



How much sea turtle bycatch is too much? A stationary age distribution model for simulating population abundance and potential biological removal in the Mediterranean

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ABSTRACT: Mediterranean populations of loggerhead *Caretta caretta* and green sea turtles *Chelonia mydas* are subject to several anthropogenic threats, with documented mortality from incidental capture in fishing gear. However, how such mortalities actually affect the populations is uncertain without an estimate of population size. We derived a theoretical demographic structure for each species in the Mediterranean, assuming a stationary age distribution in a stable population with constant proportions of turtles in each life stage, using distributions of age-specific vital rates. We incorporated uncertainty into the main vital rate parameters to identify a likely order of magnitude of turtle abundance in different life stages. Through this approach, we aim to (1) provide a rough estimate of all population stage classes, particularly the juvenile classes that are most subject to fisheries interactions, (2) provide an estimate of reproductive life span, (3) identify and review the key demographic parameters, and (4) identify the priority gaps in our information in need of further investigation. The range of population abundance estimates from the models constructed with uncertainty (95% CI) was 0.81–3.38 million loggerheads and 0.26–2.21 million green turtles, Mediterranean-wide. When we calculated the potential biological removal for the segment of the population at risk of fisheries capture, our estimates were comparable to or lower than the estimated bycatch levels in fisheries. Although the model assumes a stable population and provides only a rough estimate of abundance, these results suggest that the current bycatch level should be regarded as unsustainable for Mediterranean turtle populations.

KEY WORDS: Loggerhead turtle · *Caretta caretta* · Green turtle · *Chelonia mydas* · Demography · Incidental capture

INTRODUCTION

Three sea turtle species occur in the Mediterranean Sea (Casale & Margaritoulis 2010): the leatherback turtle *Dermochelys coriacea*, the green turtle *Chelonia mydas*, and the loggerhead turtle *Caretta caretta*. A few leatherback turtles enter the Mediterranean from the Atlantic but do not breed in the basin (Casale et al. 2003), while the other 2 species

have Mediterranean populations recognized as regional management units (Wallace et al. 2011).

The loggerhead turtle is the most abundant sea turtle species in the Mediterranean, and reproduces mainly in Greece, Turkey, Cyprus, and Libya (Casale & Margaritoulis 2010). Loggerhead turtles frequent the entire marine area of the Mediterranean, with high occurrence reported in the oceanic zones of the westernmost part of the basin (from the Alboran Sea

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to the Balearic Islands), the Strait of Sicily, and the Ionian Sea. The foraging areas of the western basin are frequented by loggerheads of both the Mediterranean and the Atlantic populations from the Americas (Carreras et al. 2011). Loggerheads are also found in high abundance in the neritic zones of the northern Adriatic, off Tunisia, Libya, Egypt, and the southeast coast of Turkey (Casale & Margaritoulis 2010). Green turtles primarily frequent shallow neritic areas in the easternmost part of the basin and reproduce on nesting beaches in Turkey, Cyprus, and Syria (Casale & Margaritoulis 2010).

In the Mediterranean, these 2 sea turtle species are subject to several anthropogenic threats, including degradation of coastal habitats, incidental catch in fishing gear, collision with boats, and intentional killing, mainly for food (Tomás et al. 2008, Casale & Margaritoulis 2010, Casale et al. 2010, Casale 2011). These anthropogenic impacts appear to increase overall mortality (loggerheads: Casale et al. 2007, 2010, 2015) and as a whole represent a high level of threat for both species (Wallace et al. 2011). Nevertheless, nest counts at monitored nesting beaches do not show a clear trend for the Mediterranean as a whole, with individual nesting beaches showing increases, decreases, or no trend (Ilgaz et al. 2007, Türkozan & Yilmaz 2008, Casale & Margaritoulis 2010, Margaritoulis et al. 2011). For instance, no significant trend was observed at the single most important loggerhead nesting site over a 26 yr period from 1984 to 2009 (Zakynthos, Greece; Margaritoulis et al. 2011). However, because sea turtles are long-lived and take many years, even decades, to reach maturity, the population is primarily composed of juveniles, and nest counts are often poor indicators of population status because they are indicators of adults only (Heppell et al. 2002, National Research Council 2010). Likewise, trends based on nest counts can be affected by environmental factors that influence the frequency of reproduction (Hays 2000, Solow et al. 2002, Mazaris et al. 2004).

The main threat for sea turtles at the regional level is probably the mortality induced by incidental capture in fishing gear (Casale 2011). Fisheries bycatch studies usually estimate the number of catches that are then converted to number of deaths if immediate and delayed mortality rates are known. However, these extrapolations do not estimate the decrease in overall survival probability at the population level because the total number of turtles is unknown. For the Mediterranean, Casale (2011) estimated over 132 000 turtle captures yr^{-1} and an associated annual mortality of over 44 000 deaths, but how such a loss

actually affects local populations is uncertain without an estimate of population size. Only the number of adult females nesting annually in the Mediterranean has been estimated to date (loggerheads: 2280–2787; green turtles: 339–360 (Broderick et al. 2002). However, this represents only a subset of all adult females and a very small part of the total population (Heppell et al. 2002). Therefore, estimating the abundance of the population as a whole would represent a valuable contribution to sea turtle management that could better contextualize the magnitude and potential impacts of bycatch.

Estimates of population abundance will allow application of the potential biological removal (PBR) approach, developed for marine mammals (Wade 1998). This approach is based on the concept that the anthropogenic mortality of a population should not exceed 50% of the potential maximum productivity rate of the population, adjusted by a recovery factor which can vary from 0.1 to 1 according to the conservation status of the population. If the anthropogenic mortalities are less than the PBR, then a depleted population should recover. PBR is a very simple approach with some basic assumptions, including a logistic population growth curve (in which the maximum net productivity level corresponds to 50% of the maximum population growth rate). However, differently from marine mammals, the size and demographic structure of sea turtle populations are commonly unknown, and the numbers of nests or adult females are used as abundance indices. In order to overcome this problem and apply PBR to sea turtle populations where only the number of adult females is known, Curtis & Moore (2013) recently developed a maximum bycatch estimation approach which uses reproductive value equivalents in place of the number of individuals, an approach that includes additional uncertainty represented by the reproductive value equivalents. In this study, we addressed the demographic problem in a different way, by estimating potential distributions of the number of individuals in the age classes subjected to anthropogenic mortality and applying the original and simpler PBR approach. As a first attempt to compare anthropogenic mortalities with population size in the Mediterranean, with the associated uncertainties, scenarios considered as unsustainable were minimized by considering maximum PBR levels derived from total instead of minimum population size.

Simple deterministic age-structured models can be used to estimate population size under the assumption of stable age distribution and constant recruitment when combined with an estimate of adult pop-

ulation size (Caswell et al. 1998, Heppell et al. 2005). One problem with this method is a lack of adequate information on the juvenile stages, in terms of fundamental parameters such as age at maturity, number of stages (and their duration), and stage-specific survival probability. In previous studies of life-history sensitivity, the number of stages was based on habitat or body size, while the survival probabilities were assumed to be constant within a stage, derived from mark-recapture field studies or size-based catch curve analyses (e.g. Frazer 1983, Crouse et al. 1987, Heppell et al. 2005). In early models, the survival rates for unobservable stages, such as the hatchling and pelagic juvenile stages, were set to achieve an asymptotic population growth rate (λ) that matched observed trends on nesting beaches (Frazer 1983, Crowder et al. 1994). Some vital rates have been measured for Mediterranean loggerheads, but considerable uncertainty remains in the estimates for

loggerheads, and demographic data for green turtles are lacking. Nevertheless, an order-of-magnitude estimate of population size for life stages affected by fisheries interactions is possible with some assumptions about population structure and the relationship between body size and annual survival probabilities (Caswell et al. 1998).

