

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/262456021>

# Annual survival probabilities of juvenile loggerhead sea turtles indicate high anthropogenic impact on Mediterranean populations

Article in *Aquatic Conservation Marine and Freshwater Ecosystems* · May 2014

Impact Factor: 2.14 · DOI: 10.1002/aqc.2467

---

CITATION

1

---

READS

123

10 authors, including:



**Paolo Casale**

46 PUBLICATIONS 1,584 CITATIONS

SEE PROFILE



**Caterina Maria Fortuna**

Institute for Environmental Protection and ...

84 PUBLICATIONS 609 CITATIONS

SEE PROFILE



**Brendan John Godley**

University of Exeter

324 PUBLICATIONS 8,416 CITATIONS

SEE PROFILE

## ***Annual survival probabilities of juvenile loggerhead sea turtles indicate high anthropogenic impact on Mediterranean populations***

PAOLO CASALE<sup>a,b,\*</sup>, DANIELA FREGGI<sup>c</sup>, GIOVANNI FURII<sup>d</sup>, CAROLA VALLINI<sup>e</sup>, PASQUALE SALVEMINI<sup>f</sup>, MICHELE DEFLORIO<sup>g</sup>, GIOVANNI TOTARO<sup>d</sup>, STEFANO RAIMONDI<sup>h</sup>, CATERINA FORTUNA<sup>i</sup> and BRENDAN J. GODLEY<sup>b</sup>

<sup>a</sup>*Department of Biology and Biotechnologies 'Charles Darwin', University of Rome 'La Sapienza', 00185 Roma, Italy*

<sup>b</sup>*Centre for Ecology & Conservation, University of Exeter, Cornwall Campus, TR10 9EZ UK*

<sup>c</sup>*Sea Turtle Rescue Centre WWF Italy, Lampedusa, Italy*

<sup>d</sup>*Centro Recupero Tartarughe Marine Legambiente, Manfredonia, Italy*

<sup>e</sup>*A.R.C.H.E', 44100 Ferrara, Italy*

<sup>f</sup>*Panda Molfetta Onlus, 70056 Molfetta, Italy*

<sup>g</sup>*Department of Animal Health and Well-being, University of Bari, Bari, Italy*

<sup>h</sup>*Legambiente Onlus, Direzione Nazionale Ufficio Aree Protette e Biodiversità, 00199 Roma, Italy*

<sup>i</sup>*Italian National Institute for Environmental Protection and Research, 00144 Rome, Italy*

### ABSTRACT

1. One of the major gaps in the knowledge of sea turtle population dynamics is survival probability, in particular of juveniles, which represent the bulk of the population and whose survival has the greatest effect on population growth. One of the major global threats to sea turtles is incidental bycatch, although not all animals die in the process. This is particularly acute for the loggerhead sea turtle (*Caretta caretta*).

2. Here fisheries-dependent monitoring is used to seek insights into patterns of survival at multiple Mediterranean foraging areas: north and south Adriatic, north Ionian, and the Tunisian shelf. Annual survival probability was estimated using the catch curve method. Size data of 2191 loggerhead turtles ranging from 19 to 92 cm curved carapace length were converted to age according to eight age–size curves available from the Mediterranean Sea.

3. The mean annual survival probabilities for the four areas were heterogeneous and ranged between 0.710 and 0.862. Results suggest that the survival probabilities for Mediterranean loggerheads, especially in some areas, are lower than would be expected from a healthy population. This is of particular concern for the Greek rookeries, which appear most affected by anthropogenic mortality occurring in the study areas. This supports the implementation in those areas of measures mitigating the main threats, notably bycatch.

Copyright © 2014 John Wiley & Sons, Ltd.

Received 17 October 2013; Revised 17 March 2014; Accepted 8 April 2014

KEY WORDS: survival probability; *Caretta caretta*; catch curve analysis; conservation; bycatch; Mediterranean

\*Correspondence to: P. Casale, Department of Biology and Biotechnologies 'Charles Darwin', University of Rome 'La Sapienza', 00185 Roma, Italy. Email: paolo.casale@tiscali.it

## INTRODUCTION

Increased fishing effort over the course of the 20th century has produced detrimental effects on marine ecosystems worldwide (Jackson *et al.*, 2001). Part of this syndrome has been rising numbers of incidental captures of non-target species or bycatch (Kelleher, 2005). Bycatch has become a serious conservation challenge for marine megafauna worldwide (Lewison *et al.*, 2004a; Soykan *et al.*, 2008) and represents one of the most serious threats to sea turtle populations (Lewison *et al.*, 2004b; Lewison and Crowder, 2007), which also face additional pressure from many human activities including direct exploitation, pollution and climate change (Lutcavage *et al.*, 1997; Hawkes *et al.*, 2009; Witt *et al.*, 2010; Keller, 2013).

The long life cycle of sea turtles makes identifying effective conservation measures and monitoring their effects difficult. For this reason, models of population dynamics have been employed to assess or predict the status of sea turtle populations under different scenarios (Crouse *et al.*, 1987; Chaloupka and Musick, 1997; Heppell *et al.*, 2003; Bolten *et al.*, 2011). Models often lack empirical estimates of various parameters, and one of the major gaps is survival probability (Heppell *et al.*, 2003), in particular of juveniles that represent the bulk of populations and whose survival has the highest effect on population dynamics (Heppell, 1998). Sea turtles frequent a range of habitats during their life cycle, therefore survival probabilities are expected to vary by species, population, area, and life stage. Although such information is growing, it is still limited to certain populations and life stages of loggerhead turtles (*Caretta caretta*) (Frazer, 1983, 1987; Heppell *et al.*, 1996; Chaloupka and Limpus, 2002; Bjorndal *et al.*, 2003b; Sasso *et al.*, 2006, 2011; Casale *et al.*, 2007c; Sasso and Epperly, 2007; Monk *et al.*, 2011), green turtles (*Chelonia mydas*) (Bjorndal, 1980; Chaloupka, 2002; Bjorndal *et al.*, 2003a; Campbell and Lagueux, 2005; Chaloupka and Limpus, 2005; Koch *et al.*, 2007; Troeng and Chaloupka, 2007; Eguchi *et al.*, 2010; Patricio *et al.*, 2011), hawksbill turtles (*Eretmochelys imbricata*) (Richardson *et al.*, 1999; Bell *et al.*, 2012; Prince and Chaloupka, 2012), Kemp's ridley turtles (*Lepidochelys kempii*) (Caillouet *et al.*, 1995), and leatherback turtles (*Dermochelys coriacea*) (Chua, 1988).

