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

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ABSTRACT

Understanding the relationship between the environmental conditions and life-history traits (such as growth, reproduction, and size at specific life stages) is important for understanding the population dynamics of a species and for constructing adaptable, relevant, and efficient conservation measures. For the endangered loggerhead turtle, characterizing effects of environmental conditions on the life-history traits is complicated by this species' longevity, global distribution, and migratory way of life. Two significant environmental factors – temperature and available food – often account for most of observed intra-population variability in growth and reproduction rates, suggesting that those two factors determine the biological responses of an individual. Adopting this hypothesis, we simulate a range of the two environmental factors to quantify effects of changes in temperature and food availability on an individual's physiology (energy investment into processes such as growth, maturation, and reproduction) and the resulting life-history traits. To represent an individual, we use a previously developed mechanistic dynamic energy budget (DEB) model for loggerhead turtles. DEB models rely on one of the empirically best validated general ecological theories, which captures rules of energy acquisition and utilization. We found that the ultimate size (length and mass) is primarily affected by food availability, whereas growth and maturation are primarily affected by temperature whilst also showing positive correlation with available food. Reproduction increases with both food availability and temperature because food availability determines energy investment into egg production, and temperature affects the rate of related processes (such as vitellogenesis). Length at puberty varies between simulated scenarios by only a small proportion, suggesting that inter-individual variability plays a larger role for length at puberty than the environmental factors do.

1. Introduction

Inter-individual and between-population differences in growth, maturation, and reproduction of loggerhead turtles (*Caretta caretta*) obstruct design of general conservation measures applicable to all regional management units and/or populations of this species (Wallace et al., 2011). Like other marine turtles, loggerheads are extremely vulnerable to natural and anthropogenic pressures due to temperature-dependent sex determination (TSD), long period required to reach puberty and reproduce, migratory way of life, and global distribution encompassing terrestrial habitats (beaches), open seas, and coastal waters (Chaloupka et al., 2008; Hawkes et al., 2009; Robinson et al., 2009; Witt et al., 2010). In addition to the conditions present on land (e.g., predators, nest infestations, nest overheating or inundation, pressures related to tourism), the abiotic and biotic conditions in the *marine* environment also greatly affect the development (growth and maturation) and survival of individuals, thus determining the success of conservation measures.

Food availability and temperature could be the major determinants of an individual's growth rate and, because faster growth might increase chances of turtle's survival (Salmon and Scholl, 2014), also the major determinants of the individual's survival. Even though the variability in the observed growth rates of loggerhead turtles has been partially attributed to inter-individual variability within (Stokes et al., 2006; Braun-McNeill et al., 2008) or between (Mendonça, 1981; Piovano et al., 2011) populations, most often differences in growth rates have been either partially (Mendonça, 1981; Braun-McNeill et al., 2008; Piovano et al., 2011) or mostly (Bjorndal and Bolten, 1988; Bjorndal et al., 2000, 2003,

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2013) attributed to the differences in experienced temperature and food abundance. Loggerhead turtles are a migratory species, and both males and females had been observed to follow certain types of temperature and food fronts (Godley et al., 2007), and/or exhibit fidelity to specific feeding areas (Pajuelo et al., 2012; Pikesley et al., 2015). Growth can be up to 30% faster in a neritic habitat (Snover, 2002 as cited in Peckham et al. (2011)). As neritic habitats are characterized by food of higher energy content and higher temperatures (Peckham et al., 2011), the higher growth rate in a neritic habitat further supports the thesis that food and temperature are the chief determinants of loggerhead turtle growth.

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

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

Furthermore, mechanisms by which changes in food availability and temperature *independently* affect the biological processes are extremely hard to study empirically for a long lived, large, and widely distributed species such as the loggerhead turtle. Hence, these mechanisms have only partially been explored and remain largely unquantified. Mechanistic deterministic models can generally help, especially with quantifying the consequences of a wide range of environmental conditions and with predicting the biological responses of individuals to environmental change (Chaloupka et al., 2008; Keith et al., 2014), but have not been used to investigate effects of environmental factors on loggerhead turtles.

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

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

2. Methods

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

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

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

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