ORIGINAL PAPER

Growth rates and age at maturity of Mediterranean loggerhead sea turtles estimated from a single-population foraging ground

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Abstract

In sea turtles, somatic growth rates and Age at Sexual Maturity (ASM) are important parameters for investigating population dynamics. Moreover, ASM informs on the time lag needed to observe the effects of past environmental variables, threats and conservation measures acting at nesting beaches on future numbers of clutches or nesting females, that are the most monitored indices. Assessing ASM of mixed populations that share the same foraging areas is difficult, as in the case of the Mediterranean Sea that is frequented by turtles originating from both the Mediterranean and the Atlantic. Here we investigated growth rates of loggerhead sea turtles (*Caretta caretta*) foraging in the Adriatic Sea, known to be frequented only by individuals of Mediterranean origin. Capture–mark–recapture records of 79 turtles provided growth rates ranging from – 1.1 to 9.6 cm yr^{-1} which were analyzed through Generalized Additive Models. When integrated with previous data on growth rates in the first years of life, results indicate a non-monotonic growth curve, likely due to an ontogenetic shift from oceanic to neritic areas. Using an integration equation, we estimated mean ASM to be 29.5 or 25.0 year based on mean nester size in Greece (83.4 cm curved carapace length, CCL) or across the Mediterranean (79.7 cm CCL), respectively. Growth rates and size-at-age are similar to the Atlantic population, but Mediterranean turtles mature earlier at a smaller size. The heterogenous growth rates and ASM reported so far in the Mediterranean are probably due, at least in part, to different foraging areas.

Keywords Adriatic Sea · Capture–mark–recapture · *Caretta* · Mediterranean Sea

Responsible Editor: L. Avens .

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Introduction

Understanding the anthropogenic impact on populations of threatened species requires adequate knowledge of population dynamics, which represents a scientific challenge. This includes sea turtles, since their cryptic and long life hinders access to individuals and data collection. Somatic growth rate is one of the fundamental parameters needed to assess population dynamics as it reflects variations in the status of the population and its surrounding environment (Bjorndal et al. 2017; Marn et al. 2017a, b), which in a changing climate makes sea turtles important bio-indicators. Growth rates are used in the estimation of length of life stages and Age at Sexual Maturity (ASM; Avens and Snover 2013; Stubbs et al. 2019). These parameters allow investigation of population status through models, that are often the only tools available to understand how perturbations in vital rates affect population dynamics (Casale and Heppell 2016; Stubbs et al. 2020). An up to date and more precise assessment of ASM has important implications for

conservation and management. For instance, ASM represents the time lag needed to observe changes in the number of clutches or nesting females (the most monitored population index for sea turtles) due to variations in numbers of hatchlings produced in the past because of environmental perturbations, threats, and conservation measures. In general, knowing the generation length is crucial especially in long lived animals with a delayed response to threats. Moreover, by providing the number of juvenile cohorts in a population, ASM can help to estimate abundance of juveniles, which are a less studied life-stage because of logistic constraints yet constitute the majority of a sea turtle population (Casale and Heppell 2016).

Growth patterns and ASM in sea turtles have high intra- and inter-specific variability, being influenced by continuously changing environmental characteristics (Diez and van Dam 2002; Hawkes et al. 2014) and genetic profiles (Heppell et al. 2003), as well as migration distances (Stokes et al. 2006) or human impact (Casale et al. 2011a; Eguchi et al. 2012). For this reason, ASM estimates bear a great degree of variability. North West Atlantic and West Indian populations of loggerhead turtles have similar ASM with an average, respectively, at 36.6 and 36.2 years (Tucek et al. 2014; Avens et al. 2015), both higher compared to West and East Pacific turtles average of 25 and 29 years, respectively (Limpus 2008; Turner Tomaszewicz et al. 2015). Despite the age differences, all these populations share a similar Size at Sexual Maturity (SSM) > 91 cm CCL and therefore they have different growth rates, possibly due to the quality of feeding grounds and/or genetics.

