



Inferring physiological energetics of loggerhead turtle (*Caretta caretta*) from existing data using a general metabolic theory



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

^a Ruder Bošković Institute, Bijenička cesta 54, HR-10002 Zagreb, Croatia

^b Vrije Universiteit Amsterdam, De Boelelaan 1105, 1081 HV Amsterdam, The Netherlands

^c Center of Mathematics for Social Creativity, Hokkaido University, 12-7 Kita Ward, 060-0812 Sapporo, Japan

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ABSTRACT

Loggerhead turtle is an endangered sea turtle species with a migratory lifestyle and worldwide distribution, experiencing markedly different habitats throughout its lifetime. Environmental conditions, especially food availability and temperature, constrain the acquisition and the use of available energy, thus affecting physiological processes such as growth, maturation, and reproduction. These physiological processes at the population level determine survival, fecundity, and ultimately the population growth rate—a key indicator of the success of conservation efforts. As a first step towards the comprehensive understanding of how environment shapes the physiology and the life cycle of a loggerhead turtle, we constructed a full life cycle model based on the principles of energy acquisition and utilization embedded in the Dynamic Energy Budget (DEB) theory. We adapted the standard DEB model using data from published and unpublished sources to obtain parameter estimates and model predictions that could be compared with data. The outcome was a successful mathematical description of ontogeny and life history traits of the loggerhead turtle. Some deviations between the model and the data existed (such as an earlier age at sexual maturity and faster growth of the post-hatchlings), yet probable causes for these deviations were found informative and discussed in great detail. Physiological traits such as the capacity to withstand starvation, trade-offs between reproduction and growth, and changes in the energy budget throughout the ontogeny were inferred from the model. The results offer new insights into physiology and ecology of loggerhead turtle with the potential to lead to novel approaches in conservation of this endangered species.

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1. Introduction

Seven known species of sea turtles currently inhabit the world's oceans. All seven are listed in the IUCN list of endangered species (Turtle Taxonomy Working Group (TTWG) et al., 2012) and face various threats despite conservation measures (Bolten et al., 2011). The conservation of sea turtles is complicated by a lack of understanding of their physiology and ecology, and by a long and complex life cycle, spanning multiple habitats over a wide geographical range (Hamann et al., 2010). Metabolic processes such as growth, maturation, and reproduction are key physiological and ecological determinants, the understanding of which is also crucial for

conservation efforts. These processes are influenced by genetics (Piovano et al., 2011), but also by environmental conditions, such as food availability and temperature (Bjorndal et al., 2003, 2013), that constrain the acquisition and use of energy. A way to better understand the physiology and ecology of a species is to reconstruct its energy budget using the principles of a general metabolic theory (e.g. Jusup et al., 2011, 2014; Teixeira et al., 2014). Indeed, the need for an energy budget approach in the research of sea turtles was identified almost a decade ago (Hays, 2008).

Focusing on the loggerhead turtle and one of its largest nesting aggregations, the North Atlantic population (TEWG, 2009), we aim to reconstruct the energy budget of this species from existing data. We begin with a brief overview of loggerhead turtle physiology and ecology. Next we explain the methodology used to develop the full life cycle model, and list the data sets used in parameter estimation. By estimating the parameter values, we establish a mapping between existing data and the loggerhead turtle energy budget. We

* Corresponding author.

** Corresponding author.

E-mail addresses: nina.marn@gmail.com (N. Marn), mjusup@gmail.com (M. Jusup).

analyze the validity of the mapping, and discuss physiological and ecological implications of the reconstructed energy budget.

1.1. The loggerhead turtle

Three aspects of the loggerhead turtle's physiology and ecology impede conservation efforts. These three impeding aspects are (i) a geographically wide species distribution, (ii) long and complex ontogenetic development, and (iii) late and variable reproductive output.

Loggerhead sea turtle is a migratory species with global distribution throughout the temperate zone (Turtle Taxonomy Working Group (TTWG) et al., 2012). Individuals of this species occupy habitats ranging from cold and nutrient-sparse oceanic zones to warm and food-rich neritic zones, where some of the habitat variability is related to an ontogenetic shift (McClellan and Read, 2007; Peckham et al., 2011) with important implications for the energy budget. Furthermore, the wide distribution of loggerhead turtles means that populations such as the North Atlantic one span multiple jurisdictions and legislative systems with different conservation targets, methods, and ultimately success (Hamann et al., 2010).

The ontogenetic development of loggerhead turtles exhibits numerous fascinating characteristics. The sex of embryos is determined by nest temperature in the second third of the embryonic development (Bolten and Witherington, 2003; LeBlanc et al., 2012). Throughout its ontogeny, from hatching to ultimate size, an average loggerhead turtle increases almost 25-fold in length, and 6500-fold in body mass. Straight carapace length at hatching is 4–5 cm, while body mass is around 20 g (Bolten and Witherington, 2003). By contrast, adults range between 90 and 130 cm straight carapace length and between 100 and 130 kg body mass (Bolten and Witherington, 2003; Stoneburner, 1980). Growth rates are influenced by individual characteristics (Braun-McNeill et al., 2008; Piovano et al., 2011) and/or the environment (Braun-McNeill et al., 2008; Piovano et al., 2011; Bjorndal et al., 2003, 2013), and are often deduced from capture-mark-recapture data (Casale et al., 2009; Braun-McNeill et al., 2008; Bjorndal et al., 2013) or growth marks on the bones (Snover, 2002; Parham and Zug, 1997; Bjorndal et al., 2003; Piovano et al., 2011). The reported growth rates cannot be compared directly because they are reported for a variety (often unknown) environmental conditions.