Two methods have been employed to estimate survival probabilities of sea turtles: capture–mark–recapture and catch curve analysis (Heppell *et al.*, 2003). Capture–mark–recapture requires extensive tagging in order to obtain adequate recapture events, especially at foraging grounds. Catch curve analysis requires a large sample of individuals of known age, where the age distribution is representative of the population. It was originally developed for use in fish (Ricker, 1975; Reid, 2009; Gray *et al.*, 2010; Trested and Isely, 2011; Fazli *et al.*, 2012) and has since been used on other taxa (e.g. shrimps: Baker and Minello, 2010; crabs: Diele and Koch, 2010; bivalves: Jones and Neves, 2011), including turtles (Frazer, 1987; National Marine Fisheries Service Southeast Fisheries Science Center, 2001; Bjorndal *et al.*, 2003b; Heppell *et al.*, 2005; Koch *et al.*, 2007).

The loggerhead turtle *Caretta caretta* is the most common sea turtle species in the Mediterranean. The region hosts oceanic and neritic habitats for animals belonging to two regional management units: the Mediterranean and the Atlantic (Wallace *et al.*, 2010). The Mediterranean population has reproductive habitats and main foraging grounds concentrated in the eastern basin but disperse widely throughout the eastern and western basins, both as juveniles and as adults (Casale and Margaritoulis, 2010). The main identified threats to sea turtles in the Mediterranean Sea are degradation of reproductive habitats (Casale and Margaritoulis, 2010 and references therein), incidental catch in fishing gear, collision with boats, and intentional killing (Tomás *et al.*, 2008; Casale *et al.*, 2010; Casale, 2011) that as a whole is considered to be a high level of anthropogenic threat to the Mediterranean regional management unit (Wallace *et al.*, 2011). How the current level of threat affects the Mediterranean loggerhead population is, however, unclear. Although anecdotal information suggests a decline over decadal scales (Casale and Margaritoulis, 2010), the limited information about recent trends is inconclusive (Ilgaz *et al.*, 2007; Turkozan and Yilmaz, 2008; Casale and Margaritoulis, 2010; Margaritoulis *et al.*, 2011; Casale *et al.*, 2012b).

In the Mediterranean, capture–mark–recapture could be used to estimate survival probabilities of

juvenile loggerheads, thanks to a long-term tagging project at foraging areas (Casale *et al.*, 2007c). However, the lack of a size–age relationship has prevented the use of catch curve analysis on Mediterranean loggerheads so far.

Growth curves have recently become available for Mediterranean loggerheads (Casale *et al.*, 2009, 2011a, b; Piovano *et al.*, 2011), together with adequate data sets from major foraging areas, and the present study provides the first application of catch curve analysis in the Mediterranean, with the aim of: (i) contributing to the current knowledge of sea turtle survival probabilities and specifically with estimates about juvenile loggerhead turtles in the Mediterranean, and (ii) comparing survival probabilities at different Mediterranean foraging grounds.

## MATERIALS AND METHODS

Annual survival probability ( $S$ ) of loggerhead sea turtles in the Mediterranean was calculated through the catch curve method (Ricker, 1975). This method analyses frequency distributions of age classes and assumes that (i) the age distribution of the population is stable, (ii) mortality is constant during the sampling period, (iii) mortality is constant among age/size classes considered, and (iv) above a certain age, the age structure of the sample is representative of the population. Assumptions (i) and (ii) are problematic for sea turtle populations, where such information is difficult to obtain or where populations are not stable. As noted above, there is no clear indication regarding a trend of the Mediterranean loggerhead turtle population in recent years. In particular, one of the most important rookeries, at Zakynthos, Greece, showed no significant trend during 19 years (1984–2002; Margaritoulis, 2005). Assumptions (i) and (ii) have been considered as acceptable. Regarding assumption (iii), the present study analysed separately datasets from different areas in which the common habitat, common threats and limited size range of the captured turtles minimize the potential sources of heterogeneity. Regarding assumption (iv), the present study analysed datasets collected only through sampling

methods where the effect of size on catchability is likely to be low, i.e. turtles within a certain size range have the same probability of being captured. The sample was made up of turtles caught incidentally by trawlers and longliners. Trawl nets capture all the animals they encounter and result in them being brought aboard. For large vessels, there is no problem of room on the deck and fishermen collaborating with research programmes are assumed to land turtles independently of their size. Longliners using large hooks for swordfish can capture all turtles over a certain size. However, in contrast with trawlers, longline vessels are relatively small with less room on the deck. Therefore, large turtles may be under-represented in programmes where longline fishermen are just asked to land turtles. For this reason, only longline samples collected by onboard observers were considered. Since our target was the Mediterranean population of loggerhead turtles, the samples analysed were from the eastern Mediterranean only, where the occurrence of individuals from the Atlantic is low (Maffucci *et al.*, 2006; Casale *et al.*, 2008b; Giovannotti *et al.*, 2010) in comparison with the western Mediterranean (Carreras *et al.*, 2011; Clusa *et al.*, 2014).

The selected datasets were from four areas (Figure 1), comprising 2191 loggerhead turtles: Tunisian shelf (TS, bottom trawlers; 2001–2011;  $n = 1261$ ); north Ionian (NI, pelagic longliners; 1999–2000;  $n = 124$ ); south Adriatic (SA, bottom trawlers; 2007–2013;  $n = 635$ ); north Adriatic (NA, midwater trawlers; 2000–2012;  $n = 171$ ). Length data consisted of curved carapace length notch-to-tip (i.e. nuchal scute to longest point of supracaudals; CCL) (Bolten, 1999). The analysis was limited to juveniles because in the Mediterranean adult males start migrating to breeding sites as early as October (Schofield *et al.*, 2010; Casale *et al.*, 2013) and adult females return to foraging grounds as late as October (Zbinden *et al.*, 2011), hence adults are expected to be under-represented at foraging grounds all year round, confounding mortality with migration. Since the average loggerhead female starts breeding at a size slightly smaller than the average size of nesting females (Limpus, 1990), turtles were considered as adults, and excluded from the

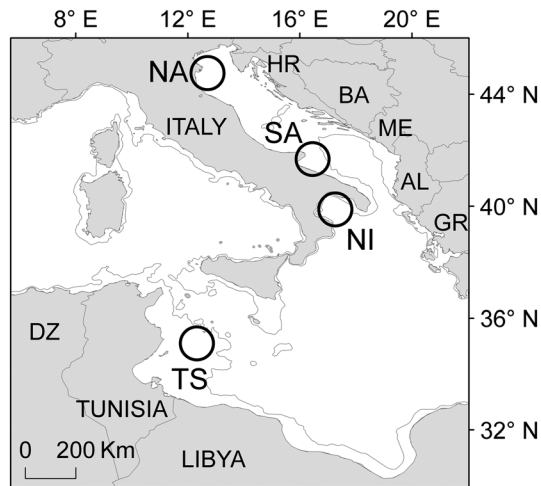


Figure 1. Mediterranean areas of capture (circles) of the loggerhead sea turtles considered in this study: north Adriatic (NA), south Adriatic (SA), north Ionian (NI), Tunisian shelf (TS). The 200 m isobath is delineated. AL, Albania; DZ, Algeria; BA, Bosnia, and Herzegovina; GR, Greece; HR, Croatia; ME, Montenegro.