Compared to other loggerhead populations throughout the world, Mediterranean loggerhead turtles (*Caretta caretta*) are the smallest at all life stages (Marn et al. 2017a), including adults (Tiwari and Bjorndal 2000). This may be due to a selective pressure for lower ASM or to a slower growth due to a suboptimal environment. Understanding factors that drive differences in growth and ASM has interesting theoretical and conservation implications. For instance, the Mediterranean was colonized by the Atlantic loggerhead population some 10,000 years ago (Bowen and Karl 2007). During the same time period, human expansion throughout the Mediterranean basin (Coll et al. 2010) altered the environment and affected species composition in this region. Mediterranean sea turtles are threatened by one of the highest fishery interaction intensity worldwide (Lewison et al. 2014). Moreover, the Mediterranean is characterized by high salinity and low productivity and this generally suboptimal environment is often considered as a main cause driving the onset of maturity at a smaller size for the Mediterranean population (Marn et al. 2019). The combination of suboptimal habitat and high levels of anthropogenic stressors has likely affected population dynamics and ASM over time.

Previous studies on loggerhead growth rates and ASM in the Mediterranean included turtles that were sampled in several areas, including Sicily Channel, the Tyrrhenian Sea, the Adriatic Sea and the Ionian Sea, which may include individuals of Atlantic or Mediterranean origin (Casale et al. 2009b, 2011a, b; Guarino et al. 2020). Piovano et al. (2011) sampled turtles in similar areas but attempted to differentiate individuals belonging to the two populations through genetic markers. Within the Mediterranean, nesting females using the major sites are reported to have high variability in size. While females nesting in Cyprus, Libya and Turkey have a similar size, Greek nesters are ca. 5–10 cm larger in average (Casale et al. 2018). This implies that there must be some underlying condition in these populations that that is driving these differences but has yet to be investigated, as size-at-age models are still lacking for Mediterranean loggerheads.

This study aims to provide new estimates of growth rates and ASM for the Mediterranean loggerhead turtle population through the most direct approach: capture–mark–recapture. To this aim, we used a large dataset from long-term capture–mark–recapture programs in the Adriatic Sea, which is known to be frequented only by turtles of Mediterranean origin and mostly from Greek breeding sites (Lazar et al. 2004; Zbinden et al. 2011; Schofield et al. 2013; Cardona et al. 2014; Tolve et al. 2018).

Materials and methods

Data collection

Capture–Mark–Recapture (CMR) records of loggerhead turtles were provided by the following organizations: Arché, ARC; ARCHELON, ARL; Fondazione Cetacea, FC; Herpetofauna Albanian Society, HAS; Legambiente, LEG; Associazione Panda Molfetta, MOL; University of Primorska, UP. Turtles ($n = 79$) were encountered between 2003 and 2020 through incidental capture in fishing gears, stranding, or gathered while floating at sea or nesting, mainly in Italian waters and coasts, but also in Slovenia, Croatia, Albania and Greece. At first encounter, turtles were tagged on front or rear flippers with a variety of tags: 681 Monel, 681 Inconel, 681 Metal (National Band and Tag Company, KY, USA), and Titanium (Stockbrands, Australia). All turtles were measured according to the Curved Carapace notch-to-tip in centimeters (CCLn-t, hereafter CCL; Bolten 1999) at both release and re-encounter. Despite this standardization, measurements bear some uncertainty because they were taken by different people.

To limit analyses to turtles foraging in the Adriatic, only turtles both tagged and re-encountered in the Adriatic or turtles encountered one time in the Adriatic and the other while breeding in Greece were included in this study. Since no

genetic divergences have been found in the two areas where most data were collected (Tolve et al. 2018), the Adriatic Sea was considered as a uniform foraging area. To avoid biases due to seasonal effects or too long re-encounter intervals (Bjorndal et al. 2000b) only CMR histories with intervals between 1 and 4 years were included.

Data analysis

Growth rate (G; cm yr^{-1}) was calculated for each turtle as

$$CCL_{(re-encounter)} - CCL_{(release)} \frac{365}{D} \tag{1}$$

where D are days elapsed between the two events. Negative and zero growth rates were included to account for any measurement errors (e.g., Bjorndal et al. 2000b) or carapace deterioration (e.g., Bell and Pike 2012) that would cause overestimation of growth rate if not included.