To contribute to our understanding of the demography and population size of Mediterranean loggerhead and green turtles, we derived a theoretical demographic structure assuming a stationary age distribution, i.e. stable population and constant proportions of turtles in each life stage, to roughly determine population size. This approach estimates the structure of the juvenile life stage in a way that balances the hatchlings produced by observed clutches and the adults laying those clutches by estimating stationary annual survival rates for each juvenile age class (1 yr class). We incorporated uncertainty into the main parameters to define a range of the order of magnitude of the abundance at different stages. Through this approach, we aimed to (1) provide an estimate of abundance of all population stages, with particular regard to the juvenile class and the part of the population at risk of capture by fishing gear, (2) provide PBR levels and compare them to the known bycatch levels, (3) provide an estimate of reproductive life span, (4) identify and review the key demographic parameters, (5) identify the priority demographic gaps in need of further investigation.

MATERIALS AND METHODS

Our model aimed to simulate the demographic structure of theoretical sea turtle populations that are as similar as possible to the actual Mediterranean loggerhead and green turtle populations, but ideally under natural conditions, i.e. not considering anthropogenic mortality. However, it cannot be excluded that the given values of some independent variables (e.g. natality) incorporate current anthropogenic effects. The resulting abundance simulations were then compared to known levels of anthropogenic mortality.

Population demographic structure and abundance

The general approach of our model can be summarized as follows (Fig. 1). From annual nest counts, we derived the annual number of hatchlings (first age class) and the total number of adults. From the latter

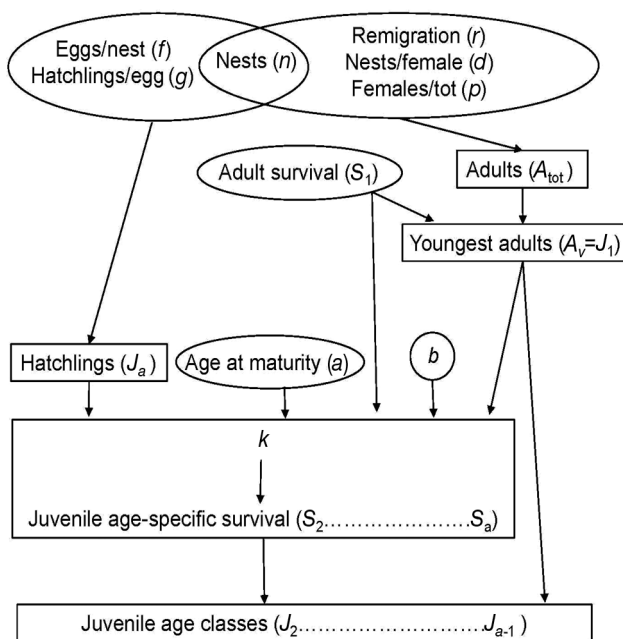


Fig. 1. Main steps of the model to estimate abundance of Mediterranean sea turtle populations. The 9 fundamental (independent) parameters are shown in ellipses/circles (see Table 1), and the derived parameters and variables are shown in boxes. Step 1: random values of the 9 fundamental parameters are generated from given value ranges and distributions (Table 1). Step 2: the number of adults (A_{tot}) and hatchlings (J_a) are derived (Eqs. 1 & 18). Step 3: the number of adults in the youngest age class ($A_v = J_1$) is derived (Eq. 7). Step 4: the parameter k is derived as a value that determines age-dependent S values which make J_0 and J_1 coherent in a stable population (Eq. 17). Step 5: the abundance of each juvenile age class is calculated (Eq. 16). All steps are repeated 10 000 times to obtain 95% CI. b : parameter for non-linearity of S -age relation

and adult survival, the demographic structure of the adult stage was derived to determine the abundance of the youngest adult age, from which all younger juvenile age classes were derived, working backwards to the first age class (hatchlings). Finally, the model forced this number of hatchlings derived by age class simulation to match the number of hatchlings determined by nest count, under the assumption of a stationary age distribution (constant annual survival rates by life stage and constant recruitment of new hatchlings each year). The resulting age-specific annual survival probabilities were then used to reconstruct the abundance of the juvenile age classes.

For convenience, we modeled the adult and juvenile stage classes separately, defining them on the basis of age at sexual maturity (a ; also commonly known as ASM) and annual survival probability (S). We defined the adult class as those turtles equal to or older than ASM, and having a constant annual survival probability (S_1 , see below). Therefore, this definition is independent from the actual breeding activity that occurred during a given year or age, which is defined by the remigration interval (r , see 'Adults' below). The juvenile class included turtles younger than a (ASM) and with a variable annual survival probability depending on age (S_t , see 'Juveniles' below).

Adults

The first step to estimate population size was to estimate the total number of adults A_{tot} as:

$$A_{\text{tot}} = \frac{nr}{pd} \quad (1)$$

where n is the number of nests yr^{-1} , r is the remigration interval (years between nesting years, or 1/proportion of adult females nesting in a particular year), d is the number of nests $\text{female}^{-1} \text{ season}^{-1}$, and p is the proportion of adults that are females. This assumes that reproduction parameters and sex ratio are constant for all adult age classes (see 'Model parameters' below).

We then estimated the number of adults in the youngest adult age class. Although this can be estimated from the proportion of adults that are 'neophytes,' or turtles breeding for the first time, we preferred to generate a distribution of the number of adult turtles in all adult age classes for 2 reasons. First, the proportion of neophytes is not well known in the Mediterranean, and this parameter is likely to

vary from one nesting site to another, together with the abundance trend. Second, with our approach, we could also estimate the reproductive life span. We assumed a constant annual survival probability and stationary adult age classes. A constant survival probability for each adult age class is plausible because, unlike juveniles, sea turtle adults show reduced or even negligible somatic growth (Carr & Goodman 1970, Limpus & Chaloupka 1997, Broderick et al. 2003, Casale et al. 2009b, 2011a). Therefore, if size affects survival, it is unlikely to vary much among adult age classes. Also, adults keep the same lifestyle and frequent the same habitats. Constant adult survival is also supported by some empirical data (e.g. Frazer 1983), and has been commonly applied in sea turtle modeling studies (e.g. Chaloupka & Limpus 2005, Heppell et al. 2005, Mazaris & Matsinos 2006, Dethmers & Baxter 2011, Lamont et al. 2014) With a known total adult abundance and a constant annual survival probability, the number of age classes and their abundances can be easily derived. In this model, the abundance of each adult age class was calculated from the next older age class (A_{t-1}), where t denotes a specific age class (in adults this ranges from 1 to v); therefore, from the oldest to the youngest age classes:

$$A_t = \frac{1}{S_1} A_{t-1} = \frac{A_1}{S_1^{t-1}} \quad (2)$$

where S_1 is the adult survival probability, and A_1 is the oldest class which, for convenience, may include more than 1 age class. The sum of all adult age classes equals the total number of adults (A_{tot}). If we set v as the number of adult classes (i.e. the number of annual age classes + A_1), then

$$A_{\text{tot}} = A_1 \sum_{m=1}^v \frac{1}{S_1^{m-1}} = A_1 \frac{1-(1/S_1)^v}{1-(1/S_1)} \quad (3)$$

from which v can be derived:

$$v = \frac{1}{\ln S_1} \ln \frac{S_1 A_1}{S_1 A_1 + A_{\text{tot}}(1 - S_1)} \quad (4)$$

