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Using an individual-based model for assessment of sea turtle population viability

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Abstract Marine turtle species have a complex life history characterized by interannual variability in reproductive performance and a long life span. These ecological features in combination with the animals' highly migratory nature create numerous difficulties when trying to assess population dynamics. This study attempts to couple existing information on species demographics and behavioral strategies with simple energetic rules in a theoretical framework. We study sea turtle population dynamics using an individual-based model that incorporates known behavioral-ecological characteristics of the species. Methodology used to design the model was based on the superindividual approach (Scheffer et al. *Ecol Model* 80:161–170, 1995). We constructed our simulation experiment on a virtual sea turtle population, which was parameterized by using recent literature reviews with emphasis on reproductive parameters of the Mediterranean loggerhead sea turtle population. Switching rules describing critical processes of reproductive performances were established as theoretical functions of efficiency of energy transfer. In order to explore the significance of variable reproductive patterns upon population dynamics and persistence, a series of simulations was performed. The model was also run under fluctuated demographic variables to perform a sensitivity analysis of critical parameters and life-history stages. Based on the specific model parameterization, simulation results show that population persistence was most sensitive to fecundity and to survival at the pelagic juvenile stage. Additionally a surprising finding is the relatively high importance of egg survival in terms of both hatching and hatchling success. We conclude that

enhancing the population with new individuals by increasing survival in the early life stages could compensate for additional losses in other age classes. The need for further research regarding biological and behavioral features as well as basic demographic insights into the endangered loggerhead sea turtle is also highlighted.

Keywords Individual-based model · Superindividual · Population dynamics · Sea turtle · *Caretta caretta* · Critical parameters

Introduction

Prioritizing needs for the protection of wildlife species through better understanding of the mechanisms underlying population dynamics is a matter of major interest for ecologists. A survey of the literature reveals a series of studies conducted worldwide in an attempt to explore sea turtle population dynamics and understand and describe key life-history features that are influencing abundance and persistence of the population. Due to the fact that sea turtles spend most of their lifetime in the ocean and are such long-lived animals, reliable demographic data of different life stages are lacking. Accordingly, annual censuses of nesting females have been used so far as an approximation to evaluate population trends and to detect demographic rates (Meylan 1982; Frazer 1983, 1984; Bjørndal et al. 1993, 1999; Chan and Liew 1996). Consequently, in the absence of long data series, deterministic modelling approaches became widely used as a theoretical tool for studying sea turtle population dynamics (Laurent et al. 1992; Crowder et al. 1994; Heppell et al. 1996a, b; Siddeek and Baldwin 1996; Grand and Beissinger 1997; Heppell et al. 2003). In order to counterbalance the uncertainty arising from the lack of information, stochastic models have also been developed (Chaloupka 2002, 2003).

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As in most wildlife species, a varying environment seems to be an important parameter controlling sea turtle life history and also the abundance of populations. Environmental conditions are likely to affect breeding cycles (Limpus and Nicholls 1988; Broderick et al. 2001) in a direct or indirect way by controlling feeding conditions or regulating body conditions. The hypothesis that variations in the number of nesting females can be caused by specific behavioral characteristics of the species, such as interannual fluctuation in the remigration interval rate, was made a long time ago (Carr and Carr 1970), and has been further supported by theoretical (Hays 2000) and empirical studies (Bjorndal et al. 1999). Since this annual variation in nesting female numbers and reproduction is strongly linked with species' behavioral and biological adaptations and strategies, sophisticated approaches to evaluate species population dynamics and interactions with the environment are needed.

In the present study, an attempt is made to overcome problems that arise with the use of the traditional modelling approaches such as age- or size-structured models (DeAngelis and Rose 1992). Herein, we introduce a stochastic individual-based model (IBM) for assessing sea turtle population dynamics. Simulation experiments were performed by applying the IBM to a virtual sea turtle population. Environmental and demographic stochasticity is incorporated in different life stages and processes, while varying survivorship is also introduced in order to realistically describe species life history. A series of relevant studies of sea turtle populations was used for model parameterization. The simulated system illustrates a generalization of individuals' dynamic interactions at different life stages. A series of simulations was performed under several scenarios and the results were examined. The effects of stochastic processes and dynamic energetic flows upon population persistence were also investigated.

Model

General model structure—initial conditions

In this study we used the superindividual modelling approach (Scheffer et al. 1995). The superindividual approach is a method that permits reduction in the number of individuals in an individual-based model. The concept of the superindividual has several similarities with the Lagrangian Ensemble Method (Woods and Onken 1982) since both methods attempt to model large populations by compressing varying number of organisms. Benefits of the superindividual method in individual-based models are summarized by Scheffer et al. (1995). The total number of individuals comprising the population is divided into units (superindividuals) that represent classes of population individuals. Each superindividual (SI) is affected by dynamic demographic processes. All individuals within the SI have the same age and share the same characteristic biological behav-

iors and strategies. The SI as the fundamental unit of the model could grow, mature, breed and die following a typical life history of the species.

Input parameters of the modelled system were based on several algorithms developed for describing dynamic functions of growth rate, multi-year reproductive cycles, size fluctuations and loss processes. To include temporal variability in the model we consider several life-history stages affected by environmental and demographic stochastic processes.

All animals grouped into the same simulated biological entry were subject to the same developmental and physiological processes. At each time step, each SI as an aggregate of animals, was characterized by its age and its length. In addition, each SI was also described by the energetic status that was associated with breeding, which could change after a breeding season. The model assumes an age-specific mortality and growth rate, while animals exceeding the maximum age are assumed to die. Annual size increment corresponding to growth was stochastically modelled as a function of the fluctuating environment, while for estimating time of sexual maturation and breeding we used a fixed threshold of body condition that had to be reached.

In our model, new superindividuals were introduced by grouping the released eggs laid by each nesting superindividual. Therefore, a new entity would be assigned for every breeder (SI) that had successfully participated in the nesting process during the current breeding season by laying at least one nest. Reproductive output was individually determined for each SI by the number of nests laid annually and a clutch-size component (eggs per clutch) depending on breeders' length. Therefore, reproductive output was the same for all individuals in an SI. Then the total number of eggs produced by a breeding SI was calculated as an aggregate by multiplying the reproductive output with the total number of animals within this SI. This aggregate represented the number of animals within the new SI produced by the specific breeder. The final number of alive new SIs was then estimated by accounting for the first year cohort lost.

The new individuals that have entered the population as a result of the breeding process are subjected to a minimum size (L_0) and joint model functions as in their first year. New individuals are also characterized by an initial energy budget (E_{initial}), which would be devoted to future breeding attempts.

