Chapter 6

General Conclusion

The overall aim of this research was to study the environmental (food density and temperature) and anthropogenic (plastic pollution) pressures on loggerhead turtles, and to provide new insights into the biology and ecology of loggerhead turtles. I focused on the processes important to the life cycle and ecology (growth, maturation, and reproduction), and thus the protection of loggerhead sea turtles, and my methods included using obtained experimental and collected literature data, and developing a life cycle model based on the Dynamic Energy Budget (DEB) theory. By far the most shocking result was the effect of plastic ingestion on the energy budget of loggerhead turtles, however several other results deserve attention as they provide valuable insight into the biology and ecology of loggerhead turtles.

Making sense of conflicting data. By comparing two neighboring regional subpopulations of the North Atlantic loggerhead turtles, and three life stage subsets, I was able to identify that the reported inconclusive differences in the expressions used for relating different types of length and width measurements are mostly due to the differences in the carapace shape of small loggerheads (posthatchlings and juveniles before moving to a neritic habitat) compared to that of larger juveniles, and adults. Generally, although the results of Chapter 2 suggest that growth is slightly more preferential in length after a certain size (possibly connected to recruitment to neritic habitats), the calculated \( \leq 5\% \) deviation from isomorphic growth is small enough to be disregarded for the purpose of mathematical approximations, as any model is, due to necessary assumptions and simplifications, at most a sketch of the reality. It was therefore concluded that a single set of expressions can be used for the whole size span (life cycle) in most practical applications. However, using the correct type of the expression to convert the measurements is crucial for methods that completely rely on two measurements of size to maintain the same ratio throughout the life cycle, such as those using the diameter and marks on a bone intersection to deduce the carapace length and age of sea turtles (e.g. \cite{264, 214}). It would be interesting to see whether the change in the relationship of bone diameter-to-carapace length \cite{214} occurs simultaneously with the slight change in shape throughout ontogeny which was suggested by results in Chapter 2. Furthermore, using the correct relationship of width and body depth to length is important while planning protection measures that rely on the size and shape of the individuals, such as openings in fishing nets (Turtle Excluder Devices or TEDs) that are aimed to reduce the largest cause of mortality, fisheries bycatch \cite{57}.
DEB parameters and model predictions  Focusing first on the North Atlantic (Chapter 3), and then on the Mediterranean population (Chapter 4), the estimated set of parameters characterized the whole life cycle of loggerhead turtles in a satisfactory way. The parameter values were consistent both in the context of the species (when two populations were compared) and in the context of other two sea turtles (Kemp’s ridley and leatherback turtle) for which the DEB parameters have previously been estimated and uploaded to the “Add my pet library” (see Chapters 3 and 4). The energy budget and the predictions for loggerhead turtles were realistic when compared directly to the observations about growth and reproduction (see Chapters 3 and 4), and when the estimated parameters were used to infer the food conversion ratio, and the daily energy need and expenditure of a fully grown adult (see Chapter 5).

Deviations of model predictions from observed data  Because of such a good fit with so many observations, deviations of model predictions from data, where present, received more attention. For example, the length and weight at hatching were overpredicted, growth of posthatchlings was underpredicted, and the age at puberty was at the lower end of the reported (estimated) values for wild individuals, while newer estimates mostly suggest values closer to the higher end of the range (e.g. [209]). Analysis of these deviations suggested interesting patterns and changes in parameter values that would have been hard to identify with a different approach. It would be worth further exploring: (i) the embryo phase, to identify the possible reasons for the mismatch between the observed and predicted size at hatching (such as metabolic acceleration, [113]); (ii) the posthatchling growth, to validate current results (suggesting increased assimilation, somatic maintenance, and reserve mobilization, with the combination resulting in an increased maximum reserve density), and to compare the predictions with the growth patterns of other species under similar environmental and evolutionary pressures; (iii) the growth of juveniles, to gain further understanding into the extent to which it deviates from the most often assumed von Bertalanffy growth (as suggested by Ref. [40] and discussed in Ref. [38]), and to identify the most important causes of this growth pattern, be it the conditions in the oceanic and the neritic habitat, or a change in physiology of loggerhead turtles.