For convenience, we defined the number of adult annual age classes ($v - 1$) as the number of age classes that include 99.9% of adults, with the oldest adult class (A_1) including all of the remaining oldest age classes (comprising 0.1% of adults). In other words, only 1 in 1000 adult turtles would survive until A_1 , and therefore $v - 1$ can be regarded as the maximum reproductive life span (e.g. Frazer 1983). Therefore, A_1 is set as:

$$A_1 = A_{\text{tot}} 10^{-3} \quad (5)$$

From Eqs. (4) & (5), v can be calculated as:

$$v = \frac{1}{\ln S_1} \ln \frac{S_1}{S_1 + (1 - S_1)10^3} \quad (6)$$

Note that this relation is now independent from A_{tot} , i.e. the number of adult age classes v can be derived by S_1 only. The abundance of the youngest adult age class (A_v) was derived from Eqs. (2) & (5), with v obtained from Eq. (6):

$$A_v = \frac{A_1}{S_1^{v-1}} = \frac{A_{\text{tot}}10^{-3}}{S_1^{v-1}} \quad (7)$$

It should be noted that this first adult age class is not equivalent to first-time breeders (neophytes), except in cases when turtles breed every year ($r = 1$). If $r > 1$, then only $1/r$ of the adults (in any age class) would breed in a given year. The non-breeding fraction of an adult age class will be subject to annual mortality and will then enter the next age class and again have a probability $1/r$ of breeding, and so on. Therefore, the proportion (c) of female neophytes observed on a nesting beach in a given year is:

$$c = U_{\text{tot}} \frac{r}{A_{\text{tot}}p} \quad (8)$$

where U_{tot} is the sum of the female neophytes of different age classes (U_m):

$$\begin{aligned} U_{\text{tot}} &= \sum_{m=1}^v U_m = \sum_{m=1}^v \frac{A_v p}{r} \left(\frac{r-1}{r} S_1 \right)^{m-1} \\ &= \frac{A_v p}{r} \sum_{m=1}^v \left(\frac{r-1}{r} S_1 \right)^{m-1} \\ &= \frac{A_v p}{r} \times \frac{1 - \left(\frac{r-1}{r} S_1 \right)^v}{1 - \left(\frac{r-1}{r} S_1 \right)} \end{aligned} \quad (9)$$

Then, combining Eqs. (8) & (9):

$$c = \frac{A_v}{A_{\text{tot}}} \times \frac{1 - \left(\frac{r-1}{r} S_1 \right)^v}{1 - \left(\frac{r-1}{r} S_1 \right)} \quad (10)$$

Note that if turtles breed every year ($r = 1$), then the proportion of first breeders (neophytes) is equivalent to the proportion of adults in the youngest adult age class (A_v).

In order to describe the age distribution of adults, we calculated the number of age classes that include the youngest 25, 50, 75, and 95% of the adult population (v_z) as follows:

$$v_z = v - v_{1-z} \quad (11)$$

with

$$\begin{aligned} v_{1-z} &= \frac{1}{\ln S_1} \ln \frac{S_1 A_1}{S_1 A_1 + A_{\text{tot}}(1-z)(1-S_1)} \\ &= \frac{1}{\ln S_1} \ln \frac{S_1}{S_1 + (1-S_1)(1-z)10^3} \end{aligned} \quad (12)$$

where v_{z-1} is the number of age classes that include the remaining oldest part of the adult population, derived from Eqs. (4) & (5), with z assuming the value of 0.25, 0.50, 0.75, or 0.95, respectively. Furthermore, the average reproductive life span (ARL) of the adult population was calculated as the sum of the individual reproductive ages divided by the number of adults:

$$\text{ARL} = \frac{\sum_{t=1}^v A_v S_1^{t-1} \times t}{\sum_{t=1}^v A_v S_1^{t-1}} = \frac{\sum_{t=1}^v S_1^{t-1} \times t}{\sum_{t=1}^v S_1^{t-1}} \quad (13)$$

where A_v is the youngest adult age class which, however, disappears in the final step of the formula and is not needed for calculating ARL. Because v is calculated from S_1 only (Eq. 6), S_1 is the only parameter needed to calculate ARL.

Juveniles

The largest fraction of a sea turtle population consists of juveniles, due to high fecundity and the large number of age classes from hatchling to adult. The primary aim of our calculations was to estimate the abundance of juveniles in each annual age class, which we could then sum to obtain the total juvenile population size estimate and the segment of the population at risk of capture by fisheries. Two parameters primarily affect the estimation of juvenile abundance: ASM (a), which determines the duration of the juvenile stage and the number of juvenile age classes, and the annual survival probability (S) of turtles within this stage. Previous models considered S as constant for the entire juvenile class (e.g. Frazer 1986) or for each of a few juvenile stages that included several age classes, with annual survival rates for each stage based on size and derived from field estimates (Heppell et al. 2002). We considered S as a variable dependent on age and hence on size, because annual growth of juveniles is significant (for Mediterranean loggerheads: Casale et al. 2009a,b, 2011a,b, Piovano et al. 2011), and it is reasonable that body size may affect survival through several factors

such as defense from predators, feeding capability, thermoregulation, etc. We considered S to be a positive function of age and avoided any arbitrary division of the juvenile class into stages (e.g. oceanic and neritic) because such stages are not supported for loggerheads in the Mediterranean context (Casale et al. 2008). Moreover, we allowed S to vary non-linearly with age, because faster change of S is more likely at young ages than at older ages, when turtles are growing more slowly.

The model made the following assumptions: (1) the duration of the juvenile stage (hatchling to adult) is the same for all turtles (i.e. all turtles enter the adult stage at the same age, a); (2) survival probability increases with age, therefore S of a given juvenile age class is higher than that of the previous younger age class; (2) the population is stable and has a stable demographic structure; and (4) all age classes have the same sex ratio.

The abundance of each juvenile age class J was calculated from the next older age class, from the oldest to the youngest:

$$J_t = \frac{1}{S_t} J_{t-1} \quad (14)$$

where S_t is the survival probability of the juvenile age class t , with t increasing with decreasing age, from 1 to a (number of age classes = ASM). The initial age class (J_1) to calculate all juvenile age classes from J_2 onward, is actually the youngest adult age class (A_v , Eq. 7) here named J_1 for convenience (and included in the adult count only, not juvenile), and J_a is the youngest juvenile age class (first year of life, i.e. hatchlings). The model considers S as age class-specific, increasing with age, and allows non-linear change of S :

$$\begin{aligned} S_t &= S_{t-1} \frac{k-1}{k} (a-t+1)^b \\ &= S_1 \left(\frac{k-1}{k} \right)^{t-1} \left[\frac{(a-1)!}{(a-t)!} \right]^b \end{aligned} \quad (15)$$

where S_1 is the survival probability of adults, k is a parameter which determines the general slope of the relationship between S and age, and b is the parameter which determines the degree of non-linearity of this relationship. The parameter b was allowed to vary within a range of values between 0 and a maximum value arbitrarily set for each of the models with different a (ASMs, see below) as the maximum value below which S increases with age, ranging from $b = 0.01$ for $a = 34$ to $b = 0.06$ for $a = 21$ for loggerhead turtles and from $b = 0.001$ for $a = 50$ to $b = 0.12$ for $a = 18$ for green turtles.