The maximum life span of the species was assumed to be 54 years (Crouse et al. 1987). For each model run, the population was initialized with a stock of a total of 80 superindividuals, providing a population with entities in all age classes. Therefore, we initialized our virtual population by progressively increasing the age of the 80 superindividuals starting from age 1. When an assigned SI reached the maximum age (54 years), the next SI entered the population, starting from age 1. By using this approach the initial population consists of two SIs for each age class between 1 and 28 years, and one SI for every age class between 29 and 54 years. The number of

animals that forms each superindividual unity was derived by an exponential function, $N_{i,0} = N_0 e^{-\text{age}(i)z}$, in order to gradually reduce the numbers of individuals in older age classes.

We also assume a 1:1 sex ratio of the population, and consider only female turtles to be grouped into the biological entries. The time step of the model was 1 year, reflecting new breeding seasons.

Model rules

A brief description of the parameters used in the model, including their values and literature sources, is given in Table 1. For the sake of simplicity, from here on in this text, the equations describing several procedures are given with respect to individual animals. However, as clearly defined in the former part, all individuals within an SI have the same age and share the same biological and behavioral characteristics, thus each described action refers to all animals in the same SI when describing the biology, development and behavior of the specific SI.

Individuals' length and growth rate

Available data on the individual growth rates of the Mediterranean loggerhead sea turtles are available only for adult females, and even those are based on relatively

small sample sizes (Broderick et al. 2003). We tried to circumvent this problem by developing a theoretical model for estimating the growth patterns. Based on the fact that the sea turtle's growth rate gradually slows and stops as individuals approach maturity (Frazer and Ehrhart 1985; Bjorndal et al. 2001), we used an exponential decreasing function to describe the annual specific growth rate of individuals.

Bjorndal et al. (2001), in an extensive study, used the von Bertalanffy equation to model growth rates of loggerhead sea turtles in the North Atlantic. They estimated that the duration required for a loggerhead turtle to grow to 87 cm would be approximately 26.5 years. They described this size class as "...the upper limit of the subadult stage," hence the minimum size at which species attain sexual maturation (Bjorndal et al. 2001). The estimated age at that size was used as a first approximation of the age of sexual maturity in our model. The approximations of the minimum age at sexual maturation estimated by Bjorndal et al. (2000b, 2001) were adopted for our population sizes (Margaritoulis et al. 2003). Thus, we assumed that individuals experience a similar pattern of growth, even if the two populations differ in the maximum body length, since loggerheads found in the Mediterranean are among the smallest found in the world (Broderick and Godley 1996; Tiwari and Bjorndal 2000).

For reasons of simplicity the minimum age of sexual maturation was set at the age of 26 rather than 26.5, to

Table 1 Parameter descriptions. Where a parameter is assumed or fitted from preliminary model runs, it is noted as "assumed" and "fitted," respectively

Parameter	Description	Value	Source
SI_{initial}	Initial number of superindividuals (SI)	80	Assumed
N_0	Coefficient determining initial population size	60,000	Assumed
L_0	Individual size at age 1	0.04	Margaritoulis 1982
z	Coefficient determining shape of initial population size	0.12	Assumed
β	Shape coefficient for the age-specific annual growth rate	0.058	Fitted
g_{mean}	Mean annual growth rate	1.7	Fitted
g_0	Constant expressing demographic stochasticity in annual length gain	0.04	Fitted
E_{mean}	Constant energy compound added annually	1.3	Fitted
E_0	Constant expressing demographic stochasticity in maturation time	0.5	Fitted
E_{crit}	Critical threshold condition determining first breeding	5	Fitted
L_{mature}	Average length of breeding individuals	75.4	Fitted
B_{mean}	Constant energy amount added annually to each individual's energy store	1.2	Fitted
B_{crit}	Critical threshold condition determining reneating interval	5	Fitted
B_0	Constant expressing demographic stochasticity in reneating interval	0.5	Fitted
d	Shape coefficient determining reproductive output	1.3537	Fitted
l	Coefficient determining reproductive output	2.6951	Fitted
S	Sex ratio	0.5	Assumed
HS_{mean}	Mean hatching success	0.715	Margaritoulis 2005
ES_{mean}	Mean hatchling emergence success	0.666	Margaritoulis 2005
$C_{\text{laid}, i}$	Number of clutches	1–5	Broderick et al. 2003
C_{mean}	Mean number of clutches	2.5	Assumed
R_{mean}	Mean clutch size (eggs/clutch)	116.6	Margaritoulis 2005
v	Constant determining whether mortality would be calculated for each individual within SI	600	Assumed
NS_i	Annual mean nesting success	0.257	Margaritoulis 2005
Nsd	Standard deviation term of the annual mean nesting success	0.04	Margaritoulis 2005
	Mean annual survival probability of pelagic juveniles	0.6445	Chaloupka 2002
	Mean annual survival probability of benthic juveniles	0.8804	Chaloupka 2002
	Mean annual survival probability of subadults	0.8474	Chaloupka 2002
	Mean annual survival probability of adults	0.9482	Chaloupka 2002

be consistent with our simulation cycles. Moreover, we assumed that the average time of maturation was 30 years by adding a deviation term to the first approximation of 26 years. The deviation term was estimated based on Limpus (1990) who suggested that after the enlargement of immature turtles' oviducts to the mature adult size, first breeding might occur after 2–4 years; he also mentioned that it is more common for females to ovulate 2 or even 3 years after their first vitellogenesis. In forming the growth model we assumed that 8 years after the age of minimum sexual maturity (26), turtles would have reached their maximum size. Moreover, we accounted for the minimum time lag by assuming that 4 years from the age of 26 would be needed for an average female population to become sexually mature. Following these assumptions we drew a life table for the species in which age classes were defined based on growth distribution until the age class of 30 years. After possible minimum maturation age (26), the decline in growth rate was assumed to be exponential towards zero.