analysis, if larger than 79.7 cm CCL, which is the mean size of nesting females in the Mediterranean weighted for rookery abundance (number of nests per year) (Table S1 in the Supplementary material). Each of the four samples was analysed separately and age distribution was derived from size distribution as follows. Each turtle was assigned to a 1-year age class (i.e. year 1, 2, 3, etc. of life) on the basis of eight different growth curves available for loggerheads in the Mediterranean, obtained through capture–mark–recapture (CMR), length–frequency analysis (LFA1-2), and skeletochronology (SKEL1-5) (Casale *et al.*, 2009, 2011a, 2011b; Piovano *et al.*, 2011). Thirty-two age distributions resulted from the eight growth curves applied to the samples from the four study areas. For each of these 32 age distributions, the annual survival probability was estimated by a catch curve analysis (Bjorndal *et al.*, 2003b). The natural logarithm of the number of turtles in each age class was plotted against the corresponding age class. In each age distribution, the age class including the highest number of individuals was assumed to be the first age class with full recruitment at the foraging ground with the sampling method used, and younger age classes were excluded from the analysis. A linear regression was fitted to the remaining data and the instantaneous mortality rate ( $Z$ ) was estimated as the descending slope. Survival probability was calculated as  $S = e^{-Z}$ .

For each of the eight age–size relationships an ANCOVA (R Development Core Team, 2013) was conducted, and in case heterogeneity of slopes was detected among the four areas (north Adriatic, south Adriatic, north Ionian, Tunisian shelf), a post-hoc Tukey test was also conducted to detect which pairs were significantly different. These pairs were then also tested for confirmation through pair-wise comparisons of the slopes ( $Z$ , instantaneous mortality rate) as follows (Zar, 1999):

$$t = \frac{Z_1 - Z_2}{s_{Z_1 - Z_2}} = \frac{Z_1 - Z_2}{\sqrt{s_{Z_1}^2 + s_{Z_2}^2}}$$

where  $s_z$  is the standard error of the slope  $Z$ . Significantly different slopes were assessed from  $t$  distribution ( $\alpha = 0.05$ ; two tailed;  $df = n_1 + n_2 - 4$ ).

## RESULTS

Curved carapace lengths (CCL) of all turtles (before selection for the analyses) ranged from 23.5 to 85.0 cm (mean: 55.4; SD: 14.4;  $n = 171$ ) for the north Adriatic, from 21.3 to 92.0 cm (mean: 56.5; SD: 11.9;  $n = 635$ ) for the south Adriatic, from 19.0 to 77.5 cm (mean: 44.2; SD: 11.0;  $n = 124$ ) for the north Ionian, and from 19.0 to 89.0 cm (mean: 53.3; SD: 13.1;  $n = 1261$ ) for the Tunisian shelf (Figure S1 in the Supplementary material). Regression slopes ( $Z$ , instantaneous mortality rate) were calculated for different age intervals, depending on the age–size relationship and area (Figure 2; Table 1). Linear regression had a moderate coefficient of determination  $r^2$  in most age distributions of the north Adriatic. The ANCOVA revealed a significant difference ( $P < 0.001$ ) among the slopes. Slopes ( $Z$ ) of the eight age–size relationships for the south Adriatic were significantly different from one or more of the other three areas (Table 1), indicating a lower survival probability. In some cases, slopes were significantly different between the north Ionian and the Tunisian shelf (Table 1). The mean of the eight estimated annual survival probabilities (Figure 3) was lower for the south Adriatic (mean: 0.710; range: 0.656–0.790), than for the Tunisian shelf (mean: 0.862; range: 0.840–0.904), the north Adriatic (mean: 0.839; range: 0.801–0.891), and the north Ionian (mean: 0.817; range: 0.786–0.885).

SURVIVAL PROBABILITIES OF LOGGERHEAD TURTLES

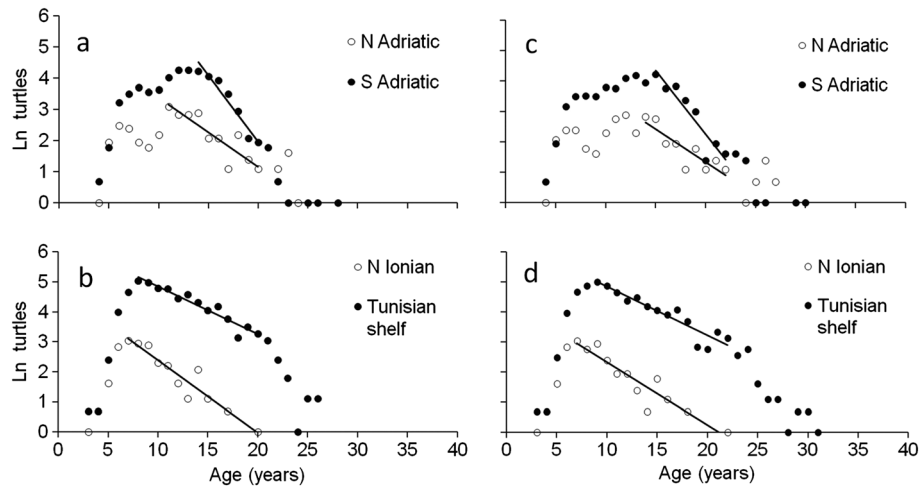


Figure 2. Examples of age distribution of loggerhead turtles ( $\ln$ ) from four Mediterranean areas, converted from size data. Only distributions obtained from the two growth curves with highest coefficients of determination ( $r^2$ ) are shown (see Table 1): SKEL3 (a, b) and SKEL1 (c, d). Regression lines are shown for the age range between the most abundant age class and the age at maturity.

On the basis of the mean value of the coefficients of determination ( $r^2$ ) of the four areas for each age–size relationship, the ranking of fit of the different age–size relationships would be: SKEL3, SKEL1, CMR, SKEL2, LFA1, SKEL4, SKEL5, LFA2 (Table 1). This ranking suggests a better fit of age–size relationships with an estimated  $L^\infty$  and a low age at maturity (e.g. SKEL3, SKEL1, CMR) than age–size relationships with a fixed  $L^\infty$  and a high age at maturity (e.g. LFA2, SKEL5).

## DISCUSSION

This study provides estimates of annual survival probabilities of Mediterranean juvenile loggerheads, which will feed future population dynamics models, and also provides evidence of spatial differences, possibly associated with area-specific anthropogenic threats. The only previous estimate of juvenile survival probability in the Mediterranean Sea (0.73) was obtained through capture–mark–recapture and it was considered an underestimate owing to tag loss (Casale *et al.*, 2007c). If a tag loss of about 0.1 is considered (Casale *et al.*, 2007c), the corrected survival probability of about 0.83 would be similar to the survival probabilities estimated by the present study, with the exception of one area (south Adriatic).