From Eqs. (14) & (15):

$$J_t = \frac{J_1 \prod_{u=1}^t (a-u)!^b}{S_1^{t-1} \left(\frac{k-1}{k} \right)^{\frac{t^2-t}{2}} (a-1)!^{bt}} \quad (16)$$

from which it is possible to obtain the value that k should have in a stable population, by setting $t = a$, with the first age class as J_1 ($= A_v$, youngest adult age class) and the last age class as J_a (hatchlings, age class 1):

$$k = \frac{1}{1 - \frac{\frac{a^2-a}{2} \sqrt{J_1 \prod_{u=1}^a (a-u)!^b}}{J_a S_1^{a-1} (a-1)!^{ba}}} \quad (17)$$

where J_a is calculated as:

$$J_a = nfg \quad (18)$$

where n is the number of nests yr^{-1} , f is the number of eggs nest^{-1} , and g is the number of hatchlings per egg which reach the sea. This 'backward' numeration allowed us to easily vary the total number of juvenile age classes, based on different values of a (ASM).

To estimate distributions of population size with uncertainty, we randomly drew values from pre-determined parameter distributions (10 000 replicates) based on previously published estimates or best guess values (Table 1). Monte Carlo simulations were run with the PopTools add-in for Microsoft Excel (www.poptools.org). Separate simulations were run for different a (ASM) values.

Model parameters

The estimation model is based on 8 fundamental (independent) biological parameters which describe a population (a, n, r, d, p, f, g, S_1) plus the parameter b , which controls the degree of non-linear relation between S and age (see Table 1 for values and sources of these 9 parameters). However, 2 of these parameters are particularly important for the model and are described below in detail.

Number of nests per year

The average number of loggerhead turtle nests yr^{-1} , n , in the Mediterranean based on data available from monitored beaches is about 7250 (Casale & Margaritoulis 2010). However, this figure represents

Table 1. Parameters, values, and distributions for a stationary age model of the Mediterranean (Med) loggerhead and green turtle populations. A triangular distribution was adopted if a likely value could be identified; otherwise a uniform distribution within the range was adopted to account for maximum uncertainty. Positive or negative relationships of the individual parameters with the resulting estimate of population abundance are indicated with + and –, respectively. Sources: 1: Broderick et al. (2003), Ilgaz et al. (2007), Hays et al. (2010); 2: Broderick et al. (2003); 3: Rees & Margaritoulis (2004), Casale et al. (2005, 2006, 2014), Zbinden et al. (2007), Rees et al. (2013), Godley et al. (2001); 4: Broderick et al. (2003), Margaritoulis et al. (2003), Türkozan et al. (2003), Margaritoulis (2005), Özdemir et al. (2008), Türkozan & Yilmaz (2008); 5: Türkozan et al. (2003), Türkozan & Yilmaz (2008), Margaritoulis (2005); 6: Heppell et al. (1996, 2002), Monk et al. (2011); 7: Stokes et al. (2014); 8: arbitrary wide range, in order to include high uncertainty, and considering results by Kaska et al. (1998) and Casale et al. (2000); 9: Türkozan et al. (2011); 10: Heppell et al. (2002), Campbell & Lagueux (2005). Sources given as ‘see text’ refer to ‘Materials and methods: Model parameters’

Parameters	Single or likely value	Min	Max	Distribution	Source	Area	Effect on pop. estimate
Loggerhead turtles							
Age at sexual maturity (ASM) (<i>a</i>)	21–34				See text	Med	+
Nests per year (<i>n</i>)	8300	7250	8800	Triangular	See text	Med	+
Female remigration interval (years/breeding) (<i>r</i>)	2.3	2	3.35	Triangular	1	Med	+
Nests per female per breeding season (<i>d</i>)	1.9	1	5	Triangular	2	Med	–
Sex ratio (proportion female) (<i>p</i>)		0.40	0.75	Uniform	3	Med	–
Eggs per nest (<i>f</i>)		73	116	Uniform	4	Med	+
Hatchlings to sea per egg (<i>g</i>)		0.583	0.666	Uniform	5	Med	+
Adult survival (S_1)		0.85	0.91	Uniform	6	World	–
Parameter for non-linearity of <i>S</i> –age relation (<i>b</i>)		0	0.01–0.06	Uniform	Arbitrary, see text		–
Green turtles							
ASM (<i>a</i>)	18–50				See text	Med	+
Nests per year (<i>n</i>)		1600	1840	Uniform	See text	Med	+
Female remigration interval (years/breeding) (<i>r</i>)	3	3	4	Triangular	7	Med	+
Nests per female per breeding season (<i>d</i>)	3	1	4	Triangular	7	Med	–
Sex ratio (proportion female) (<i>p</i>)		0.50	0.9	Uniform	8	Med	–
Eggs per nest (<i>f</i>)		103	119	Uniform	9	Med	+
Hatchlings to sea per egg (<i>g</i>)		0.58	0.85	Uniform	9	Med	+
Adult survival (S_1)		0.82	0.95	Uniform	10	World	–
Parameter for non-linearity of <i>S</i> (<i>b</i>)		0	0.001–0.12	Uniform	Arbitrary, see text		–

an underestimate, for 2 reasons. First, many nests are scattered along minor or unknown nesting beaches along the Mediterranean coasts; in Greece, these nests are estimated to comprise about 15% of the monitored ones (Margaritoulis et al. 2003). Second, about 66% of sandy beaches in Libya (total 1089 km) have never been surveyed (Hamza 2010) and might support high nesting levels. We therefore considered 7250 as the minimum, 8300 (7250 + 15%) as the most likely figure, and 8800 (including 500 hypothetical additional nests from Libya) as the maximum number of nests yr^{-1} (Table 1).

Based on data available from monitored beaches, the average number of green turtle nests yr^{-1} in the Mediterranean is about 1600 (Casale & Margaritoulis 2010). Because additional unmonitored nesting activ-

ity probably occurs, we considered 1600 as the minimum number and 1840 (1600 + 15%) as the maximum number of nests yr^{-1} (Table 1).

Number of juvenile age classes

Age at maturity (*a*) was calculated from the mean values of 8 age-at-length relationships obtained in the Mediterranean through capture-mark-recapture, length-frequency, and skeletochronology (Casale et al. 2009b, 2011a,b, Piovano et al. 2011). The size at maturity of loggerhead turtles in the Mediterranean was assumed to be the average size of nesting females, because female loggerhead turtles begin breeding at a size slightly smaller than the average

size of all nesting females (Limpus 1990). The mean size (weighted for rookery size in terms of number of nests) of loggerheads nesting in the Mediterranean is ca. 80 cm curved carapace length (CCL) (see Table S1 in the Supplement, available at www.int-res.com/articles/suppl/n029p239_supp.pdf), and males appear to reach maturity at a similar size (Casale et al. 2005, 2014). The mean age at 80 cm CCL determined from the 8 growth curves resulted in an average a of 25 yr (range: 21–34 yr). To consider the uncertainty of these estimations and to provide indications of the effects of a on the model, 14 models were built with a ranging from 21 to 34 yr.

Because no growth curve is available for Mediterranean green turtles, we adopted the highest uncertainty possible for a (ASM) of this species, represented by the range of ASMs estimated for other green turtle populations around the world, viz. 18 to 50 yr (Avens & Snover 2013). A total of 17 models were built with a (ASM) ranging from 18 to 50 yr (1 model for every 2 yr of possible ASM).

General sensitivity analysis

The relative importance of each parameter on the population abundance estimate was assessed by comparing results from simulations for the set values of 1 parameter at a time either (1) increased or decreased by 20% for parameters with positive or negative relationships with population abundance, respectively, or (2) fixed at the minimum and maximum values considered for the model (see Table 1).

Bycatch and PBR

Segment of the population at risk of capture

Available bycatch data indicate that only turtles >20 cm CCL are generally captured (Casale 2011) and were therefore considered to be at risk of capture in our model; this approximately corresponds to turtles older than 2 yr from hatching (Casale et al. 2009a, Goshe et al. 2010). However, this is a minimum size threshold, and such small turtles are not commonly caught (Casale 2011); therefore, we considered turtles >40 cm CCL to be at higher risk of capture. For Mediterranean loggerheads, this size range corresponds to turtles older than 7 yr from hatching (Casale et al. 2009b, 2011a,b, Piovano et al. 2011). The lack of growth data for Mediterranean

green turtles makes an estimate of age at that size highly uncertain for this species, so the higher risk category was not considered for green turtles.