We defined the effect of environmental processes and individual life history upon growth rate and applied them using specific probability distributions. Based on initial model assumptions, all individuals in each SI were growing at the same rate, while the dynamic size increment of each individual at each age class (Fig. 1) was computed as

$$L_{i,t} = L_{\text{age}(i)}(1 + g_{\text{mean}}\exp[-\beta L_{\text{age}(i)}] + g_{i,0,t}) \quad (1)$$

where $L_{i,t}$ is the length of individual i , at time t . The proportion expressed by the lognormal function corresponds to the age-specific annual growth rate of the individual at age $\text{age}(i) \in [0, \text{age}(\text{max})]$, β is a constant and $L_{\text{age}(i)}$ is the mean length of individuals aged $\text{age}(i)$ years

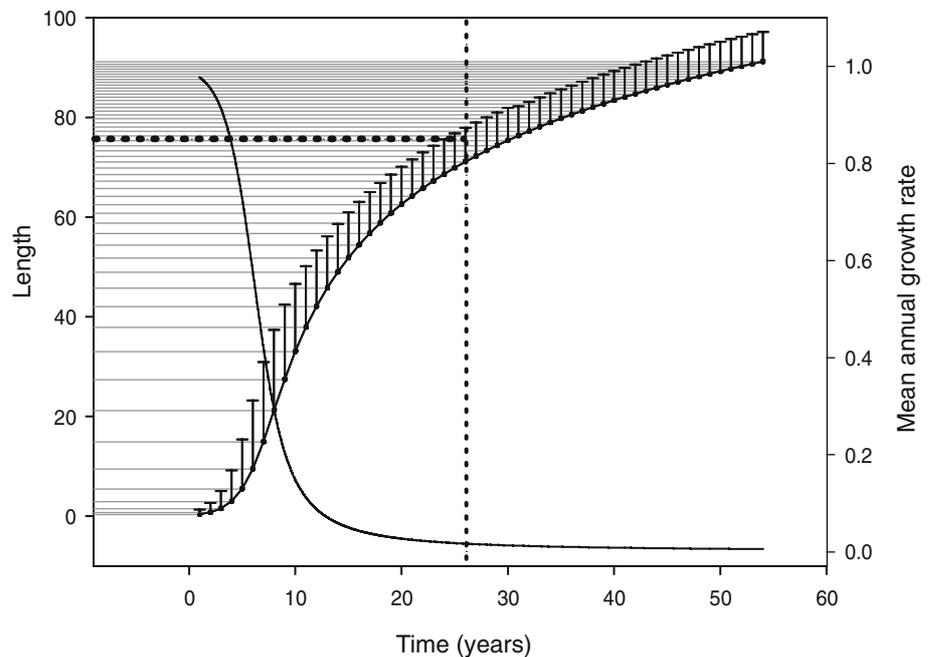
old computed as $L_{\text{age}(i)} = L_{\text{age}(i-1)}(1 + \exp[-\beta L_{\text{age}(i-1)}])$. L_0 is the individual size at age 1, g_{mean} is the mean annual growth rate, $g_{i,0,t}$ is the stochastic term that is readjusted to take into account the maximum annual length gain under favorable environmental conditions, generated by a normal distribution $\sim N(0, g_{i,0})$. Mean annual growth rate was adjusted individually for each age class, such that an animal that has been subjected to a constant size increment could reach sexual maturation at the minimum possible age (26 years).

Maturation and first breeding

Understanding reproductive cycles is of great importance for realistically describing population trends (Carr and Carr 1970; Hays 2000). However, no data exists on the exact age of turtle maturation. We circumvent this problem by using two theoretical conditions regarding the first age of sexual maturation and the time of the first breeding. The dynamics of the maturation of each individual were computed based on the stochastic size component, Eq. 1. Therefore a turtle could be considered as mature as soon it has reached the critical maturation length (L_{mature}) determined as the maximum size that an animal could achieve under constant environmental conditions through the average age of maturation.

In addition, the first breeding attempt after maturation was assumed to occur only if the individual had reached a threshold body condition (E_{crit}). When turtles have entered into the sexually mature stage they are assumed to have already started to accumulate energy to be devoted to their first breeding. This initial energy component (E_{initial}) was randomly established for each

Fig. 1 Mean annual growth rate (*thin line*) during the life cycle of an individual (54 years) and the increment weight curve. The *error bars* (indicating only the “positive” environmental influence) show maximum length increment caused by stochastic process, while the *gray lines* indicate the successively decreased function of the annual length increment. *Dotted lines* indicate the minimum age at which an individual can reach sexual maturity with 26 as the minimum maturation age under a favorable environment



individual by sampling from a random number generator $\in [0, E_{\text{crit}}]$. Moreover, immediately after maturation energy storage allocated for breeding begins to cause a progressive increase in an energy budget year after year, until the first breeding. The annual energy increment is described by:

$$E_{\text{incr},i,t} = E_{\text{mean}} + E_{i,0,t} \quad (2)$$

where $E_{\text{incr},i,t}$ is the annual energy accumulation of individual i at time t , E_{mean} is a fixed energy compound added annually, and $E_{i,0,t}$ is a stochastic parameter reflecting demographic variability in energetic accumulation, generated by a normal distribution with mean zero and SD equal to E_0 , $\sim N(0, E_0)$.

Therefore, for an animal that has reached maturation size at time $t-n$, the dynamic energy budget is then calculated by adding fixed proportions of energy storage including variance components in energy accumulation due to environmental effects:

$$E_{i,t} = E_{\text{initial},i} + E_{\text{incr},i,t-n} + E_{\text{incr},i,t} \quad (3)$$

where $E_{i,t}$ is the energetic status of individual i , at time t ; E_{initial} is an initial proportion of an individual's energy; $E_{\text{incr},i,t}$ is the energy increment of year t ; and $E_{\text{incr},i,t-n}$ represents the progressive annual increase in the energy state. Thus, the first breeding attempt is defined as:

Breeding is attempted if $L_{i,t} \geq L_{\text{mature}}$ and $E_{i,t} \geq E_{\text{crit}}$.

In the model, all parameters of the dynamic energy function (Eq. 3) were readjusted in order to ensure that, under favorable conditions, all individuals that have reached critical maturation length (L_{mature}) between the ages of 26 and 30 will definitely attempt to breed at the time $t-n$ with $n=4$. After an individual has successfully attempted to breed for the first time, the initial energy storage is reset to zero, and any successive breeding events follow an alternative dynamic process that incorporates the multi-annual reproductive cycles of the species (see below).

Periodic breeding-remigration interval

Breeding was modelled as a dynamic process occurring once a year. For mature animals the duration between two successive breeding periods varied from 1–4 years corresponding to the reneating interval. It was assumed that the time between successive non-breeding periods has a cumulative effect upon the energetics.

For all age classes above the mean maturation age and for individuals that have completed their first nesting attempt, the breeding period was determined by a dynamic energy status, described by the function:

$$B_{i,t} = B_{i,t-\mu} + B_{\text{mean}} + B_{i,0} \quad (4)$$

where $B_{i,t}$ is the dynamic energy status of individual i at age t , $B_{i,t-\mu}$ represents the progressive annual increase in the energy budget starting at year $t-\mu$, B_{mean} is a fixed energy amount added annually to each individual's energy level, and $B_{i,0}$ is a stochastic parameter reflecting demographic variability in energetic accumulation. This was implemented by multiplying B_0 with a random variable generated from a normal distribution.

The above formulation was developed by assuming that, under constant energy accumulation, individuals would fulfil the body condition requirements and would be ready for breeding at any time within a 4-year period, with the maximum period between two successive breeding attempts for all individuals being the 4th year after their maturation and first breeding attempt.