Generalized Additive Models (GAMs) with a Gaussian family and an identity link were used to investigate the nonlinear relationship between growth rate (response variable, G) and two explanatory variables: mean size (S) and mean year ($\bar{Y}$), both averaged between release and re-encounter (Figure S1 and S2, respectively). Mean size is considered an adequate measure for size, especially for short time intervals (Bjorndal et al. 2000b). Mean year is preferred to release or re-encounter year and accounts for the effect of environmental variation during the growth period, although it cannot be clearly distinguished from age and cohort effects (Bjorndal et al. 2000a; Casale et al. 2009b; Colman et al. 2015). The expected size-specific growth rate function was estimated for the range of mean size values of the dataset (41.8–87.8 cm CCL) through two models, in the form $G \sim s(S)$ and $G \sim s(S) + s(\bar{Y})$, that were fitted through package *mgcv* (Wood 2006) in R (R Core Team 2022).

ASM was calculated in two steps from two separate estimates: (i) the time needed to growth from the smallest size of the present dataset to SSM and (ii) the age of the smallest size observed. For the first step, to predict time in years needed to grow from the smallest size of the observed sample (S_{min}; 41.8 cm CCL) to adulthood (A_m), we set the Size of Sexual Maturity (SSM), size at which A_m is attained, to the mean size of female nesters in Greece (83.4 cm CCL; see Casale et al. 2018), because of the predominant Greek origin of the loggerhead turtles foraging in the Adriatic Sea (Lazar et al. 2004; Zbinden et al. 2011; Schofield et al. 2013; Cardona et al. 2014; Tolve et al. 2018). Time needed to grow to 79.7 cm CCL as the mean size of Mediterranean nesters was also estimated for comparison with previous growth rate studies in the Mediterranean, summarized by Casale et al. (2015). Then, the following integration equation (Colman et al. 2015; Bellini et al. 2019) was used for each turtle, after ordering turtles by S:

$$A_i = A_{i-1} + \frac{\left(\bar{S}_i - \bar{S}_{i-1}\right)}{G_i} \tag{2}$$

where A_i is the age of turtle i (with $A_0 = 0$ being the age of the turtle with S_{min}), S_{i-1} is the mean size of the previous turtle, A_{i-1} is the estimated age of the previous turtle, G_i is the growth rate predicted by the GAM for the size S_i. Finally, to obtain A_m, the integration equation was calculated using A_{i-1}, $\bar{S}_{i-1}$ and G_i as the ones of the size immediately lower to SSM.

For the second step of estimating the age at $\bar{S}_{min}$ (41.8 cm) we took advantage of the age at 28 cm already estimated by another study (mostly based on turtles found in the southern Adriatic Sea; Casale et al. 2009a). Therefore, what remained to be estimated was the time needed to grow from 28 to 41.8 cm (S_{min}) and this was accomplished as follows. First, for each 5-cm size class (S*) in the original sample size range we estimated G through a GAM in the form $G \sim s(S^*)$. Second, we combined these G–S^* values with those regarding turtles < 30 cm CCL available as such from Casale et al. (2009a). Third, a GAM in the form $G \sim s(\bar{S}_r)$ was fitted to predict G for each 1-cm size class in the missing intermediate size interval (from 28 cm to S_{min}). Fourth, we estimated the age from 28 cm to the S_{min} through the integration equation above (2), obtaining A_{min}. Finally, ASM was estimated as $ASM = A_{min} + A_m$.

To compare present results with other studies, the Von Bertalanffy (1938) growth function was estimated in the form:

$$L_t = L_\infty - \left(L_\infty - L_0\right)e^{(-kt)} \tag{3}$$

The parameter k (growth coefficient) was estimated through a Nonlinear Least Squared approach (function *nls* of package *stats*). The starting values of k was estimated through the function *vbStarts* of the package *FSA* (Ogle et al. 2022). The value of L_∞ was set at 102 cm CCL (the largest size recorded for Mediterranean loggerhead turtles; see Casale et al. 2018). L_0 was set at S_{min} and t was the age estimated from the fittest GAM model for each S (L_t).