PBR

The PBR approach for protected species was developed for marine mammals (Wade 1998) and is based on the concept that the anthropogenic mortality of a population should not exceed 50% of the potential maximum productivity rate of the population (R_{\max}), adjusted by a recovery factor (F) which can vary from 0.1 to 1 according to the conservation status of the population (0.1 for endangered, 0.5 for threatened, and 1 for other populations; Barlow et al. 1995). PBR is calculated through a simple equation requiring 3 factors: minimum population size (N_{\min}), R_{\max} , and F , as follows:

$$\text{PBR} = 0.5R_{\max}FN_{\min} \quad (19)$$

For R_{\max} , we used maximum population growth rates observed at nesting sites: 0.064 yr⁻¹ for loggerheads (Brazil; Marcovaldi & Chaloupka 2007) and 0.139 yr⁻¹ for green turtles (Florida, USA; Chaloupka et al. 2008). These maximum population growth rates were chosen because the observed populations were at low density and are thought to have similar life history traits to the Mediterranean populations of each species. PBR was calculated for each of 3 values of F (0.1, 0.5, and 1; Wade 1998). Although minimum population abundance should be used, we calculated PBR for all mean and 95% CI abundance estimates of the Mediterranean populations, thereby providing both a range and maximum PBRs in a context with high uncertainty.

Estimated bycatch removal

Available bycatch data (Table S2 in the Supplement) aggregate Mediterranean green turtles and Mediterranean and Atlantic loggerheads together; as such, they are difficult to compare with PBRs estimated by this study. Data regarding the eastern Mediterranean (29 500 deaths yr⁻¹) are here considered to be an approximation of the removal level of Mediterranean loggerheads, considering that this subpopulation mostly frequents the eastern basin, while in the western basin, Mediterranean loggerheads mix with Atlantic loggerheads. Data regarding the Levantine basin (8450 deaths yr⁻¹) are considered as an approximation of removal levels of Mediterran-

ean green turtles considering that they mostly frequent the Levantine basin and to a lesser extent other areas of the eastern basin, and that they share the Levantine basin with loggerhead turtles.

RESULTS

Population demographic structure and abundance

Loggerhead turtles

The estimated mean number of adults was 15 843 (95% CI: 6915–31 958). The maximum number of

adult age classes, exceeded by only 0.1% of adults (e.g. Frazer 1983), was 38 (95% CI: 31–47), which can be considered as the maximum reproductive life span. However, 95% of adults were included in only 23 age classes (95% CI: 18–29), and ARL was 8.2 yr (95% CI: 6.5–10.4; Table S3 in the Supplement). Because the adult model assumed a constant adult survival probability for all age classes, the above estimations should be regarded as maximum values, and somewhat shorter reproductive life spans are expected if the adult survival probability decreases with age.

The effect of a (ASM) on age-specific S is shown in Fig. 2. The resulting ranges of S fit the empirical

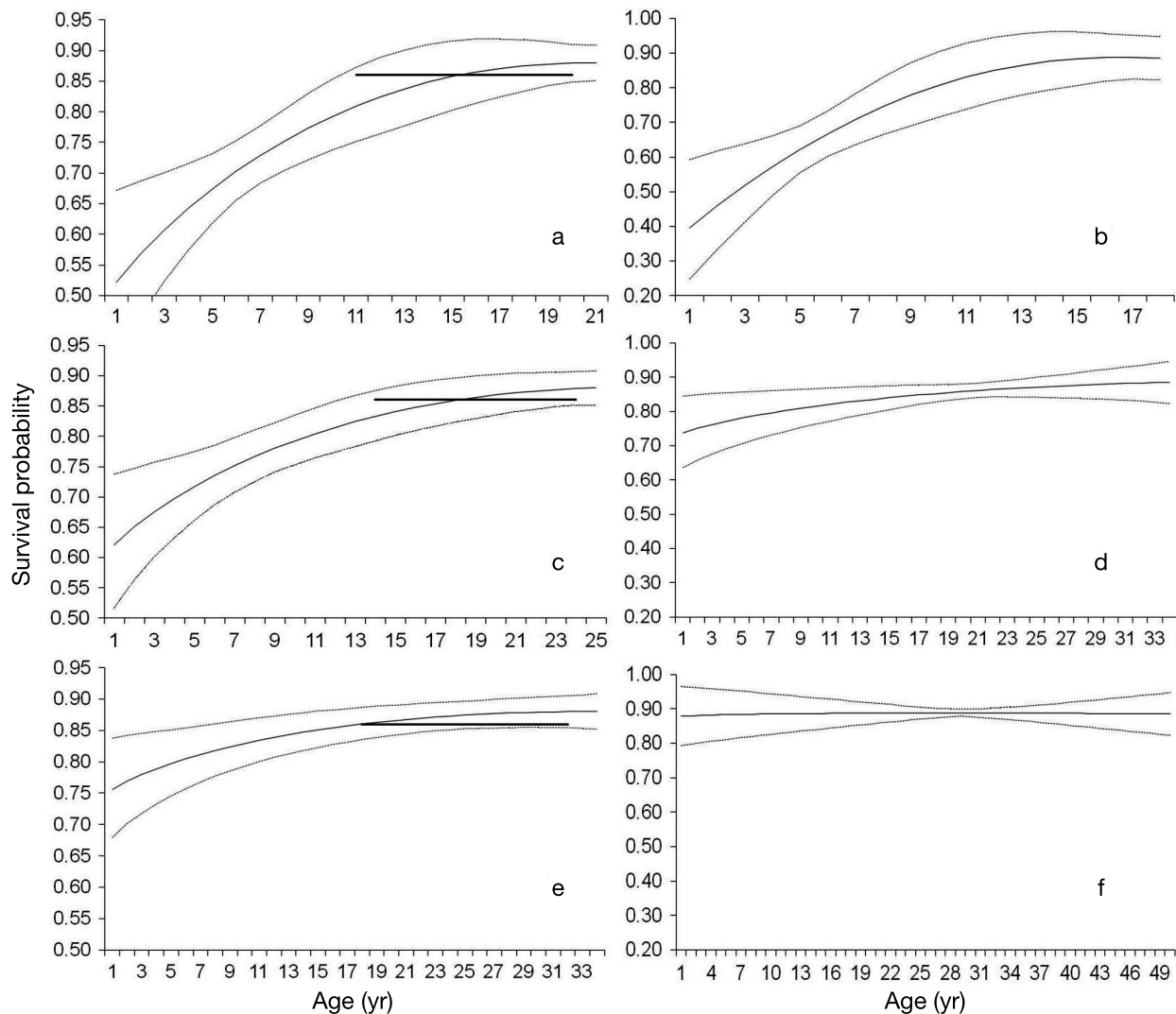


Fig. 2. Mean and 95% CI of survival probability of (a,c,e) loggerhead *Caretta caretta* and (b,d,f) green turtles *Chelonia mydas* in each age class from year 1 (hatchlings) to age at sexual maturity (ASM) from the 3 ASM values (loggerheads: 21, 25, and 34 yr; green turtles: 18, 34, and 50 yr). The solid horizontal bars represent the highest annual survival probability of loggerheads estimated in Mediterranean foraging grounds to date (0.86; Tunisian Shelf; Casale et al. 2015). The bars span the age range to which this probability applies

estimation of juvenile survival probability (Fig. 2). Combining the results for adults and juveniles, total population abundance estimates for different *a* values are shown in Fig. 3, and detailed results of 3 specific scenarios with the minimum, mean, and maximum ASM values (21, 25, and 34 yr) are presented in Table 2 and in Fig. S1 in the Supplement. Population abundance was higher with higher *a*, ranging from an average of 1 197 087 turtles (95 % CI: 805 658–1 732 675) with *a* = 21, to 2 364 843 turtles (95 % CI: 1 611 085–3 376 104) with *a* = 34 (Table 2).