The present data are in the range of estimates available from other loggerhead turtle populations (range 0.410–0.918; Table 2). However, a healthy

population would be characterized by higher survival probabilities, and the highest values known for oceanic juveniles, neritic juveniles and adults are above 0.91 (Table 2). Caution is needed when comparing results obtained from different populations with different methods. Notwithstanding, these results suggest that the survival probabilities of Mediterranean loggerheads, especially in some areas, are somewhat lower than what would be expected from a healthy population. This may be caused by the high bycatch levels in the basin, that represent the most important source of anthropogenic mortality at sea (Casale, 2011) and by other, less studied threats (pollution; Lazar and Gračan, 2011; Lazar *et al.*, 2011).

In the north Ionian, turtles were captured by pelagic longliners and were probably foraging mainly upon pelagic prey. Loggerhead turtles frequent different habitats during their life, with a general tendency to frequent oceanic habitats first followed by neritic habitats. Recruitment to neritic habitats on the Tunisian shelf and the Adriatic from the oceanic area in the north Ionian has previously been inferred in the Mediterranean from tag returns (Casale *et al.*, 2007b). Hence, in the north Ionian, mortality induced by fishing gear (Deflorio *et al.*, 2005) may be confounded by permanent emigration to neritic habitats, possibly resulting in underestimated survival probabilities (Bjorndal *et al.*, 2003b). This would represent a violation of assumption (iv) and makes the

Table 1. Instantaneous mortality rate ( $Z$ ) and annual survival probability ( $S$ ) of loggerhead turtles from four Mediterranean areas, estimated from age distributions obtained through the eight age-size curves available for the Mediterranean Sea and based on capture-mark-recapture (CMR), length-frequency analysis (LFA), and skeletochronology (SKEL). The coefficient of determination ( $r^2$ ) of the linear regression is also provided. The von Bertalanffy growth function parameters  $L_\infty$  (mean asymptotic carapace length) and  $k$  (growth coefficient) are provided for each of the eight growth curves: CMR (Casale *et al.*, 2009), LFA1-2 (Casale *et al.*, 2011b), SKEL1-4 (Casale *et al.*, 2011a), SKEL5 (Piovano *et al.*, 2011). Pairwise significant differences ( $P < 0.05$ ) between  $Z$  values of different areas are indicated by symbols \* or †

	CMR	LFA1	LFA2	SKEL1	SKEL2	SKEL3	SKEL4	SKEL5	Mean
$L_\infty$	95.63	99	99	103.88	99	119.32	99	99	
$k$	0.077	0.066	0.051	0.062	0.066	0.052	0.072	0.042	
Age at 79.7 cm CCL (yrs)	23.4	23.3	29.0	22.9	24.2	20.6	22.2	34.1	
<b>North Adriatic (n = 171)</b>									
Age classes	12-22	14-22	17-27	14-22	14-23	11-20	13-21	12-22	
$Z$	0.185°	0.156°	0.116°	0.216°	0.193°	0.222°	0.199°	0.128°	
$S$	<b>0.831</b>	<b>0.856</b>	<b>0.891</b>	<b>0.806</b>	<b>0.824</b>	<b>0.801</b>	<b>0.819</b>	<b>0.880</b>	<b>0.839</b>
$r^2$	0.840	0.601	0.325	0.756	0.618	0.785	0.508	0.519	0.619
<b>South Adriatic (n = 635)</b>									
Age classes	15-23	14-23	17-28	15-22	13-23	14-20	14-22	20-34	
$Z$	0.383*o	0.348*o+	0.276*o+	0.417*o+	0.312*o+	0.422*o+	0.359*o+	0.236*o+	
$S$	<b>0.682</b>	<b>0.706</b>	<b>0.759</b>	<b>0.659</b>	<b>0.732</b>	<b>0.656</b>	<b>0.699</b>	<b>0.790</b>	<b>0.710</b>
$r^2$	0.793	0.811	0.857	0.866	0.907	0.938	0.892	0.755	0.852
<b>North Ionian (n = 124)</b>									
Age classes	8-22	7-22	6-27	7-22	7-23	7-20	7-21	6-32	
$Z$	0.224	0.207+	0.163+†	0.209+	0.233+‡	0.241+‡	0.222+	0.123+†	
$S$	<b>0.800</b>	<b>0.813</b>	<b>0.849</b>	<b>0.811</b>	<b>0.792</b>	<b>0.786</b>	<b>0.801</b>	<b>0.885</b>	<b>0.817</b>
$r^2$	0.825	0.858	0.861	0.882	0.852	0.907	0.880	0.832	0.862
<b>Tunisian shelf (n = 1261)</b>									
Age classes	8-23	7-23	8-28	9-22	9-23	8-20	9-22	11-34	
$Z$	0.169*	0.151*	0.120*‡	0.161*	0.155*‡	0.158*‡	0.172*	0.101*	
$S$	<b>0.844</b>	<b>0.860</b>	<b>0.887</b>	<b>0.851</b>	<b>0.856</b>	<b>0.854</b>	<b>0.842</b>	<b>0.904</b>	<b>0.862</b>
$r^2$	0.890	0.882	0.878	0.877	0.882	0.927	0.848	0.833	0.877
mean $r^2$	0.837	0.788	0.731	0.845	0.815	0.889	0.782	0.735	

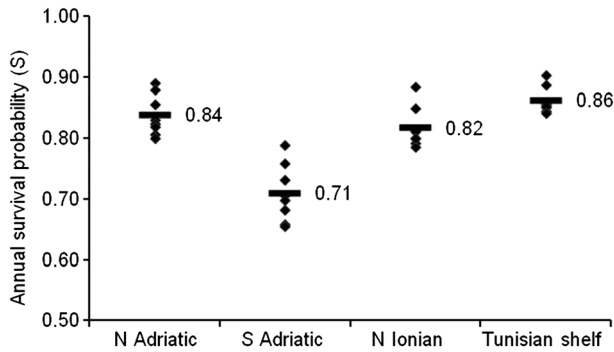


Figure 3. Annual survival probability ( $S$ ) of loggerhead turtles from four Mediterranean areas, estimated from age distributions obtained through the eight age–size curves available for the Mediterranean Sea and based on capture–mark–recapture (Casale *et al.*, 2009), length–frequency analysis (Casale *et al.*, 2011b), and skeletochronology (Casale *et al.*, 2011a; Piovano *et al.*, 2011). Average values for each area are given and indicated by solid bars. See Table 1 for complete results.

