < E_H^p$ $\frac{dE_H}{dt} = 0$ , otherwise	S3; $E_H^p$ is maturity at puberty marking the beginning of the adult stage (see Fig. B.12. In this stage, investment into maturation gets redirected into reproduction: $\frac{dE_R}{dt} = \dot{p}_R$ (auxiliary variable R1 in Figure B.12)

Table B.8: **Energy flows** appearing in the system of equations for state variables (Table B.7), modified from Marn et al. [19]. All model parameters are conveniently summarized in Table 2.

Process	Equation	Note
Assimilation	$\dot{p}_A = \{\dot{p}_{Am}\}fL^2$	P1; The fraction of the daily feed ration that gets fixed into reserve, where $\{\dot{p}_{Am}\}$ (unit $\text{J cm}^{-2} \text{d}^{-1}$ ) 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.
Mobilization	$\dot{p}_C = E(\dot{v}/L - \dot{r})$	P2; The flow of energy mobilized from reserve to power metabolic processes, where parameter $\dot{v}$ (unit $\text{d}^{-1}$ ) 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 $\text{J cm}^{-3} \text{d}^{-1}$ ) is the volume-specific somatic maintenance rate.
Somatic maintenance	$\dot{p}_M = [\dot{p}_M]L^3$	P3; The flow of mobilized reserve energy needed to maintain the structure of given size $L^3$ .
Growth	$\dot{p}_G = \kappa\dot{p}_C - \dot{p}_M$	P4; The flow of mobilized reserve energy invested into the increase of structure after satisfying the somatic maintenance needs.
Maturity maintenance	$\dot{p}_J = \dot{k}_J E_H, E_H \leq E_H^p$	P5; 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 $\text{d}^{-1}$ ) is called the maturity maintenance rate coefficient.
Maturation	$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$	P6; The flow of mobilized reserve energy towards increasing the level of maturity ( $E_H$ ), after satisfying the maturity maintenance, $\dot{p}_J$ .
Reproduction	$\dot{p}_R$	P7; At the onset of the adult stage when the level of maturity reaches $E_H^p$ , the organism starts to invest energy into reproduction instead of maturation. Hence, reproduction starts and maturity stops increasing.

664 We first used the parameter set for the North Atlantic (NA) population of loggerhead  
665 turtles (*'pars<sub>NA</sub>'*) to run the model and get predictions for environmental characteristics de-  
666 scribing the Mediterranean Sea (Fig B.13, see Section 2.2 for more details). We compared  
667 predictions (life history traits, growth curves, reproduction output etc.) to observations for  
668 Mediterranean (MED) loggerhead turtles to calculate the goodness of fit [21, 58, this issue].  
669 In the second step, we used the observations (on life history traits, growth, and reproduc-  
670 tion) in addition to *'pars<sub>NA</sub>'* and environmental characteristics, and with the covariation  
671 routines obtained a new parameter set (*'pars<sub>MED</sub>'*) and model predictions. The covariation  
672 routines (integrated into DEBtool [61]), use the Nelder-Mead method and symmetric-bound  
673 loss function for parameter estimation [57, 58, this issue].

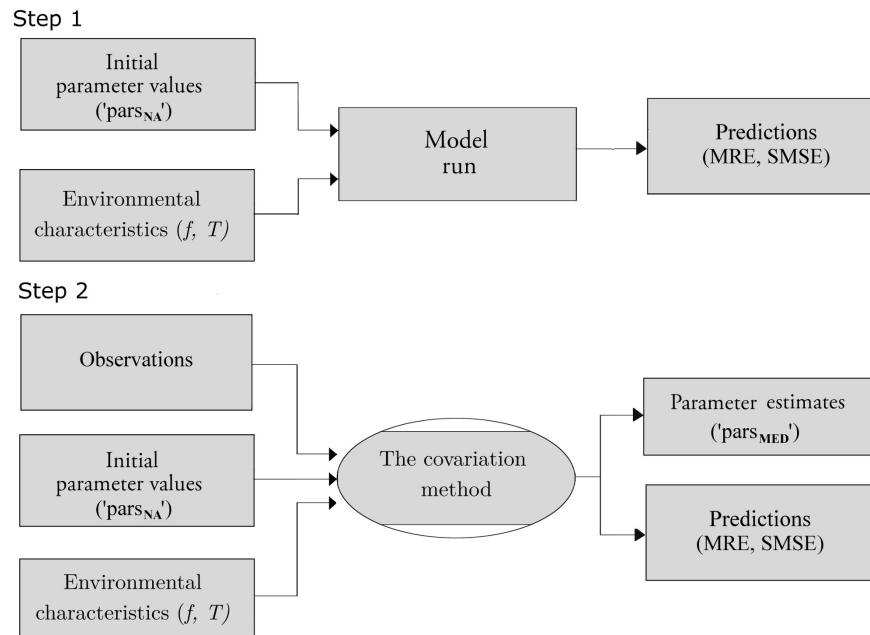


Figure B.13: **Schematic representation of the two steps used in the mechanistic approach.** Parameter set ' $pars_{NA}$ ' was estimated with the covariation method previously using only data for North Atlantic (NA) loggerhead turtles (Marn et al. [19] and AmP *Caretta caretta* [dataset] [71]). Parameter set ' $pars_{MED}$ ' pertains to the Mediterranean (MED) loggerhead turtles. Goodness of fit to data is expressed as mean relative error (MRE) and symmetrical mean squared error (SMSE). See Section 2.2 for more details

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