Therefore, completion of the energetic requirements for breeding occurred when an individual's energy budgets exceeded a critical threshold level (Hays 2000; Broderick et al. 2001), B_{crit} , i.e., when $B_{i,t} \geq B_{\text{crit}}$. Once an individual has successfully bred, the surplus energy that was concentrated to be devoted for reproduction was reset to zero, and energy accumulation process was initialized.

Success of the nesting attempts

During the breeding season, female turtles leave the water and crawl up to the beach where they look for a favorable place to lay a nest; however not all these attempts results in nest construction. The proportion of emergences that successfully result in a nest is defined as nesting success. In our model, for all individuals that have successfully fulfilled the energetic requirements of maturation and are attempting their first nesting or reneating, nesting success was a random deviate with mean (Ns_{mean}) and variance (Nsd) (Margaritoulis 2005). If a random number drawn from a uniform distribution [0,1] was lower than the probability of nesting success, the nesting attempt was then assumed to be successful.

Reproductive output

A common feature of the sea turtle species is that the number of nests laid per breeding female and the eggs laid per clutch (clutch size) may vary individually and annually (Broderick et al. 2002, 2003), while body size is related to the number of eggs laid (Elgar and Heaphy 1989; Hays and Speakman 1991; Van Buskirk and Crowder 1994; Miller 1997). In the context of our model all individuals in each SI breed at the same time. We defined reproductive output as a varying process based on specific individual characteristics of each nesting SI. The number of clutches laid by each female ($C_{\text{laid},i,t}$) was randomly sampled within the recorded values for the loggerhead population nesting at Cyprus (Broderick et al. 2003).

The clutch size of each nester was individually determined using a lognormal distribution. Its parameters were estimated by assuming that an individual at the minimum age (reflecting the minimum body length for a mature animal) for sexual maturation will lay fewer eggs; likewise the maximum clutch size will be laid at the maximum age, reflecting the maximum obtained body size. To model this suggestion we used maximum (132) and minimum (65) values derived by the mean range of clutch size for loggerheads nesting on Greek coasts (Margaritoulis et al. 2003). An equation describing animals' clutch sizes can be written as:

$$R_{i,t} = s C_{\text{laid},i,t} (d L_{i,t} - l) \quad (5)$$

where $R_{i,t}$ is the total number of eggs laid by individual i at time t , s is the sex ratio assumed for the eggs (1:1), $C_{\text{laid},i,t}$ is the number of nests laid, while the value within the parentheses describes the dynamic clutch size of the individual with length $L_{i,t}$, with d and l as constants. After calculating Eq. 5, the number of eggs was then determined by rounding the result to an integer value.

Clutch survival

Eggs and hatchlings are vulnerable to several biotic and abiotic factors. In an attempt to account for losses at these first stages we defined the clutch survival rate as:

$$Cs = H_{s_{\text{mean}}} E_{s_{\text{mean}}} \quad (6)$$

Where Cs is the clutch survival rate, calculated by accounting for the percentage of eggs that hatched (hatching success, $H_{s_{\text{mean}}}$) and the probability of the hatched eggs producing hatchlings that successfully exit the nest (hatchling emergence success, $E_{s_{\text{mean}}}$). The probability of clutch survival was then determined by drawing a random number [0,1] and comparing it with clutch survival rate. It was assumed that a clutch survived when the random number was lower than Cs . For the total number of nests produced by each SI, clutch survival was individually modelled.

Mortality

Due to the fact that survival rates are very low for the Mediterranean population and our estimates had to be based primarily on expert knowledge and incomplete studies, we used for this part of our model the survivorship rates used by Chaloupka (2002) for the southern Great Barrier Reef (GBR) green turtle population, which was justified by the overall similarity of population trends for the two cases (Poiner and Harris 1996; Chaloupka and Limpus 2001; Margaritoulis 2005). The GBR green turtle stock represents one of the most well-studied populations of sea turtles, with detailed and well-documented information on demographic parameters for most of the age classes. Therefore, the adopted

survivorships were used as inputs to our novel superindividual modelling approach; more accurate local estimates would undoubtedly enhance model predictions.

Assumptions and processes for the estimation of mortality rates are described by Chaloupka (2002). The age classes' specific survivorships (a) were transformed into age-class mortality rates ($M = 1 - a$), and applied to our model. Species life history was then divided into four different stages, including small juveniles, large juveniles, subadults and reproductively mature individuals (including all ontogenetic stages that include novice breeders, first year remigrants and mature breeders). For the duration of stages, we used suggestions by Bjørndal et al. (2000b, 2001) and Crouse et al. (1987). Bjørndal et al. (2000b) used a growth model for the size-frequency distribution of pelagic and neritic individuals, giving an 8.2-year duration for the pelagic stage (small juveniles). This estimate was rounded to the integer value of 8 to fit our simulation time steps. The duration of the large juvenile stage was set to 7 years (Crouse et al. 1987), while the remaining variable period before individuals reach their minimum maturation age was defined as the duration of the subadult stage.

Demographic variability was also included by adding a quantity produced by the multiplication of a constant ($m_d = 0.003$) with a random number sampled by a normal distribution:

$$M_{i,\text{age}(i),t} = M_{\text{age}(i)} + m_{d,t} \quad (7)$$

where $M_{i,\text{age}(i),t}$ is the mortality rate of individual i , aged $\text{age}(i)$, at time t , $M_{\text{age}(i)}$ is age-class mortality derived from the literature, and $m_{d,t}$ is the stochastic parameter reflecting demographic variability.

Based on the stochastic age-specific mortality rate (7), the annual mortality risk for a SI was then calculated as:

$$Pd_{\text{age}(i),t}^j = 1 - \exp[-M_{i,\text{age}(i),t}] \quad (8)$$

where $Pd_{\text{age}(i),t}^j$ is the annual mortality risk of the superindividual j , consisting of individuals aged $\text{age}(i)$, at time step t , and $M_{i,\text{age}(i),t}$ is the calculated mortality rate for the individuals with age equal to $\text{age}(i)$ that form the SI at time t .

Each individual in the SI was subjected to the mortality process before nesting; two additional procedures were employed depending on the number of individual animals within each SI. We assumed that if the number of individuals within an SI exceeded a given value (v), the numbers of survivors was found directly by multiplying the abundance of the specific superindividual by $Pd_{\text{age}(i),t}^j$. In the case that the number of individuals in an SI was less than v , mortality was calculated for each animal individually as in Scheffer et al. (1995).