Table 2. Annual survival probabilities of loggerhead sea turtles per area and life stage (rounded to the third decimal place). Source: a, Heppell *et al.* (1996); b, Chaloupka and Limpus (2002); c, Frazer (1983); d, Monk *et al.* (2011); e, Sasso *et al.* (2011); f, National Marine Fisheries Service Southeast Fisheries Science Center (2001); g, Sasso *et al.* (2006); h, Frazer (1987); i, Bjorndal *et al.* (2003b); j, Sasso and Epperly (2007); k, Casale *et al.* (2007c)

Life stage	Area	Survival	Source
Adult	Australia (Heron Reef)	0.910	a
	Australia (Mon Repos)	0.782	a
	Australia	0.875	b
	South-east USA	0.809	c
	North Carolina, USA	0.850	d
	Florida, USA	0.410–0.600	e
Neritic juvenile	Australia	0.885	a
	Australia	0.830	a
	Australia	0.918	b
	South-east USA	0.893	f
	North Carolina, USA	0.810	g
	South-east USA	0.700	h
Oceanic juvenile	South-east USA	0.680	h
	Azores	0.911	i
	Atlantic USA	0.814	j
Juvenile	Mediterranean	0.730	k
	Mediterranean	0.710–0.862	present study

interpretation of results from this area more difficult than in other areas. In contrast, the other three areas are neritic habitats, and can be assumed to be relatively final recruitment areas. Furthermore, satellite tracking has revealed a certain degree of fidelity by juvenile loggerhead turtles foraging in these areas (Casale *et al.*, 2012a, c; Casale, unpubl. data) and this suggests that the observed survival probabilities are area-specific, at least in part, and therefore are affected by local anthropogenic

sources of mortality. High bycatch levels have been recorded in two of these areas, the Tunisian shelf (Casale *et al.*, 2007a; Jribi *et al.*, 2007, 2008; Echwikhi *et al.*, 2010, 2012) and the north Adriatic (Lazar and Tvrtković, 1995; Casale *et al.*, 2004; Fortuna *et al.*, 2010), and represent the most likely explanation for the reduced survival probability suggested by the present results. The third neritic area, the south Adriatic, was only recently recognized as an important foraging area, where loggerheads are incidentally captured in high numbers (Casale *et al.*, 2012d). The particularly low survival probabilities estimated in this area, significantly lower than the other two neritic areas, highlights the need for specific investigation on the mortality induced by fishing gear in this area that has not yet been fully quantified.

It is important to relate the survival probabilities and the threats occurring in these areas to the rookeries of origin of the turtles. Genetic markers indicate that the main origin of turtles foraging in the north Adriatic is Greece and to a lesser extent Turkey (Giovannotti *et al.*, 2010; Garofalo *et al.*, 2013) supporting previous information from tag returns of adult females nesting in Greece (Lazar *et al.*, 2004; Zbinden *et al.*, 2008). A similar situation probably occurs in the south Adriatic, although no information is available from this area yet. The north Ionian is probably a developmental area for loggerheads born in the adjacent Greek rookeries, as suggested by dispersal models (Casale and Mariani, 2014) and by the small turtles found stranded in that area (Casale *et al.*, 2010), and genetic markers indicate that it is also frequented by turtles from Turkey (Garofalo *et al.*, 2013). The Tunisian shelf is frequented by turtles from several Mediterranean rookeries and also by some Atlantic turtles. Recent information from genetic markers (Garofalo *et al.*, 2013) and satellite tracking (Casale *et al.*, 2013) highlights the importance of this area for turtles from Libya, and to a lesser extent from Greece, as previously indicated by tag returns (Margaritoulis *et al.*, 2003) and satellite tracking (Zbinden *et al.*, 2011). Therefore, the observed reduced survival probabilities, and especially those frequenting the Adriatic Sea, may imply that Greek rookeries are particularly affected by anthropogenic mortality occurring in these areas.



Size data indicate that full recruitment occurs at a different size in the sampled neritic areas. Although benthic feeding by small turtles was observed both in the Adriatic Sea (Lazar *et al.*, 2008) and in the Tunisian shelf (Casale *et al.*, 2008a), the present results provide evidence that early recruitment to neritic habitats is more common in the Tunisian shelf than in the Adriatic Sea.

Identifying reliable methods for estimating demographic parameters is considered a priority for sea turtle conservation and management (Hamann *et al.*, 2010). Although catch-curve-analysis is based on several assumptions about mortality and on the knowledge of an age-size relationship, data are relatively simple to obtain in comparison with capture-mark-recapture which requires extensive tagging and long time series. In the Mediterranean, further studies on survival probabilities are desirable, and intensive in-water sampling should be conducted at major foraging areas. In-water sampling can be accomplished either through direct capture (Rees *et al.*, 2013) or by taking advantage of incidental catches by fishing gears, in particular trawlers, as in the present study. Intensive in-water sampling can greatly reduce the data collection period for catch-curve-analysis and hence can resolve one of its most important assumptions, i.e. stable population structure during the sampling period. Intensive in-water sampling can also provide data for capture-mark-recapture if associated with tagging and if extended for several years, and can also contribute to catch-curve-analysis by providing further age-size relationships. Furthermore, monitoring possible change of survival probability across time, in index areas, will greatly inform assessments of conservation status and help parameterize the magnitude of local threats. Ultimately, strong survival probability data will support the implementation, at specific areas, of conservation measures to reduce the impact of threats on the populations, for instance technical modifications of fishing gears to reduce bycatch levels (Lucchetti and Sala, 2010) or onboard best practice to reduce post-release mortality rates (Gerosa and Aureggi, 2001).

#### ACKNOWLEDGEMENTS

We are greatly indebted to all the fishermen who collaborated with this study and to the volunteers

who supported WWF Italy's Sea Turtle Centre in Lampedusa and the A.R.C.H.E. project. Special thanks to Michele and Ciro Conoscitore and all the fishermen of Manfredonia for their help on the south Adriatic part of the study. We also thank the Italian Forestry Department (Corpo Forestale dello Stato), the Harbour Offices and Consorzio Nazionale Interuniversitario per le Scienze del Mare (CoNISMa) for their support, as well as the Province of Ferrara and Banca Popolare di Milano that supported part of our activities. A part of the data collected in the northern Adriatic Sea between 2006 and 2012 were obtained within the framework of research and monitoring activities related to the Italian implementation of the Regulation (EC) n. 812/2004. These activities were funded by the General Directorate of Maritime Fisheries of the Italian Ministry of Agriculture, Food and Forestry. We thank an anonymous reviewer and the Editor for their helpful comments.

#### REFERENCES

- Baker R, Minello T. 2010. Growth and mortality of juvenile white shrimp *Litopenaeus setiferus* in a marsh pond. *Marine Ecology-Progress Series* **413**: 95–104.
- Bell I, Schwarzkopf L, Manicom C. 2012. High survivorship of an annually decreasing aggregation of hawksbill turtles, *Eretmochelys imbricata*, found foraging in the northern Great Barrier Reef. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**: 673–682.
- Bjorndal KA. 1980. Demography of the breeding population of the green turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. *Copeia* **1980**: 525–530.
- Bjorndal KA, Bolten AB, Chaloupka MY. 2003a. Survival probability estimates for immature green turtles *Chelonia mydas* in the Bahamas. *Marine Ecology-Progress Series* **252**: 273–281.
- Bjorndal KA, Bolten AB, Martins HR. 2003b. Estimates of survival probabilities for oceanic-stage loggerhead sea turtles (*Caretta caretta*) in the North Atlantic. *Fishery Bulletin* **101**: 732–736.
- Bolten AB. 1999. Techniques for measuring sea turtles. In *Research and Management Techniques for the Conservation of Sea Turtles*, Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds). IUCN/SSC Marine Turtle Specialist Group: Washington, DC; 110–114.
- Bolten AB, Crowder LB, Dodd MG, MacPherson SL, Musick JA, Schroeder BA, Witherington BE, Long KJ, Snover ML. 2011. Quantifying multiple threats to endangered species: an example from loggerhead sea turtles. *Frontiers in Ecology and the Environment* **9**: 295–301.
- Caillouet CWJ, Fontaine CT, Manzella-Tirpack SA, Shaver DJ. 1995. Survival of head-started Kemp's ridley sea turtles (*Lepidochelys kempii*) released into the Gulf of