Results

A total of 79 loggerhead turtles released or re-encountered between 2003 and 2020 were considered (Fig. 1). Two turtles were re-encountered two times and one three times, but all the events were considered independently for a total of 83 release-re-encounter pairs. Turtles size ranged 34.0–88.5 cm (median = 63, IQR = ± 12.3) and 48.5–87.5 cm (median = 67, IQR = ± 10), at release and re-encounter, respectively. S ranged from 41.8 to 87.8 cm (median = 65, IQR = ± 11.3). $\bar{Y}$
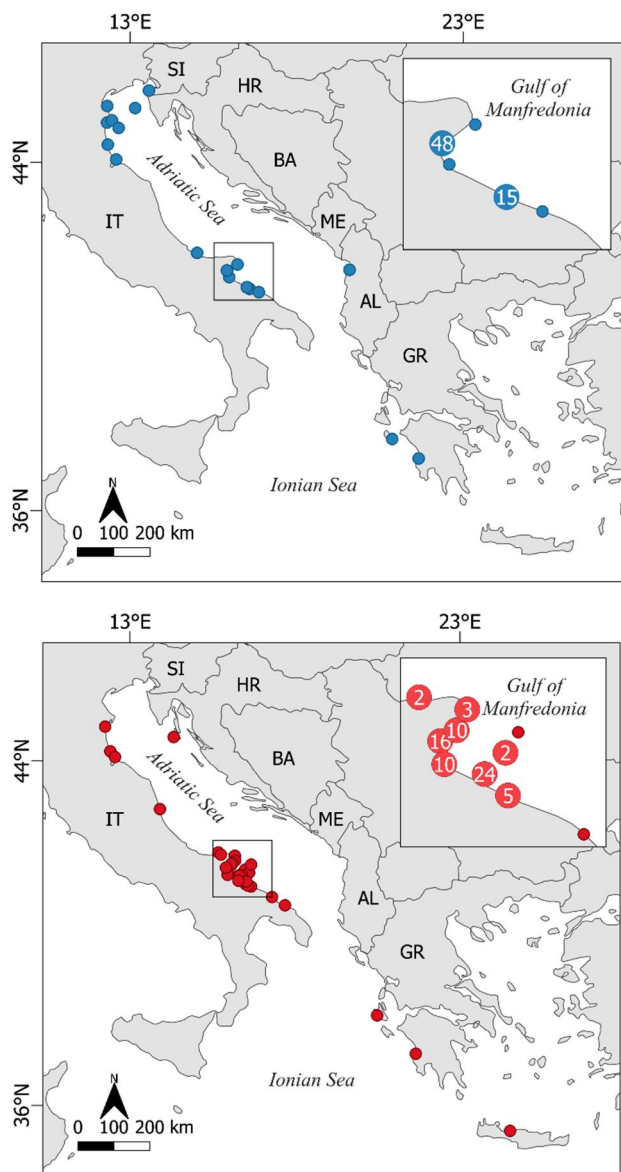
Fig. 1 Distribution of loggerhead sea turtles' releases (blue) and re-encounters (red) in the Adriatic Sea and Greece. Maps in top right show clustered points with number of releases or re-encounters per cluster. Country codes (clockwise): *IT* Italy, *SI* Slovenia, *HR* Croatia, *BA* Bosnia and Herzegovina, *ME* Montenegro, *AL* Albania, *GR* Greece

ranged from 2003 to 2019 (median = 2015, IQR = ± 5). Calculated G ranged from − 1.1 to 9.6 cm yr^{-1} (median = 2.0, IQR = ± 1.9). Both GAM models provided relatively good fit with an R^2 of 0.30 and 0.38, respectively for $G \sim s(S)$ and $G \sim s(S) + s(\bar{Y})$, with both explanatory variables investigated having a significant effect on G ($P < 0.05$) and the more complex model had a lower AIC (Akaike information criterion) (Table 1). Growth and age functions estimated through the two GAMs (Fig. 2) were monotonic.

The growth function estimated from data of the present study combined with Casale et al. (2009a)'s data was non-monotonic (Fig. 3). Predicted G for each S are summarized in Table 2. Estimated $A_{\min}$ for the size of 42 cm was 6.8 years. The S closest to 83.4 cm was 83 cm with an estimated A_i of 22.2 years. Applying the estimated G of 0.8 cm yr^{-1} at that size, A_m and ASM for turtles nesting in Greece was estimated at 22.7 and 29.5 years, respectively. The estimated age at 79.7 cm (for comparison with previous growth rate studies) was 25.2.