Simulation

In an attempt to evaluate the relative importance of each life stage upon population dynamics and persistence, the

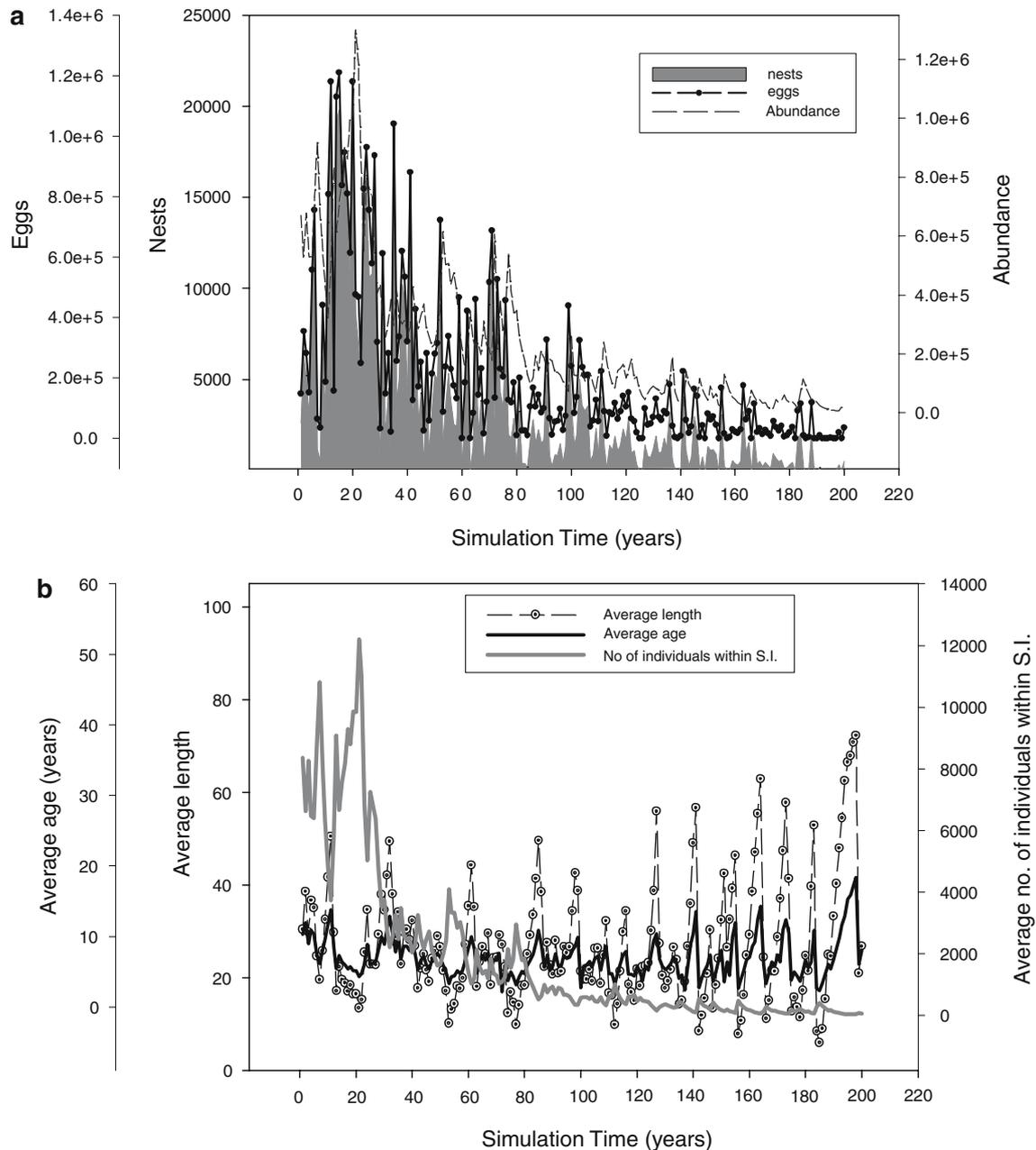


Fig. 2 a A typical population trajectory of the total number of individuals in the population (*dashed line*) and the total number of nests (*gray area*) and eggs (*dashed line with circles*) laid. **b** Average

length (*thin line*) and average age (*dotted line*) are presented with the mean number of individuals (*thick line*) within each superindividual through time

model was initially run allowing for a 5% increase and decrease in each age-specific mortality, while 5% changes were also applied to mean clutch success.

The importance of reproductive performance upon population extinction probability was examined by performing an additional set of simulations. Two basic simulation sets were distinguished by incorporating stable and variable reproductive conditions. For model runs under constant reproductive parameters, we assumed that all individuals that have reached the critical maturation size will breed, and successive nestings (remigration interval) will occur every 2 years. Under

these scenarios the number of nests laid annually (C_{mean}) by a breeding female was 2.5, and nesting success ($N_{s_{\text{mean}}}$) and clutch size were assumed to be constant and equal to mean observed values (Margaritoulis 2005). To investigate further model responses under constant reproductive performances with respect to varying demographic parameters, simulation runs were constructed allowing for a 5% increase and decrease in mean clutch success and age-specific mortalities. The model was also run under stochastic environmental conditions by using constant renesting intervals of 3–6 years.