Comparison of the North Atlantic and the Mediterranean population  Developing and applying the model made it possible to explore the variability of individuals within populations and among populations. Comparing the Mediterranean and North Atlantic individuals (Chapter 4) on the basis of size (length, weight, and the ratio of the two, i.e. the condition index) and physiology (that is, model parameters) I simultaneously explored the directly observable and more “hidden” characteristics. An interesting result was a similar maximum reserve density of adults from both populations, coinciding with the calculated similar condition indices of the adults from both populations, as well
as the higher maximum reserve density of the posthatchlings, coinciding with higher (compared to adults) condition indices of hatchlings from both populations. It is however necessary to calculate the condition indices while accounting for the interindividual variability for any firmer conclusions. It would also be interesting to further study other possible metabolic adaptations of the Mediterranean individuals, such as those to the higher salinity of the Mediterranean sea. The energetic cost of osmoregulation has not been studied in detail, and it is yet to be determined how important the difference of few ppt (between 36 and 39 ppt) is. Identifying the level of maturity at puberty as the main physiological difference between the two populations, and the one most responsible for different size at puberty, would be impossible without a mechanistic model that includes maturity, and also puberty as one of the maturity switches. Switches happening at a certain maturity density rather than maturity level might become an important factor for other populations of other species that have been genetically isolated for a longer period, and have been exposed to different environmental pressures.

**Influence of temperature and food availability on the energy budget of individuals**

The same model which was used to compare the differences between individuals and populations was used to study the influence of selected global and local pressures on the loggerhead turtle (Chapter 5). Knowing the relationship between the food density and temperature on one side, and the response of an individual (growth, development, reproduction) on the other, is a valuable tool for understanding the observed differences between individuals and populations. In this study mostly constant conditions were simulated, directly relating to individuals that spend most of their lives in a similar type of habitat. The formulation and the mechanistic nature of the model allow, however, simulations of fluctuating conditions, as well as prolonged periods of stable yet different conditions (such as a long period in the oceanic zone followed by transitions between the oceanic and neritic zone), which could be explored further. It would be interesting to validate the model predictions on populations for which adults with bimodal feeding strategies have been observed, such as the population nesting in Japan [80] and in Cape Verde [82, 85].

**Effects of plastic ingestion on the energy budget of the individuals**

The effects of plastic ingestion on the energy budget and processes of growth, maintenance, matura-
tion, and reproduction of loggerhead turtles were greater than I initially assumed. The results suggest that the effect of ingested plastic taking up just 3% of the gut volume but with a (3 times) longer-than-food residence time, can have tremendous effects on the life cycle of a loggerhead turtle, and consequently on the whole population (as the turtle would not reproduce). Two major hurdles in studying the effect of plastic were that (1) representative control data is lacking, and (2) the mechanism by which plastic ingestion affects the energy budget was not known. To overcome the first issue, I assumed the
data used for DEB parameter estimation describes individuals which had not ingested any plastic. For the second issue, I used the concept of Synthesizing (i.e. Assimilation) Units, and arrived at the kinetics similar to that of enzymes when in an environment with inhibitors. Several other assumptions were needed in the process: for example, I assumed that most of the individuals in the wild were without any plastic in their digestive system (assumed “control” value of $f = 0.81$), and that they were exposed to more or less constant environmental conditions resulting in a von Bertalanffy growth. Keeping in mind the previous results (namely biphasic growth), the growth curve might look markedly different, resulting in a later age at puberty, suggesting that the effects of plastic ingestion are even more serious. Also, individuals normally exposed to a higher food level than that simulated as chronic exposure to a certain plastic density, would grow to a larger size than was the ultimate size in the simulation. A larger size includes a higher maintenance cost, suggesting that when exposed to a high load of plastic the loggerhead turtle could not acquire enough energy to satisfy its energy need, and would die of starvation. Now that a mechanism of modeling plastic ingestion has been defined, simulating such an acute exposure to plastic is one of the possible future studies.

Another important point identified by this approach is the plastic ingestion analysis, as there is currently no standardized way of reporting the occurrence of ingested anthropogenic marine debris. Debris is often reported as absolute volume or mass (wet and/or dry), or the proportion of stomach contents, sometimes jointly for all individuals in a study (e.g. [121, 233, 75]). While all these reports are valuable, a more unified approach, ideally reporting the percentage of total gut occupied by debris, would provide even more information needed to mechanistically study the effects of plastic ingestion.

**Outlook**  Finally, while all of the results, and especially the model obtained in this study are extremely useful, they are all, like DEB theory, individual-based. Luckily, like DEB theory, they are applicable in many forms. One of the applications is an individual-based population model (e.g. [139]), which could account for interindividual variability in some parameter values. The model, in combination with rules for interaction between individuals and models for the environment, also specifies the behavior of populations. One additional possibility is a multi-species parameter exploration, where a number of interesting properties could be studied with respect to the parameter values of loggerhead and other sea turtles in relation to parameter values of other reptiles or even other animal groups. Linking some traits, e.g. temperature dependent sex determination present in many reptile groups [265] to a specific combination of parameter values would surely be something only a theory applicable on a large number of species and groups can yield.