Green turtles

The estimated mean number of adults was 3390 (95 % CI: 1894–6552). The maximum number of adult age classes, exceeded by only 0.1 % of adults (e.g. Frazer 1983), was 42 (95 % CI: 27–73), which can be considered as the maximum reproductive life span. However, 95 % of adults were included in only 26 age classes (95 % CI: 15–50), and ARL was 9.4 yr (95 % CI: 5.5–17.4; Table S3). Because the adult model assumed a constant adult survival probability for all age classes, the above estimations should be regarded as maximum values, and somewhat shorter reproductive life spans are expected if the adult survival probability decreases with age.

The effect of *a* (ASM) on age-specific *S* is shown in Fig. 2. Combining the results

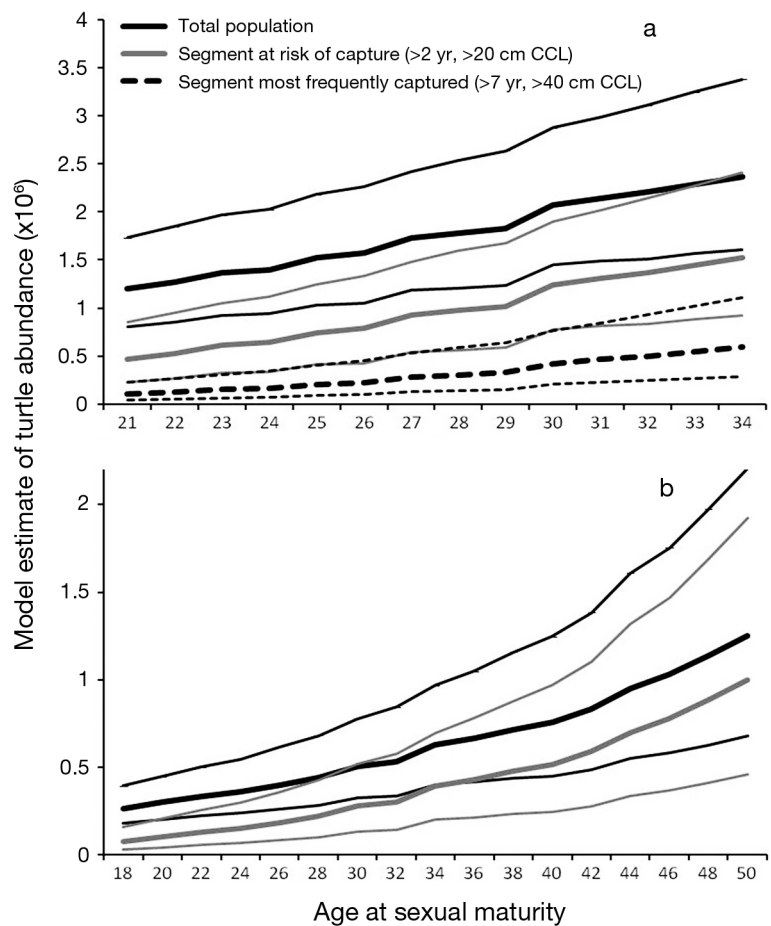


Fig. 3. (a) Estimated loggerhead turtle *Caretta caretta* population abundance from 14 models with age at sexual maturity (ASM) from 21 to 34 yr, and (b) green turtle *Chelonia mydas* population abundance from 17 models with ASM from 18 to 50 yr (every 2 yr). Mean (thick lines) and 95 % CI (thin lines) are shown for each of the 3 segments of the population: the total population, the fraction of the population that is at risk of capture by fisheries (>20 cm curved carapace length, CCL), and the fraction of the population that is most represented in fisheries bycatch (>40 cm CCL). See ‘Materials and methods’ for further details about these 2 components of the population

Table 2. Abundance (mean and 95 % CI) for the Mediterranean loggerhead *Caretta caretta* and green turtle *Chelonia mydas* populations estimated through a stationary age distribution model, for 3 age at sexual maturity (ASM) values. The estimates for the category ‘most at risk’ of being captured by fisheries are given for loggerheads only, for which growth curves are available in the Mediterranean (see ‘Materials and methods’)

ASM (yr)	Total population	Population at risk of capture (>2 yr)	Most at risk (>7 yr)
Loggerhead turtles			
21	1 197 087 (805 658–1 732 675)	469 059 (229 658–853 532)	110 550 (45 276–227 072)
25	1 521 107 (1 034 839–2 178 790)	744 754 (414 729–1 245 429)	205 913 (90 533–403 324)
34	2 364 843 (1 611 085–3 376 104)	1 522 577 (922 981–2 407 930)	597 394 (290 519–1 106 122)
Green turtles			
18	261 727 (176 284–391 386)	71 329 (25 993–158 849)	
34	626 196 (397 537–967 649)	388 782 (198 002–692 427)	
50	1 252 283 (679 433–2 209 833)	995 678 (459 714–1 926 281)	

Table 3. Effect of model parameters on the population abundance estimate (simulated for loggerhead turtles *Caretta caretta* only). (a) Ratios (corrected:original) of abundance values obtained applying a 20% correction factor to each parameter (1.2 or 0.8 for parameters with a positive or negative relation to the population abundance, respectively). The effect of age at sexual maturity (ASM) was assessed by comparing ASM = 30 against 25 (mean ASM). (b) Ratios of abundance values obtained fixing each parameter at the minimum and maximum values considered for the model (see Table 1). In both cases, for parameters other than ASM, the model was run by changing 1 parameter at a time with ASM = 25. Values: the 2 values from which results of the simulation are obtained

(a)	Correction factor	N adults	Total population	Population at risk of capture (>2 yr)	Most at risk of being captured (>7 yr)
ASM (<i>a</i>)	1.2	1.0	1.3	1.4	1.8
Nests per year (<i>n</i>)	1.2	1.2	1.2	1.2	1.2
Female remigration interval (years/breeding) (<i>r</i>)	1.2	1.2	1.0	1.1	1.1
Nests per female per breeding season (<i>d</i>)	1.2	1.3	1.1	1.1	1.2
Sex ratio (proportion female) (<i>p</i>)	0.8	1.3	1.1	1.1	1.2
Eggs per nest (<i>f</i>)	0.8	1.0	1.2	1.1	1.1
Hatchlings to sea per egg (<i>g</i>)	1.2	1.0	1.2	1.1	1.1
Adult survival (S_1)	0.8	1.0	2.3	3.3	5.5
(b)	Values	N adults	Total population	Population at risk of capture (>2 yr)	Most at risk of being captured (>7 yr)
ASM (<i>a</i>)	21–34	1.0	2.0	3.2	5.4
Nests per year (<i>n</i>)	7250–8800	1.2	1.2	1.2	1.2
Female remigration interval (years/breeding) (<i>r</i>)	2.00–3.35	1.6	1.1	1.2	1.4
Nests per female per breeding season (<i>d</i>)	1–5	5.0	1.4	1.8	3.1
Sex ratio (proportion female) (<i>p</i>)	0.40–0.75	1.9	1.1	1.3	1.5
Eggs per nest (<i>f</i>)	73–116	1.0	1.5	1.4	1.2
Hatchlings to sea per egg (<i>g</i>)	0.583–0.666	1.0	1.1	1.1	1.0
Adult survival (S_1)	0.85–0.91	1.0	1.3	1.5	1.9
Parameter for non-linearity of <i>S</i> (<i>b</i>)	0.00–0.03	1.0	1.4	1.9	1.9