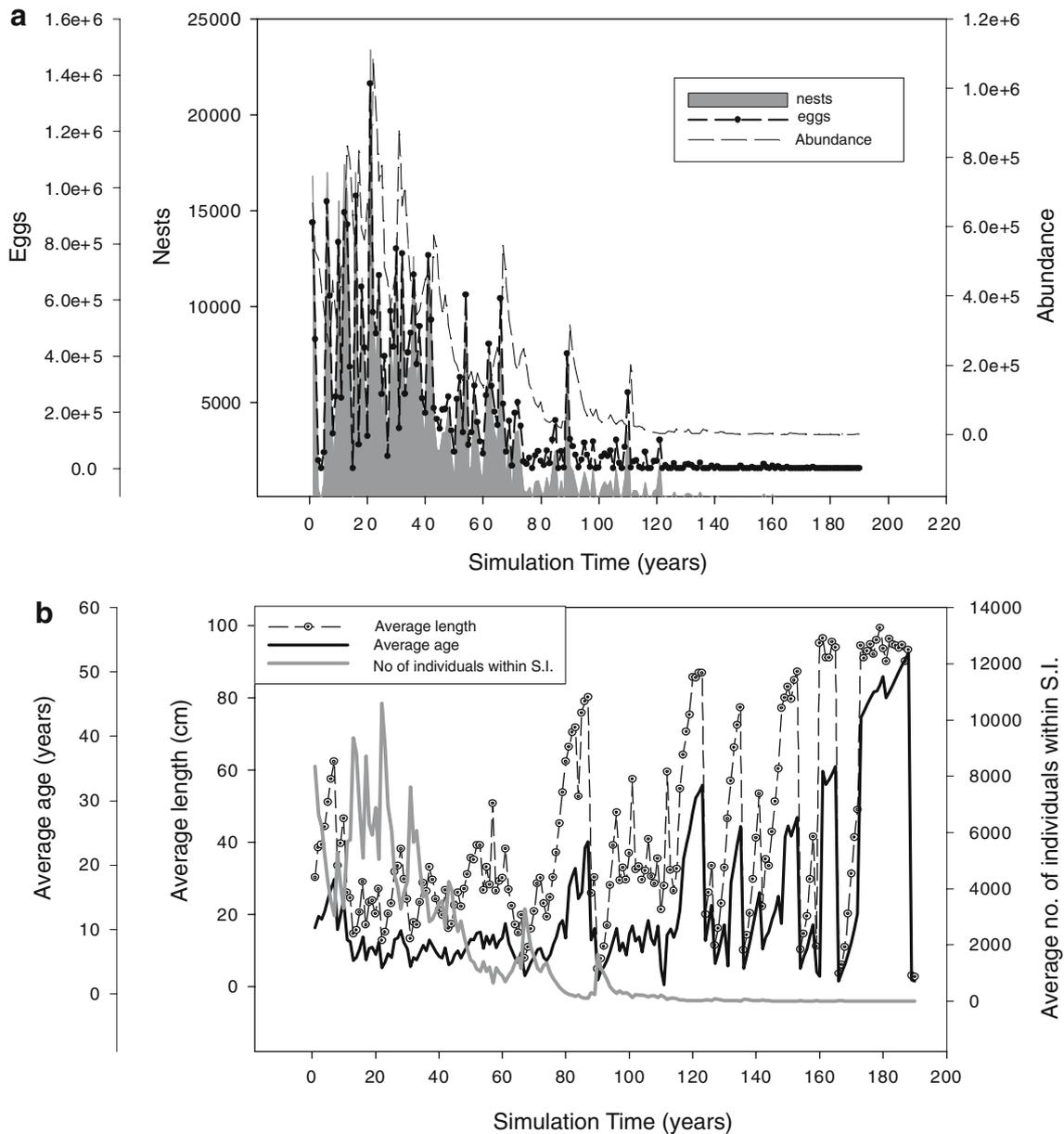


Fig. 3 a A typical population trajectory of the total number of individuals in the population (*dashed line*) and the total number of nests (*gray area*) and eggs (*dashed line with circles*) laid. **b** Average

weight (*thin line*) and average age (*dotted line*) are presented with the mean number of individuals (*thick line*) within each super-individual through time

Persistence probabilities were calculated for each simulation set by running the model 1,000 times using a 200-year forecast horizon. The population was assumed to be extinct when all individuals died.

Results

Figures 2 and 3 show two typical trajectories of population dynamics under a variable environment. In Fig. 2a, a population, presented as an aggregation of individual animals, fluctuates following reproductive cycles and stochastic mortalities. While a gradual

population decline is observed, it survives through the simulation time. It is also apparent that the number of eggs produced is proportional to the laid nests while they both follow overall population trends. In the second simulation (Fig. 3a) there is clear evidence of population increase during the first years, with the increased reproductive output contributing to the total population size. However, at around year 70 of the simulation, population fluctuates and gradually decreases, ending in extinction after about 170 years. It is also clear that nest construction and thus egg laying are significantly reduced after the 70th year of the simulation. After this time nest construction and egg-laying are characterized

by two main peaks at about 20-year intervals (around years 90 and 110).

Some interesting findings regarding risk of population decline in terms of population abundance arise when

examining additional figures of each trajectory (Figs. 2b, 3b). The fluctuation in average size and average age of superindividuals is illustrated, providing a sample of the mean number of individuals within each superindividual.

Fig. 4 Probability of population extinction under a variable environment with constant egg survival (*gray bars*), increased mean egg survival (*dark gray bars*) and a 5% reduction in egg survival (*black bars*) under different mortalities. *Dashed line* denotes 90% probability of extinction. Simulation groups 1–9 illustrate changes in mortality rates: the 1st simulation set was run with mean annual age-class mortality, the 2nd, 4th, 6th and 8th with a 5% increase in mortality for small and large juveniles, subadult and adult stages, respectively, and the 3rd, 5th, 7th and 9th sets were run assuming a 5% reduction in mortality over the former stages

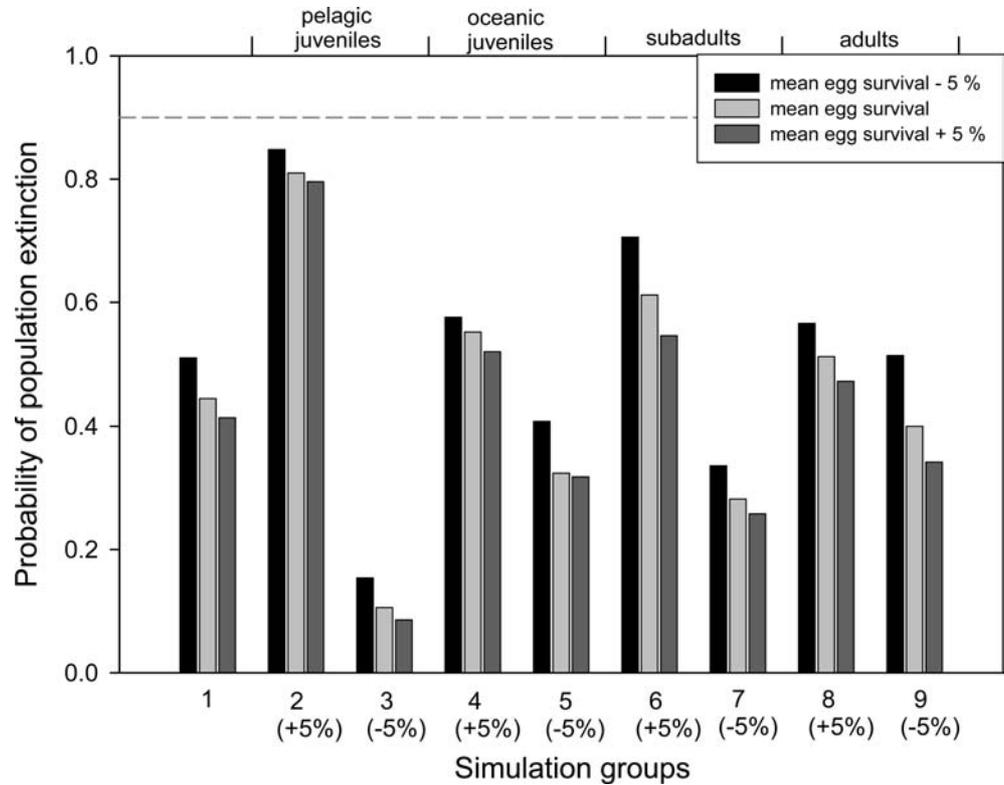


Fig. 5 Probability of population extinction under constant reproduction rates with constant egg survival (*gray bars*), increased mean egg survival (*dark gray bars*) and a 5% reduction in egg survival (*black bars*) under different mortalities. Simulation groups 1–9 illustrate changes in mortality rates: the 1st simulation set was run with mean annual age-class mortality, the 2nd, 4th, 6th and 8th with a 5% increase in mortality for small and large juveniles, subadult and adult stages, respectively, and the 3rd, 5th, 7th and 9th sets were run assuming a 5% reduction in mortalities over the former stages