Estimates for the von Bertalanffy growth parameters was $k = 0.059$ (95% CI = 0.058–0.061) from the $G \sim s(S) + s(\bar{Y})$ model. These estimates and values from other studies in the Mediterranean and elsewhere are provided in Table 2 for comparison (but see also Ramirez et al. 2021).

Discussion

Growth rates calculated in this study allowed a direct estimate of ASM for the Mediterranean population. Our study was unique because, contrary to other Mediterranean areas investigated by most previous studies, the Adriatic Sea is not frequented by Atlantic turtles, but only by Mediterranean turtles and mainly by turtles from nesting sites in Greece (Lazar et al. 2004; Zbinden et al. 2011; Schofield et al. 2013; Cardona et al. 2014; Tolve et al. 2018). An estimation of growth rates for Mediterranean turtles, instead of a potential mix of Mediterranean and Atlantic individuals as in previous studies, allows a better comparison with other regions.

Present results and other studies (Braun-McNeill et al. 2008; Casale et al. 2011b; Bjorndal et al. 2013; Avens et al. 2015), indicate that loggerhead turtles in the Mediterranean Sea have comparable growth rate and size-at-age to the Atlantic. Given that Mediterranean adult turtles are smaller, similar growth rates suggest that Mediterranean loggerhead turtles mature at a younger age than Atlantic turtles (Heppell et al. 2003; Scott et al. 2012; Avens et al. 2015; Chasco et al. 2020). Mediterranean turtles are also smaller than counterparts in the Indian and Pacific oceans and have a lower ASM (Hatase et al. 2004; Limpus 2008; Tucek et al. 2014; Turner Tomaszewicz et al. 2015). The smaller size of Mediterranean loggerhead turtles, that represent a genetically distinct population (Carreras et al. 2011), may be an adaptation to specific local conditions or may be due to a general pattern. For instance, the Mediterranean is at the extreme of the loggerhead turtles distribution range and Tiwari and Bjorndal (2000) observed a negative correlation of body size and latitude.

The ASM of 29.5 and 25.2 years estimated for the Greek and the Mediterranean adults respectively (with SSM of 83.4 cm and 79.7 cm, respectively) falls within the range of ages estimated for turtles sampled in various areas of the

Table 1 Summary of parameter estimates of the GAM models

Model	R^2	Dev. explained (%)	REML	AIC	Param	Estimate	Std. Err	t value	F	P
$G \sim s(\bar{S})$	0.30	31.8	153.1	305.4	Intercept	2.2	0.2	13.5		< 0.001
					$s(\bar{S})$				3.9	< 0.001
$G \sim s(\bar{S}) + s(\bar{Y})$	0.38	41.2	150.4	297.3	Intercept	2.2	0.2	14.3		< 0.001
					$s(\bar{S})$				4.0	< 0.001
					$s(\bar{Y})$				1.1	0.003
$G \sim s(\bar{S}_r)$	0.98	99.4	24.7	20.6	Intercept	4.0	0.1	36.8		< 0.001
					$s(\bar{S})$				91.0	< 0.001
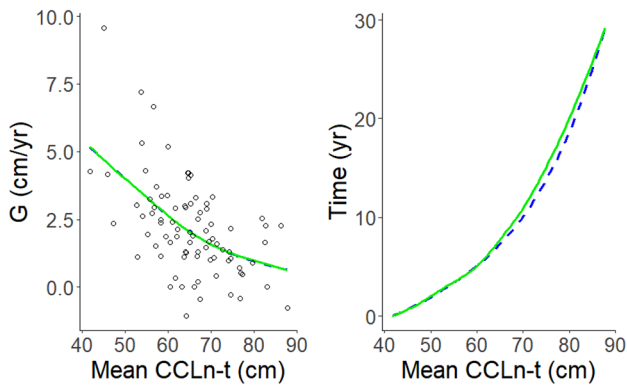
Fig. 2 Size-specific (Mean CCLn-t in x axes) predicted growth rate (G) and the time (years) to grow from the smallest size observed and a specific size estimated from the integration equation following the GAM models $G \sim s(\bar{S})$ in dashed blue (less visible due to overlapping) and $G \sim s(\bar{S}) + s(\bar{Y})$ in solid green. Data are shown as dots
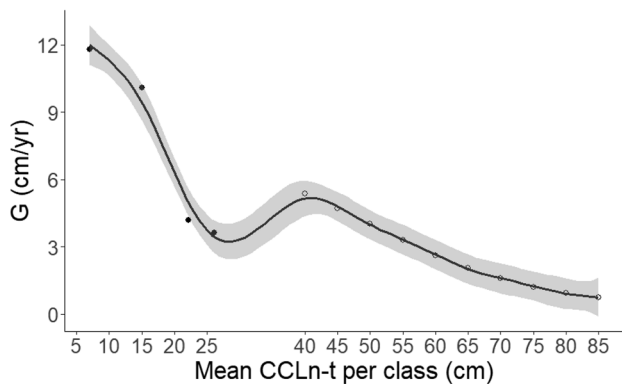