Table 4. Potential biological removal (PBR) values (number of turtles) calculated from abundance estimations of the Mediterranean loggerhead *Caretta caretta* and green turtle *Chelonia mydas* populations at risk of capture (Table 2). Although minimum population abundance should be used, PBRs are provided for the entire range (mean and 95% CI) of abundance estimates, in order to also include maximum PBRs in a context with high uncertainty. PBR was calculated for each of 3 values of the recovery factor *F*: 0.1 for endangered, 0.5 for threatened, and 1 for other populations (sensu Wade 1998). ASM: age at sexual maturity

ASM (yr)	Population at risk of capture (>2 yr)			Most at risk of being captured (>7 yr)		
	0.1	0.5	1	0.1	0.5	1
Loggerhead turtles						
21	1501 (735–2731)	7505 (3675–13 657)	15010 (7349–27 313)	354 (145–727)	1769 (724–3633)	3538 (1449–7266)
25	2383 (1327–3985)	11 916 (6636–19 927)	23 832 (13 271–39 854)	659 (290–1,291)	3295 (1449–6453)	6589 (2897–12 906)
34	4872 (2954–7705)	24 361 (14 768–38 527)	48 722 (29 535–77 054)	1912 (930–3540)	9558 (4648–17 698)	19 117 (9297–35 396)
Green turtles						
18	496 (181–1104)	2479 (903–5520)	4957 (1807–11 040)			
34	2702 (1376–4812)	13 510 (6881–24 062)	27 020 (13 761–48 124)			
50	6920 (3195–13 388)	34 600 (15 975–66 938)	69 200 (31 950–133 877)			

for adults and juveniles, total population abundance estimates for different *a* values are shown in Fig. 3, and detailed results of 3 specific scenarios with the minimum, mean, and maximum ASM values (18, 34, and 50 yr) are presented in Table 2 and Fig. S2. Population abundance increased with higher *a*, ranging from an average of 261 727 turtles (95% CI: 176 284–391 386) with *a* = 18, to 1 252 283 turtles (95% CI: 679 433–2 209 833) with *a* = 50 (Table 2).

General sensitivity analysis

The biological parameters with the largest effect on population abundance estimates were ASM (*a*), nests female⁻¹ season⁻¹ (*d*), and adult survival probability (S_1) (Table 3). Also, the parameter for non-linearity of *S* (*b*) showed a relatively large effect, indicating that population abundance is strongly affected by how juvenile *S* changes across age classes.

Bycatch and PBR

Loggerhead turtles

Mean PBR estimates varied from 1501 to 48722 loggerhead turtles for the fraction of the population at risk of capture and from 354 to 19117 turtles for the fraction of the population at highest risk of capture (Table 4). PBR *sensu stricto* (calculated on the minimum population abundance) was lower than the estimated bycatch removal, as were PBRs in most scenarios (Fig. 4). A frequency distribution of PBR results for an example case is shown in Fig. S3.

Green turtles

Mean PBR estimates varied from 496 to 69200 green turtles for the segment of the population at risk of capture (Table 4). PBR *sensu stricto* (calculated on the minimum population abundance) was lower than the estimated bycatch removal, as were PBRs in many other scenarios (Fig. 4).

DISCUSSION

Population demographic structure and abundance

We simulated the demographic structure of theoretical sea turtle populations with stationary age distributions using independent biological parameters available for the Mediterranean populations of loggerhead and green turtles. This represents the first attempt to estimate population sizes for these populations using a simulated demographic structure. We used wide ranges of values for all parameters, and likely captured the true abundances in our 95% CI ranges. The most problematic assumption of the model is the stationary age distribution, which is a function of time-constant survival rates and age at maturity. It is improbable that a sea turtle population is perfectly stable and in a stationary condition. In the case of a decreasing or increasing population, the abundance obtained by our stationary age distribution model would be over- and underestimated, respectively. However, the available long-term data sets of nest counts do not show a clear overall trend in the Mediterranean populations (Ilgaz et al. 2007, Türkozan & Yilmaz 2008, Casale & Margaritoulis 2010, Margaritoulis et al. 2011); this is even more uncertain for green turtles. Our model also has other simplifications. For instance, all turtles are assumed to enter the adult stage at the same age, and this stage is assumed to have a constant annual survival probability. The theoretical populations are also assumed to be living under natural conditions (although it cannot be excluded that the given values of some independent variables incorporate current anthropogenic effects), while anthropogenic mortality is considered at a second step, by comparing known levels

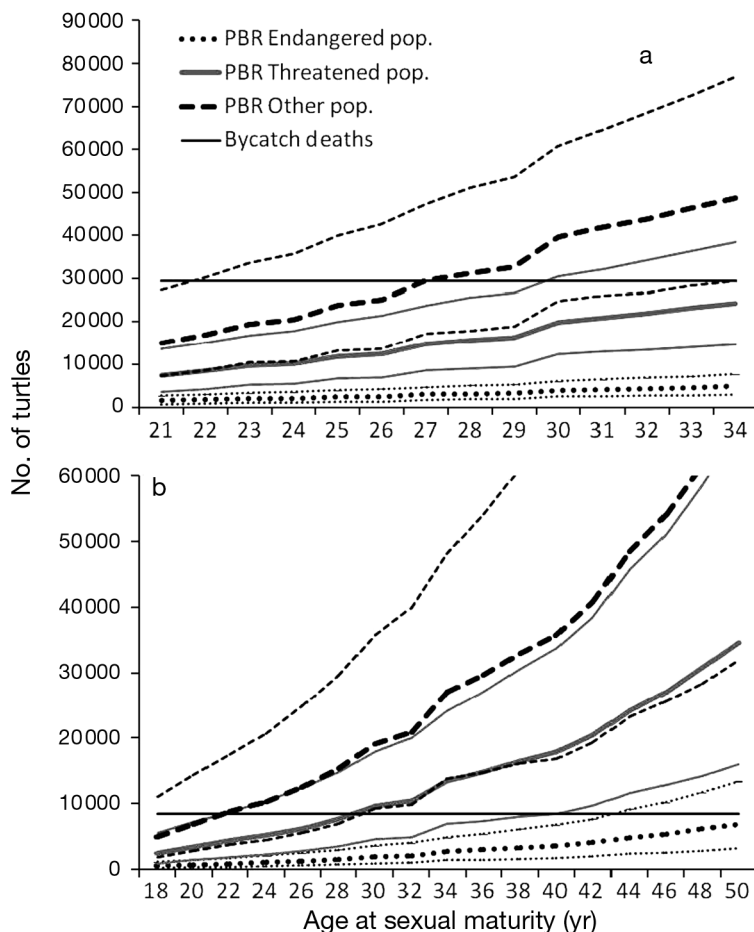


Fig. 4. Potential biological removal (PBR) levels calculated from abundance levels for the fraction of the population at risk of capture by fisheries (>20 cm curved carapace length, CCL or >2 yr) of Mediterranean (a) loggerhead *Caretta caretta* and (b) green turtle *Chelonia mydas* populations estimated through a stationary age distribution model for a range of age at sexual maturity (ASM) values. Mean (thick lines) and 95% CI (thin lines) are shown for each of 3 PBRs calculated for endangered, threatened, and other populations (recovery factor $F = 0.1, 0.5$, and 1 respectively; see 'Materials and methods' for details). The horizontal solid bar shows the level of removal estimated from bycatch data; therefore, scenarios below the bar should be considered unsustainable

of anthropogenic mortality with PBR obtained from the simulations. Therefore, the present estimates can be regarded as an attempt to provide an order of magnitude for the abundance of Mediterranean turtle populations, although the exact figures should be considered preliminary.