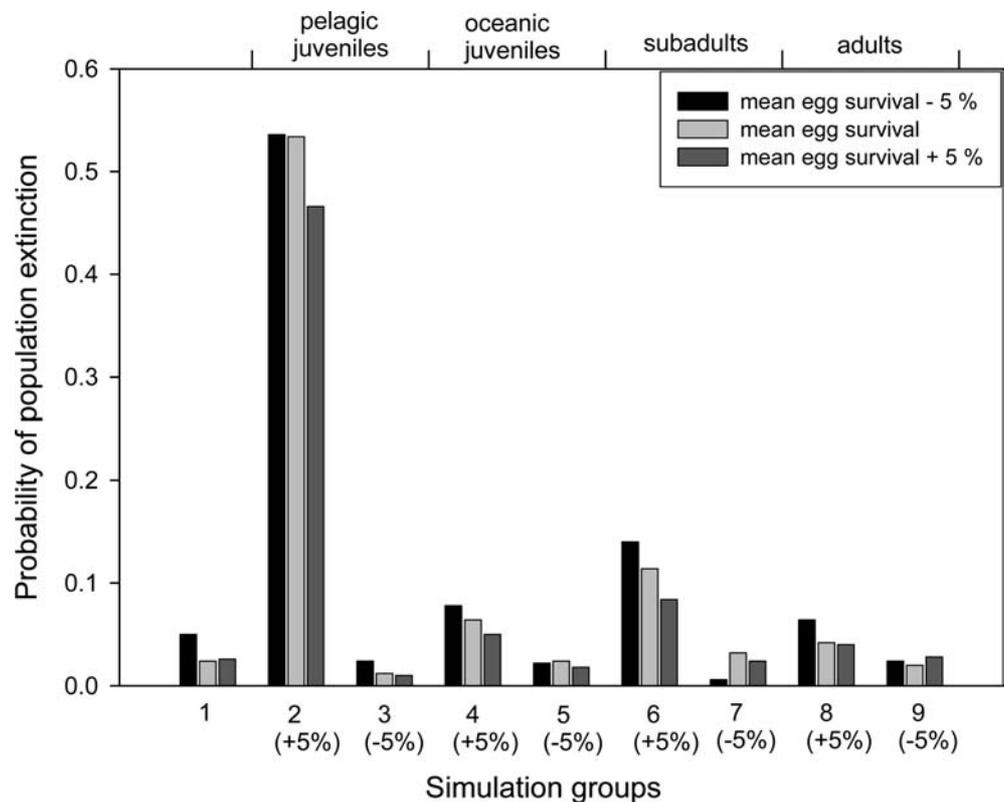
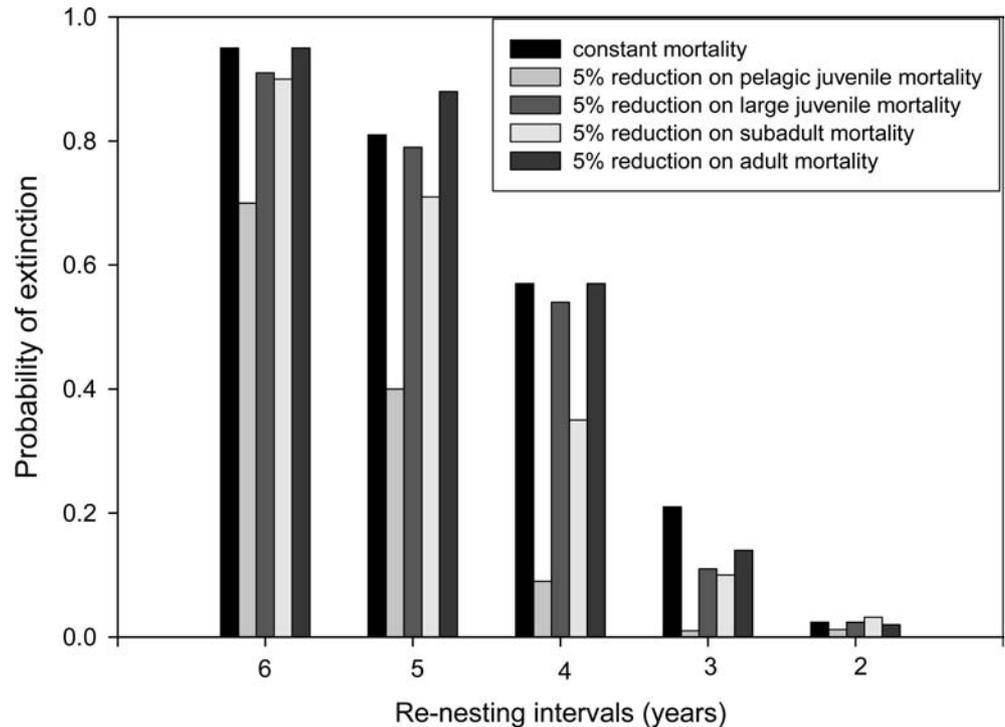


Fig. 6 Probability of population extinction under constant egg production, clutch size, nesting success and egg survival, a 5% reduction in mortalities, and varying re-nesting intervals (2–5 years)



Whether significant population declines occur, a relative increase in older age classes becomes most apparent at the cohort structure. However, at this simulation time, contribution of this relatively abundant stage to population, in terms of egg and newborns, seems to be insufficient to prevent extinction. This could be explained by both high mortalities that new animals face at the pelagic juvenile stage, and also by considering the possible low number of adult individuals during this time step. In Fig. 2b, this feature of a relative increase in the age-specific individual distribution is observed during the first simulation years, showing a significant change in average length and age distribution. Over the simulation time a gradual population decline is followed by a disproportionate increase in age and size structure of the population. In Fig. 3b, a similar pattern can be seen, with the relative change in age-stage abundance observed at around year 70 of the simulation. At that time, the average age and size start to fluctuate intensively, leading to an overall increase. This change in age structure is closely associated with the overall population decline, which finally leads to extinction (Fig. 3a, b).