- Mexico or adjacent bays. *Chelonian Conservation and Biology* **1**: 285–292.
- Campbell CL, Lagueur CJ. 2005. Survival probability estimates for large juvenile and adult green turtles (*Chelonia mydas*) exposed to an artisanal marine turtle fishery in the western Caribbean. *Herpetologica* **61**: 91–103.
- Carreras C, Pascual M, Cardona L, Marco A, Bellido JJ, Castillo JJ, Tomas J, Raga JA, Sanfelix M, Fernandez G, et al. 2011. Living together but remaining apart: Atlantic and Mediterranean loggerhead sea turtles (*Caretta caretta*) in shared feeding grounds. *Journal of Heredity* **102**: 666–677.
- Casale P. 2011. Sea turtle by-catch in the Mediterranean. *Fish and Fisheries* **12**: 299–316.
- Casale P, Margaritoulis D. 2010. *Sea Turtles in the Mediterranean: Distribution, Threats and Conservation Priorities*. IUCN: Gland, Switzerland.
- Casale P, Mariani P. 2014. The first ‘lost year’ of Mediterranean sea turtles: dispersal patterns indicate subregional management units for conservation. *Marine Ecology-Progress Series* **498**: 263–274.
- Casale P, Laurent L, De Metrio G. 2004. Incidental capture of marine turtles by the Italian trawl fishery in the north Adriatic Sea. *Biological Conservation* **119**: 287–295.
- Casale P, Cattarino L, Freggi D, Rocco M, Argano R. 2007a. Incidental catch of marine turtles by Italian trawlers and longliners in the central Mediterranean. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**: 686–701.
- Casale P, Freggi D, Basso R, Vallini C, Argano R. 2007b. A model of area fidelity, nomadism, and distribution patterns of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea. *Marine Biology* **152**: 1039–1049.
- Casale P, Mazaris AD, Freggi D, Basso R, Argano R. 2007c. Survival probabilities of loggerhead sea turtles (*Caretta caretta*) estimated from capture-mark-recapture data in the Mediterranean Sea. *Scientia Marina* **71**: 365–372.
- Casale P, Abbate G, Freggi D, Conte N, Oliverio M, Argano R. 2008a. Foraging ecology of loggerhead sea turtles *Caretta caretta* in the central Mediterranean sea: evidence for a relaxed life history model. *Marine Ecology-Progress Series* **372**: 265–276.
- Casale P, Freggi D, Gratton P, Argano R, Oliverio M. 2008b. Mitochondrial DNA reveals regional and interregional importance of the central Mediterranean African shelf for loggerhead sea turtles (*Caretta caretta*). *Scientia Marina* **72**: 541–548.
- Casale P, Mazaris AD, Freggi D, Vallini C, Argano R. 2009. Growth rates and age at adult size of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea, estimated through capture-mark-recapture records. *Scientia Marina* **73**: 589–595.
- Casale P, Affronte M, Insacco G, Freggi D, Vallini C, d’Astore PP, Basso R, Paolillo G, Abbate G, Argano R. 2010. Sea turtle strandings reveal high anthropogenic mortality in Italian waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**: 611–620.
- Casale P, Conte N, Freggi D, Cioni C, Argano R. 2011a. Age and growth determination by skeletochronology in loggerhead sea turtles (*Caretta caretta*) from the Mediterranean Sea. *Scientia Marina* **75**: 197–203.
- Casale P, Mazaris AD, Freggi D. 2011b. Estimation of age at maturity of loggerhead sea turtles *Caretta caretta* in the Mediterranean using length–frequency data. *Endangered Species Research* **13**: 123–129.
- Casale P, Affronte M, Scaravelli D, Lazar B, Vallini C, Luschi P. 2012a. Foraging grounds, movement patterns and habitat connectivity of juvenile loggerhead turtles (*Caretta caretta*) tracked from the Adriatic Sea. *Marine Biology* **159**: 1527–1535.
- Casale P, Aprea A, Defflorio M, De Metrio G. 2012b. Increased by-catch rates in the Gulf of Taranto, Italy, in 20 years: a clue about sea turtle population trends? *Chelonian Conservation and Biology* **11**: 239–243.
- Casale P, Broderick AC, Freggi D, Mencacci R, Fuller WJ, Godley BJ, Luschi P. 2012c. Long-term residence of juvenile loggerhead turtles to foraging grounds: a potential conservation hotspot in the Mediterranean. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**: 144–154.
- Casale P, Simone G, Conoscitore C, Conoscitore M, Salvemini P. 2012d. The Gulf of Manfredonia: a new neritic foraging area for loggerhead sea turtles in the Adriatic Sea. *Acta Herpetologica* **7**: 1–12.
- Casale P, Freggi D, Cinà A, Rocco M. 2013. Spatio-temporal distribution and migration of adult male loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea: further evidence of the importance of neritic habitats off North Africa. *Marine Biology* **160**: 703–718.
- Chaloupka M. 2002. Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modelling* **148**: 79–109.
- Chaloupka MY, Limpus CJ. 2002. Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Marine Biology* **140**: 267–277.
- Chaloupka M, Limpus C. 2005. Estimates of sex- and age-class-specific survival probabilities for a southern Great Barrier Reef green sea turtle population. *Marine Biology* **146**: 1251–1261.
- Chaloupka MY, Musick JA. 1997. Age, growth, and population dynamics. In *The Biology of Sea Turtles*, Lutz PL, Musick JA (eds). CRC Marine Science Series, CRC Press: Boca Raton, FL; 233–276.
- Chua TH. 1988. Nesting population and frequency of visits in *Dermochelys coriacea* in Malaysia. *Journal of Herpetology* **22**: 192–207.
- Clusa M, Carreras C, Pascual M, Gaughran S, Piovano S, Giacoma C, Fernández G, Levy Y, Tomás J, Raga J, et al. 2014. Fine-scale distribution of juvenile Atlantic and Mediterranean loggerhead turtles (*Caretta caretta*) in the Mediterranean Sea. *Marine Biology* **161**: 209–519.
- Crouse DT, Crowder LB, Caswell H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**: 1412–1423.
- Defflorio M, Aprea A, Corriero A, Santamaria N, De Metrio G. 2005. Incidental captures of sea turtles by swordfish and albacore longlines in the Ionian sea. *Fisheries Science* **71**: 1010–1018.
- Diele K, Koch V. 2010. Growth and mortality of the exploited mangrove crab *Ucides cordatus* (Ucididae) in N-Brazil. *Journal of Experimental Marine Biology and Ecology* **395**: 171–180.
- Echwikhi K, Jribi I, Bradai MN, Bouain A. 2010. Gillnet fishery - loggerhead turtle interactions in the Gulf of Gabes, Tunisia. *Herpetological Journal* **20**: 25–30.
- Echwikhi K, Jribi I, Bradai MN, Bouain A. 2012. Interactions of loggerhead turtle with bottom longline fishery in the Gulf