Fig. 3 Growth rate (G) as a function of size (mean size class-specific; Mean CCLn-t) of loggerhead turtles foraging in the Adriatic Sea. Empty dots: present study. Full dots: calculated from Casale et al. (2009a, b)

Mediterranean Sea (15.4–34.9 years at 66.5–84.7 cm; Casale et al. 2009b, 2011a, b; Guarino et al. 2020; Şirin and Başkale 2021). The only exception is the ASM of 24 years at 69 cm estimated by Piovano et al. (2011) for Mediterranean turtles, who also estimated lower growth rates for individuals of Atlantic and Mediterranean origin frequenting the Mediterranean. Different foraging areas used by turtles sampled in Piovano et al. (2011) compared to our study is a possible explanation for that difference. Additionally, differences in methods used to calculate ASM by Piovano et al. (2011) compared to methods used in this study may explain the different estimates, particularly given that the ASM of Atlantic turtles estimated by Piovano et al. (2011) was higher than estimates from other studies (Heppell et al. 2003; Avens et al. 2015).

Adults breeding in Greece are larger (mean 83.4 cm CCL) than loggerhead turtles breeding in other Mediterranean rookeries (Cyprus, Turkey, Libya means ≤ 78 cm CCL; see Casale et al. 2018): they either have similar ASM but different growth rates or vice versa or a combination of the two (Omeyer et al. 2018). Assessing which is the case would have interesting biological and ecological implications, but direct age comparison with other rookeries in the Mediterranean is not possible at the moment for two reasons. First, growth data from most foraging grounds are lacking. Second, rookery-specific growth rate studies are difficult because Mediterranean foraging grounds are usually frequented by multiple rookeries (in or outside the basin), with the Adriatic being an exception.

If the larger size of Greek adults compared to other Mediterranean nesting areas is due to different growth trajectories, trophic resources and/or different environmental factors likely play a role. These turtles frequent mainly the Adriatic Sea and the Tunisian Shelf (Lazar et al. 2004; Zbinden et al. 2011; Schofield et al. 2013; Cardona et al. 2014; Tolve et al. 2018), which hosts also turtles from other major nesting sites (Haywood et al. 2020; Cerritelli et al. 2022). At present, there are little to no growth data for these other rookeries, therefore, although genetics could contribute (Balazs and

Table 2 Summary of estimated von Bertalanffy parameters, G and ASM for loggerhead turtles in the present study