Simulation results of different combinations of fluctuated mortality rates of the different life stages are shown in Fig. 4. Probability of population extinction was clearly affected by fluctuations in mortality at the small juvenile stage. First-year cohort (egg/hatchling) survival seemed to have an effect on all simulation sets, with extinction probability increasing as egg/hatchling stage survival was reduced, and was highest in simulations with lower survival of the small juvenile stages.

When our model was run under constant reproduction rates it was evident that fertility has the greatest

impact on population dynamics (Fig. 5). Assuming that each mature individual will breed every 2 years with a constant reproductive output, the probability of population extinction significantly decreases. Repeating the simulations under a 5% change in mean egg-survival processes, we can clearly see that under the initial model conditions simulating high productivity, changes in egg survival have no effect on population performance.

Figure 6 shows the probability of extinction that was calculated under constant reproductive rates and varying remigration intervals with a 5% reduction in mortality rates. It is apparent that the reduction of the re-nesting period has a significant effect on population size, while in all simulations survival at the pelagic stage is the most critical parameter.

Discussion

Using an individual-based model, we studied population dynamics of sea turtles. Simulation results of our virtual system showed that the probability of population persistence significantly depends on fertility, while survival rate at early life stages also seems to have a profound effect. When running the model under constant fecundity it was also apparent that reduction in mortality at pelagic stages is the most important parameter among stage-specific survivorship, while changes in the re-nesting interval have a large effect on population persistence.

Our findings contradict the results of other studies that have been conducted for sea turtle populations using deterministic modelling approaches (Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996a, b;

Cunnington and Brooks 1996; Siddeek and Baldwin 1996; Grand and Beissinger 1997), but it does to some extent accord with the results drawn by the stochastic simulation models of Chaloupka (2002, 2003). At this point we should mention that the results of matrix models that have been analyzed using loop analysis (Wardle 1998; Chaloupka 2002) have also highlighted the importance of fertility in population growth. However, in both former studies the proportionally higher importance of pelagic survival was overlooked.

When including stochastic events the comparisons of the relative effects indicate that increases in the annual cohort size could strongly prevent population decline. This could biologically be explained by taking into account the relatively high mortality rate at small juvenile stages. Controlling this loss process could result in a high contribution of individuals to the next stages. Following the former assumption, higher individual abundances distributed in the upper age classes would be subjected to lower mortality rates in comparison to the initial stages and could further support an increased contribution to the population due to reproduction. Note that this feature could possibly explain the ability of the Cuban hawksbill population to withstand high harvest rates (Carrillo et al. 1999); this population is characterized by higher growth rates (IUCN 2002) and also has a relative higher survivorship of hatchlings to 1 year of age (CCMA 1998).

Fluctuations in the proportion of eggs surviving and hatching also have an effect on population dynamics, while their significance is highly reduced under the deterministic scenarios. This feature could be explained by taking into consideration the higher proportional reproductive value of adults in comparison to eggs.

Furthermore, in an attempt to identify clearly the significance of multi-annual reproduction, the model was run using fixed re-nesting intervals. According to model results, the frequency of breeding attempts is a key factor for population survival, with the pelagic juvenile stage the most vulnerable life stage. We conclude that this pattern highlights the significance of the earlier age classes, which suffer higher mortality, since increased reproductive output illustrates a rather stable cohort at older age classes. Moreover, the profound effect of breeding attempts against survival at adult stages suggests that under the relative low mortality at adult stages, breeding performance is the most important of the demographic parameters for mature age classes.

Considering the results of our analysis, which highlight the importance of fecundity, in parallel with the evidence suggesting that annual variation in nesting female numbers and reproduction are strongly connected with “environmental” variability and species behavioral and biological adaptations and strategies, our suggestions in terms of conservation efforts are presented. Reduction of mortality through the early age classes could positively affect population dynamics by increasing cohort size. Furthermore, based on the fact that sea turtles spend almost all their life in the ocean and also considering the

importance of the different marine stages on species survival, conservation efforts should be oriented towards this direction. Protection measures such as turtle excluder devices (TED) and fishing regulations could be realistically applied for the protection of the different oceanic and neritic stages. Moreover, conservation efforts should also keep focusing on protection measures applied at the nesting sites (i.e. hatcheries, nest translocation, head-starting programs, reduction of predators and poachers), since hatchling production could act as a short-term preventative factor against abrupt population decline, providing useful time for population recovery. This suggestion is further supported by the fact that the probability of first-year survival (combined as hatching and hatchling emergence success) is significantly lower than survival probabilities of the other stages. Based on this, it is obvious that even minor changes in the survival of the first-year cohort could result in a relatively higher number of survivors moving to the next age class in comparison with other-year cohorts.

During model development and parameterization we made several assumptions. A critical aspect of our model is the use of parameters provided by a series of separate studies. Furthermore, in the absence of empirical data, theoretical energetic rules were developed and applied considering processes and dynamics. Even if the former rules as well as model parameterizations incorporate realistic behaviour, model outcomes are affected to a certain degree by the assumptions.

Since age-structured abundance of individuals is very difficult to reliably identify, we initialized our stock by assuming a relatively high number of sexually mature individuals (12,500), and a total maximum number of 54,399 individuals in the first population age class. We further assumed that our virtual population shared the same demography as populations in different geographic regions, while survival rates were derived from a well-studied stock. Furthermore, for both simulation groups under a constant and variable environment, the range and mean values of the reproductive cycle parameters were derived from detailed studies that were conducted in Cyprus and Greece (Broderick et al. 2002, 2003; Margaritoulis 2005). We did not include any effect of density dependence on population growth rates, since such information has not been well documented for sea turtles (for an exception, see Bjørndal et al. 2000a). Nor did we include any carrying-capacity effects in terms of spatial nest distribution on the breeding habitats. Y. G. Matsinos et al. (unpublished manuscript) have recently addressed possible implications of the reduced availability of nesting areas on nesting processes. However, in this study, they provided a theoretical, comprehensive tool for assessing future threats due to habitat loss and fragmentation rather than an estimate of the current reductions in hatching success due to the restrictive component of carrying capacity.

In summary, our simulation results oppose findings of previous studies, while presenting an alternative method for modelling sea turtle population dynamics.

Our modelling methodology could serve as a starting point for analyzing sea turtle population dynamics through a new quantitative concept, while the generalized outlook of the present study could provide some insight into sea turtle population viability analysis. However, considering the uncertainty of some critical parameters of our model (such as mean annual survival rate), as well as the lack of information concerning life-history data (carrying capacity of nesting beaches, individual interactions within space, effects of catastrophes, etc.) it should be mentioned that our results should be viewed with caution. Nevertheless, the accuracy and reliability of model results could be further increased with the addition of more accurate and representative information on the critical demographic parameters. In conclusion we would like to emphasize the need for further field research regarding biological and behavioral features as well as basic demographic properties of sea turtle populations.

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