- of Gabès, Tunisia. *Journal of the Marine Biological Association of the United Kingdom* **92**: 853–858.
- Eguchi T, Seminoff JA, LeRoux RA, Dutton PH, Dutton DL. 2010. Abundance and survival rates of green turtles in an urban environment: coexistence of humans and an endangered species. *Marine Biology* **157**: 1869–1877.
- Fazli H, Daryanabard GR, Abdolmaleki S, Bandani GA. 2012. Stock assessment and management implications of golden grey mullet (*Liza aurata* Risso, 1810) in Iranian waters of the Caspian Sea. *Journal of Applied Ichthyology* **29**: 431–436.
- Fortuna CM, Vallini C, Filidei E, Ruffino M, Consalvo I, Di Muccio S, Gion C, Scacco U, Tarulli E, Giovanardi O, et al. 2010. By-catch of cetaceans and other species of conservation concern during pair trawl fishing operations in the Adriatic Sea (Italy). *Chemistry and Ecology* **26**: 65–76.
- Frazer NB. 1983. Survivorship of adult female loggerhead sea turtles, *Caretta caretta*, nesting on Little Cumberland Island, Georgia, USA. *Herpetologica* **39**: 436–447.
- Frazer NB. 1987. Preliminary estimates of survivorship for wild juvenile loggerhead sea turtles (*Caretta caretta*). *Journal of Herpetology* **21**: 232–235.
- Garofalo L, Mastrogiacomo A, Casale P, Carlini R, Eleni C, Freggi D, Gelli D, Knittweis L, Mifsud C, Mingozi T, et al. 2013. Genetic characterization of central Mediterranean stocks of the loggerhead turtle (*Caretta caretta*) using mitochondrial and nuclear markers, and conservation implications. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 868–884.
- Gerosa G, Aureggi M. 2001. *Sea Turtle Handling Guidebook for Fishermen*. RAC/SPA, UNEP: Tunis.
- Giovannotti M, Franzellitti S, Cerioni PN, Fabbri E, Guccione S, Vallini C, Tinti F, Caputo V. 2010. Genetic characterization of loggerhead turtle (*Caretta caretta*) individuals stranded and caught as bycatch from the North-Central Adriatic Sea. *Amphibia - Reptilia* **31**: 127–133.
- Gray CA, Ives MC, Macbeth WG, Kendall BW. 2010. Variation in growth, mortality, length and age compositions of harvested populations of the herbivorous fish *Girella tricuspidata*. *Journal of Fish Biology* **76**: 880–899.
- Hamann M, Godfrey MH, Seminoff JA, Arthur K, Barata PCR, Bjorndal KA, Bolten AB, Broderick A, Campbell LM, Carreras C, et al. 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research* **11**: 245–269.
- Hawkes LA, Broderick AC, Godfrey MH, Godley BJ. 2009. Climate change and marine turtles. *Endangered Species Research* **7**: 137–154.
- Heppell SS. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* **1998**: 367–375.
- Heppell SS, Limpus CJ, Crouse DT, Frazer NB, Crowder LB. 1996. Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. *Wildlife Research* **23**: 143–159.
- Heppell SS, Snover ML, Crowder LB. 2003. Sea turtle population ecology. In *The Biology of Sea Turtles*. Volume II. Lutz PL, Musick JA, Wyneken J (eds). CRC Marine Biology Series, CRC Press: Boca Raton, FL; 275–306.
- Heppell SS, Crouse DT, Crowder LB, Epperly SP, Gabriel W, Henwood T, Marquez R, Thompson NB. 2005. A population model to estimate recovery time, population size, and management impacts on Kemp's ridley sea turtles. *Chelonian Conservation and Biology* **4**: 767–773.
- Ilgaz Ç, Türkozan O, Özdemir A, Kaska Y, Stachowitsch M. 2007. Population decline of loggerhead turtles: two potential scenarios for Fethiye beach, Turkey. *Biodiversity and Conservation* **16**: 1027–1037.
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629–638.
- Jones JW, Neves RJ. 2011. Influence of life-history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**: 57–73.
- Jribi I, Bradai MN, Bouain A. 2007. Impact of trawl fishery on marine turtles in the Gulf of Gabes, Tunisia. *Herpetological Journal* **17**: 110–114.
- Jribi I, Echwikhi K, Bradai MN, Bouain A. 2008. Incidental capture of sea turtles by longlines in the Gulf of Gabes (South Tunisia): a comparative study between bottom and surface longlines. *Scientia Marina* **72**: 337–342.
- Kelleher K. 2005. *Discards in the World's Marine Fisheries. An Update*. FAO: Rome.
- Keller JM. 2013. Exposure to and effects of persistent organic pollutants. In *The biology of sea turtles*. Volume III. Wyneken J, Lohmann KJ, Musick JA (eds). CRC Press: Boca Raton, FL; 285–328.
- Koch V, Brooks LB, Nichols WJ. 2007. Population ecology of the green/black turtle (*Chelonia mydas*) in Bahia Magdalena, Mexico. *Marine Biology* **153**: 35–46.
- Lazar B, Gračan R. 2011. Ingestion of marine debris by loggerhead sea turtles, *Caretta caretta*, in the Adriatic Sea. *Marine Pollution Bulletin* **62**: 43–47.
- Lazar B, Tvrtković N. 1995. Marine turtles in the eastern part of the Adriatic sea: preliminary research. *Natura Croatica* **4**: 59–74.
- Lazar B, Margaritoulis D, Tvrtkovic N. 2004. Tag recoveries of the loggerhead sea turtle *Caretta caretta* in the eastern Adriatic Sea: implications for conservation. *Journal of the Marine Biological Association of the United Kingdom* **84**: 475–480.
- Lazar B, Gračan R, Zavodnik D, Tvrtkovic N. 2008. Feeding ecology of pelagic loggerhead turtles, *Caretta caretta*, in the northern Adriatic Sea: proof of an early ontogenetic habitat shift. In *Twenty-fifth Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Tech. Memorandum NMFS-SEFSC-582.
- Lazar B, Maslov L, Romanic SH, Gračan R, Krauthacker B, Holcer D, Tvrtkovic N. 2011. Accumulation of organochlorine contaminants in loggerhead sea turtles, *Caretta caretta*, from the eastern Adriatic Sea. *Chemosphere* **82**: 121–129.
- Lewis RL, Crowder LB. 2007. Putting longline bycatch of sea turtles into perspective. *Conservation Biology* **21**: 79–86.
- Lewis RL, Crowder LB, Read AJ, Freeman SA. 2004a. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* **19**: 598–604.
- Lewis RL, Freeman SA, Crowder LB. 2004b. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters* **7**: 221–231.
- Limpus CJ. 1990. Puberty and first breeding in *Caretta caretta*. In *Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum NMFS-SEFSC-278: 81–83.
- Lucchetti A, Sala A. 2010. An overview of loggerhead sea turtle (*Caretta caretta*) bycatch and technical mitigation measures in the Mediterranean Sea. *Reviews in Fish Biology and Fisheries* **20**: 141–161.