The average female needs 10–30 years to reach puberty (Scott et al., 2012; Zug et al., 1986). Reproducing every 2–3 years, females lay 4–5 clutches of over a hundred eggs each (Tiwari and Bjorndal, 2000; Broderick et al., 2003). The reproduction rate was found to correlate with the average sea surface temperature (Solow et al., 2002; Hays et al., 2002a), as well as the large scale environmental oscillations (Van Houtan and Halle, 2011).

2. Methods

2.1. Full life cycle model of the loggerhead turtle

We use the Dynamic Energy Budget (DEB) theory (Sousa et al., 2008, 2010; Kooijman, 2010; Jusup et al., 2016) to model the full life cycle of loggerhead turtles. By relying on DEB theory, we ensure that our model is thermodynamically consistent, meaning that the conservation laws of mass and energy are strictly observed. Modeled loggerhead turtles also obey several homeostasis rules as a way of coping with sudden, unfavorable changes in the environment, especially in food availability. Metabolic rates (e.g., food assimilation, somatic maintenance, etc.) follow from scaling assumptions (concise statements of these assumptions are found below) appended with the kappa rule for allocation to soma

(Kooijman, 2010; Lika et al., 2011). The essence of the kappa rule is that energy is divided at a fixed fraction between soma and the reproductive cells. DEB model furthermore accounts for embryonic development, where turtle eggs start as blobs of energy received from mothers. This initial energy reserve is used by the embryo to start building structure and to mature enough in order to begin feeding on an outside energy source. The basic model prescribes the rate at which mothers commit energy to reproduction. We make a step forward and convert this energy into the number of eggs as if they were produced in a continuous manner. Modeling the timing and the duration of reproductive seasons is also possible by means of species- or population-specific rules for handling the storage of energy between reproductive seasons and the conversion of stored energy into eggs during one such season.

Free ranging animals owe their mobility in large part to a better homeostatic regulation (Kooijman and Troost, 2007; Lika et al., 2014), which in turn simplifies their energy budgets. Accordingly, in describing the full life-cycle of loggerhead turtles, we used the least complex DEB formulation called the standard DEB model (Sousa et al., 2008, 2010; Kooijman, 2010). In this model, the state of a turtle is captured by three state variables: reserve, E (energy in joules, J), structure, L (length in centimeters, cm), and maturity, E_H (J). Reserve is a maintenance-free energy buffer between the environment and the turtle that quantifies metabolic memory. Energy in reserve is readily mobilized to power metabolic processes. Structure, by contrast, is built and maintained using energy mobilized from reserve. Finally, maturity is a maintenance requiring quantity that does not contribute to body mass. It is quantified as energy that was cumulatively invested in maturation (preparation for the adult stage). Maturity controls metabolic switching (e.g., the onset of first feeding or the onset of reproduction) and, analogous to structure, is maintained with energy mobilized from reserve.

If sufficient food is available in the environment, all three state variables are increasing functions of age, yet maturity is assumed to remain constant upon reaching the adult stage. In this stage, energy previously used for maturation is redirected to reproduction. Loggerhead turtles reproduce intermittently, implying that energy is stored in a reproduction buffer. The state of the reproduction buffer is tracked using an auxiliary variable denoted E_R .

Dynamics of the state variables are determined by energy flows denoted universally \dot{p}_* (unit J d^{-1} ; Fig. 1):

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C, \quad (1a)$$

$$\frac{dL}{dt} = \frac{1}{3L^2} \frac{\dot{p}_G}{[E_G]}, \quad (1b)$$

$$\frac{dE_H}{dt} = \begin{cases} \dot{p}_R, & \text{if } E_H < E_H^p, \\ 0, & \text{otherwise,} \end{cases} \quad (1c)$$

where $[E_G]$ (unit J cm^{-3}) is the volume-specific cost of structure, and E_H^p is maturity at puberty marking the beginning of the adult stage. In this stage, we replace Eq. (1c) with $\frac{dE_R}{dt} = \dot{p}_R$.

Energy flows appearing in the system of Eq. (1) are defined as follows:

Assimilation, $\dot{p}_A = \{ \dot{p}_{Am} \} f L^2$, is the fraction of the daily feed ration that gets fixed into reserve, where $\{ \dot{p}_{Am} \}$ (unit $\text{J cm}^{-2} \text{d}^{-1}$) 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. The scaled functional response quantifies food availability (i.e., $f = 1$ under unlimited food availability and $f = 0$ when food is unavailable) and in many cases

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