The adult fraction of the population is the easiest to simulate because it is not subject to highly uncertain parameters such as ASM (or a) and S -age relationships in juveniles. The present estimate of annual nesting females is higher than the previous estimate (2280–2787 loggerheads and 339–360 green turtles; Broderick et al. 2002), mainly due to a higher overall nest count resulting from increased beach monitoring efforts. The estimated average ARL of loggerheads was 8.2 yr; with the average ASM (25 yr), this suggests an average adult age of 33 yr. Considering the ARL and ASM ranges, the average adult age would range from 28 to 44 yr. For green turtles, ARL was 9.4 yr, but ASM for the Mediterranean population is too uncertain to suggest adult age. An ARL of a few years may appear short for sea turtles, which are considered long-lived animals. However, such a consideration confounds 2 very different concepts, the potential life span (that can be long but is reached by only a small percentage of a population) and the average life span. In sea turtles, the average life span is predicted to be just a few years, i.e. most turtles never reach maturity nor even a large size. For instance, in our model, adults represent only about 1% of the total population (see also Heppell et al. 1996). In the same way, only a few adults are expected to live for decades. For example, with the adult S considered here, only about 5% of adults would live longer than 23 yr after ASM, which means longer than 48 yr in total lifespan if ASM is 25 yr. As a different perspective to think about ARL, consider that an adult female should lay an average of 10 (loggerheads) or 11 clutches (green turtles) to produce enough eggs to allow 2 of her offspring to reach ASM in order to replace herself and her mate. Any additional clutches would lead to population increase. With the average values for remigration interval and clutches female⁻¹ season⁻¹ (Table 1), the above number of clutches can be translated to 12.1 and 11 yr ARL, respectively. However, these values are probably overestimates, because current estimation of remigration intervals and clutches female⁻¹ are probably over- and underestimated, respectively, due to methodological biases. Adult life spans depend on survival probabilities that might be underestimated because of methodological limits, as suggested by Chaloupka & Limpus (2002). However, if current

methods underestimate survival probabilities in adults and juveniles, and the actual values are higher than the available estimates, then even fewer nests would be needed to replace an adult couple, and adults would breed for much longer than 'required.'

Our model considered juvenile S to be a variable dependent on age (size) and derived from other independent variables. For loggerheads, the estimated values of S (Fig. 2) can be compared to values estimated through empirical means from Mediterranean foraging grounds (Casale et al. 2015). The highest of these values can be assumed to be less affected by anthropogenic mortality and closer to the natural values, and this value is similar to the survival probabilities estimated by our model. For comparison, the highest S values for juveniles of other loggerhead populations are around 0.91 (Casale et al. 2015).

Population abundance estimates span a wide range of values, due to the uncertainty in several parameters. Empirical estimates are intrinsically difficult to provide for a marine animal spending most of the time underwater. The best method may be represented by aerial surveys that can estimate the surface abundance of turtles, followed by an estimate of the total abundance in the surveyed area through a correction factor for the time spent underwater. However, aerial surveys have been conducted in only 2 areas, representing just a small part of the Mediterranean: in Spanish waters (Gómez de Segura et al. 2006) and in the Pelagos Sanctuary (Lauriano et al. 2011), both in the western Mediterranean. In these 2 areas, 19 000 and 10 000 loggerhead turtles were estimated to occur, respectively, but these areas are frequented by loggerheads of both Mediterranean and Atlantic origin (Clusa et al. 2014). For all of the above limitations, a comparison between simulated and empirical estimates is not very informative at present.

Bycatch and PBR

Population abundance estimates from our model can be compared to estimated bycatch levels and associated mortality in the Mediterranean. Available bycatch estimates (Casale 2011) are based on data collected in different Mediterranean areas in the 1990s and 2000s; therefore, current bycatch levels might be different. However, the population abundance estimates here were derived from average nest counts and other data collected during the same period as the bycatch estimates. Bycatch levels are probably underestimated, and mortality rates have a

degree of uncertainty (Casale 2011). The empirical estimates are aggregates of Mediterranean loggerheads, Atlantic loggerheads (mainly in the western basin; Clusa et al. 2014), and Mediterranean green turtles, the latter occurring mainly in the Levantine Basin (Casale & Margaritoulis 2010). Thus, it is likely that a few tens of thousands of Mediterranean loggerheads and several thousands of green turtles are removed annually by fisheries. This amount is higher than the PBR values (*sensu stricto*, i.e. calculated on the minimum population abundance) for the segment of the population at risk of capture and even higher than most PBRs calculated on the highest population abundance estimates. Therefore, our results indicate that the available bycatch level should be regarded as unsustainable for the Mediterranean turtle populations, as previously suspected (Casale 2011). Under this scenario, the lack of evidence (from the primary nesting beaches) of a decreasing population is intriguing. We propose 3 hypotheses for further study: (1) the real abundance, and hence PBR, is higher than we thought because of major rookeries that have not yet been discovered (Libya is the best candidate for unknown rookeries; Hamza 2010); (2) the real abundance of juveniles (the bulk of the population), and hence PBR, is higher than we thought because the population is increasing (while our model considers a stable population with constant recruitment), but these abundant juvenile age classes have not yet recruited to the adult stage (the only current index of the population through nest counts); this would imply a reduction of anthropogenic impact in a recent period ($<ASM$), and the best candidate for this is protection of nesting beaches with increased natality (Casale & Margaritoulis 2010); (3) the juvenile population is actually decreasing due to an increase in bycatch mortality in a recent period ($<ASM$), but this has not yet been observed in the adult stage because of the long maturation of these animals. Although most bycatch studies have been conducted within this period (Casale 2011), it is likely that high bycatch levels also occurred before; however, a recent increase cannot be excluded, especially if this is due to cryptic fisheries bycatch in small-scale fisheries in developing countries.

Concluding remarks

By forcing the population to be stable in structure and abundance, a stationary age distribution model highlights the interdependency among several demographic parameters of a population and helps iden-

tify the minimum set of fundamental parameters (or field data) which are required to describe the population. Our model considered juvenile annual survival probability as a dependent variable (1 for each age class) obtained from 8 independent variables, of which 7 can be obtained at nesting beaches and 1 (ASM) from studies on juveniles. In our model, ASM, annual survival probability of adults, and nests female⁻¹ season⁻¹ are the most influential parameters for the abundance results, either in terms of the current range of uncertainty or in terms of a constant percentage change, or both. Therefore, these parameters should be considered as a research priority to better define the most common range of their values. A better assessment of the other parameters could also greatly reduce the overall uncertainty, as would other information to make the models more realistic. For instance, the proportion of female neophytes (first-time breeders) observed at nesting grounds can provide a direct estimate of A_v and provide useful indications about population trends (e.g. Stokes et al. 2014) that can be used or compared in population models. Abundance estimates at sea by aerial surveys at most of the major foraging grounds will be particularly needed in the future to compare with simulations and to provide trends of the juvenile age classes, which may represent a better abundance index than nest counts. Sea turtle populations consist almost entirely of juveniles which, with some exceptions, cannot be accessed by land. Monitoring, defining conservation strategies, and managing sea turtle populations on the basis of the adult fraction of the populations or its indices (nests) is not realistic, and more effort should be applied to the investigation of demography and abundance (National Research Council 2010).

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