- Lutcavage ME, Plotkin P, Witherington BE, Lutz PL. 1997. Human impacts on sea turtle survival. In *The Biology of Sea Turtles*, Lutz PL, Musick JA (eds). CRC Press: Boca Raton, FL; 387–409.
- Maffucci F, Kooistra W, Bentivegna F. 2006. Natal origin of loggerhead turtles, *Caretta caretta*, in the neritic habitat off the Italian coasts, Central Mediterranean. *Biological Conservation* **127**: 183–189.
- Margaritoulis D. 2005. Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. *Chelonian Conservation and Biology* **4**: 916–929.
- Margaritoulis D, Argano R, Baran I, Bentivegna F, Bradai MN, Caminas JA, Casale P, De Metrio G, Demetropoulos A, Gerosa G, et al. 2003. Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In *Biology and Conservation of Loggerhead Sea Turtles*, Bolten AB, Witherington B (eds). Smithsonian Institution Press: Washington; 175–198.
- Margaritoulis D, Rees AF, Dean CJ, Riggall T. 2011. Reproductive data of loggerhead turtles in Laganas Bay, Zakynthos Island, Greece, 2003–2009. *Marine Turtle Newsletter* **131**: 2–6.
- Monk MH, Berkson J, Rivalan P. 2011. Estimating demographic parameters for loggerhead sea turtles using mark-recapture data and a multistate model. *Population Ecology* **53**: 165–174.
- National Marine Fisheries Service Southeast Fisheries Science Center. 2001. Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles of the Western North Atlantic. US Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-455.
- Patricio AR, Velez-Zuazo X, Diez CE, Van Dam R, Sabat AM. 2011. Survival probability of immature green turtles in two foraging grounds at Culebra, Puerto Rico. *Marine Ecology-Progress Series* **440**: 217–227.
- Piovano S, Clusa M, Carreras C, Giacoma C, Pascual M, Cardona L. 2011. Different growth rates between loggerhead sea turtles (*Caretta caretta*) of Mediterranean and Atlantic origin in the Mediterranean Sea. *Marine Biology* **158**: 2577–2587.
- Prince RIT, Chaloupka M. 2012. Estimating demographic parameters for a critically endangered marine species with frequent reproductive omission: hawksbill turtles nesting at Varanus Island, Western Australia. *Marine Biology* **159**: 355–363.
- R Development Core Team. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna, Austria.
- Rees AF, Margaritoulis D, Newman R, Riggall TE, Tsaros P, Zbinden JA, Godley BJ. 2013. Ecology of loggerhead marine turtles *Caretta caretta* in a neritic foraging habitat: movements, sex ratios and growth rates. *Marine Biology* **160**: 519–529.
- Reid SM. 2009. Age, growth and mortality of black redbhorse (*Moxostoma duquesnei*) and shorthead redbhorse (*M. macrolepidotum*) in the Grand River, Ontario. *Journal of Applied Ichthyology* **25**: 178–183.
- Richardson JJ, Bell R, Richardson TH. 1999. Population ecology and demographic implications drawn from an 11-year study of nesting hawksbill turtles, *Eretmochelys imbricata*, at Jumby Bay, Long Island, Antigua, West Indies. *Chelonian Conservation and Biology* **3**: 244–250.
- Ricker W. 1975. *Computation and Interpretation of Biological Statistics of Fish Populations*. Canadian Department of the Environment Fisheries and Marine Service Bulletin: Ottawa.
- Sasso CR, Epperly SP. 2007. Survival of pelagic juvenile loggerhead turtles in the open ocean. *Journal of Wildlife Management* **71**: 1830–1835.
- Sasso CR, Braun-McNeill J, Avens L, Epperly SP. 2006. Effects of transients on estimating survival and population growth in juvenile loggerhead turtles. *Marine Ecology-Progress Series* **324**: 287–292.
- Sasso CR, Epperly SP, Johnson C. 2011. Annual survival of loggerhead sea turtles (*Caretta caretta*) nesting in peninsular Florida: a cause for concern. *Herpetological Conservation and Biology* **6**: 443–448.
- Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA, Hays GC. 2010. Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. *Diversity and Distributions* **16**: 840–853.
- Soykan CU, Moore JE, Zydelski R, Crowder LB, Safina C, Lewison RL. 2008. Why study bycatch? An introduction to the Theme Section on fisheries bycatch. *Endangered Species Research* **5**: 91–102.
- Tomás J, Gosalbes P, Raga JA, Godley BJ. 2008. Bycatch of loggerhead sea turtles: insights from 14 years of stranding data. *Endangered Species Research* **5**: 161–169.
- Trested DG, Isely JJ. 2011. Age, growth, mortality, and abundance of lake sturgeon in the Grasse River, New York, USA. *Journal of Applied Ichthyology* **27**: 13–19.
- Troeng S, Chaloupka M. 2007. Variation in adult annual survival probability and remigration intervals of sea turtles. *Marine Biology* **151**: 1721–1730.
- Turkozian O, Yilmaz C. 2008. Loggerhead Turtles, *Caretta caretta*, at Dalyan Beach, Turkey: nesting Activity (2004–2005) and 19-year Abundance Trend (1987–2005). *Chelonian Conservation and Biology* **7**: 178–187.
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM, Bolten AB, Chaloupka MY, Hutchinson BJ, Abreu-Grobois FA, Amorcho D, Bjorndal KA, et al. 2010. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* **5**: e15465.
- Wallace BP, DiMatteo AD, Bolten AB, Chaloupka MY, Hutchinson BJ, Abreu-Grobois FA, Mortimer JA, Seminoff JA, Amorcho D, Bjorndal KA, et al. 2011. Global conservation priorities for marine turtles. *PLoS ONE* **6**: e24510.
- Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC. 2010. Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *Journal of Experimental Biology* **213**: 901–911.
- Zar JH. 1999. *Biostatistical Analysis*, 4th edn. Prentice-Hall Inc.: Upper Saddle River, New Jersey.
- Zbinden JA, Aebischer A, Margaritoulis D, Arlettaz R. 2008. Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. *Marine Biology* **153**: 899–906.
- Zbinden JA, Bearhop S, Bradshaw P, Gill B, Margaritoulis D, Newton J, Godley BJ. 2011. Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Marine Ecology-Progress Series* **421**: 291–302.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.