Study area	n	L_∞ (cm)	k	Size (cm)	G (cm yr^{-1})	SSM (cm)	ASM (years)	Refs.
Mediterranean Sea								
Italy (Adriatic Sea)	83	102[a]	0.059 (CI=0.058–0.061)	45 55 65 75 85	4.70 3.30 2.06 1.22 0.75	79.7 83.4	25.2 29.5	1
Italy (Adriatic Sea[b])	88	29.45	0.769	7.1 15.0 22.2 26.1	11.8 10.1 4.2 3.6			2
Italy (All seas)	38	95.63	0.077	61.7	2.5±1.7	66.5–84.7	16–28	3
Italy (Lampedusa Island)	774	99[a]	0.051 0.066	32–69.5	0.37–6.5	66.5–84.7 79.7 66.5–84.7 79.7	18.8–34.9 23.3 15.4–27.8 29.0	4
Italy (Lampedusa Island)	33	103.9 99[a] 119.3 99[a]	0.062 0.066 0.052 0.072	17.3–74.5	1.4–6.2	79.7	22.9 24.2 20.6 22.2	5
Italy MO (All seas)	30	99[a]	0.042	16.5 25 35 45 55 65 74.5	5.1 3.5 2.9 2.9 4.1 4.4 3.0	69 79.7	24 34.1	6
Italy AO (All seas)	35	124[a]	0.023	16.5 25 35 45 55 65 74.5	4.6 3.2 3.0 3.0 2.1 2.7 1.5	80	38	6
Albania (Drini Bay)	26			40–84.5	0.0–4.9			7
Cyprus (Alagadi Beach)	39			63–87	−1.0 to 1.8			8
Greece (Amvrakikos Gulf)	33			53.9 to >85[c]	<0.0–2.7			9
Turkey						67	18[d]	10
Atlantic Ocean								
NWA		90.3–111.9	0.031–0.128	4.6–109	0.2–12	75–115	10–52	11
SWA				40–109	0.63–3	102.5	32	12
Indian Ocean								
SWI	137					91.3[c]	36.2	13
Pacific Ocean								
NWP	78			79.6–102.1[c]	−1.8 to 1.5			14
SWP						95.7	29	15
NEP	146					91	25	16

Published studies are listed for comparison. Study area is coded as Country (sampling area). Ranges include minimum and maximum values among all the references

CI 95% CI, *MO* Mediterranean origin, *AO* Atlantic origin, *NWA* North West Atlantic, *SWA* South West Atlantic, *SWI* South West Indian, *NWP* North West Pacific, *SWP* South West Pacific, *NEP* North East Pacific. *1* This study, *2* (Casale et al. 2009a), *3* (Casale et al. 2009b), *4* (Casale et al. 2011b), *5* (Casale et al. 2011a), *6* (Piovano et al. 2011), *7* (White et al. 2013), *8* (Broderick et al. 2003), *9* (Rees et al. 2013), *10* (Şirin and Başkale 2021), *11* (Heppell et al. 2003; Scott et al. 2012; Bjorndal et al. 2013; Avens et al. 2015; Ramirez et al. 2017, 2021; Chasco et al. 2020) and references therein, *12* (Baptistotte et al. 2003; Petitet et al. 2012; Lenz et al. 2016), *13* (Tucek et al. 2014), *14* (Hatase et al. 2004), *15* (Limpus 2008) and references therein, *16* (Turner Tomaszewicz et al. 2015)

[a]Fixed L_∞

[b]Majority of the sample

Chaloupka [2004]), this aspect cannot be further discussed. Focusing on Greek turtles, previous studies found that turtles foraging in the Adriatic are larger compared to those using the Tunisian shelf (Patel et al. [2015]). The two foraging areas differ in terms of sea surface temperature and biodiversity (Coll et al. [2010]). Growth rates from the present study seems higher also compared to the Amvrakikos Gulf (Rees et al. [2013]). Such a difference may be due to the different features of the two areas: the Amvrakikos Gulf is a small fjord connected to the Ionian Sea characterized by waters often shallower than 2 m and an anoxic seafloor (Rees et al. [2013]). Similar cases are known from other areas and for several species including loggerheads (Hatase et al. [2002]; Eder et al. [2012]; Vander Zanden et al. [2014]; Benscoter et al. [2022]), green turtles (Balazs and Chaloupka [2004]; Chaloupka et al. [2004]; Eguchi et al. [2012]) and hawksbills (Diez and van Dam [2002]; Hawkes et al. [2014]) and were attributed to differences in environmental conditions. Optimal trophic resources allow higher growth rates and permit turtles to reach SSM at a larger size thereby increasing their reproductive output, which would be a favored strategy under those conditions (Omeyer et al. [2018]). However, when resources are suboptimal or limited reaching maturity at smaller sizes could be more advantageous, since fewer resources are allocated to growth and, being smaller, less energy is required for reproduction (Broderick et al. [2003]). Present results suggest that the Adriatic Sea offers better trophic resources that determine higher growth rates than other foraging areas.

On the other hand environmental and anthropogenic stressors have been reported to negatively influence various aspects of sea turtle biology, including growth rates (Bjorndal et al. [2017]) and breeding (Le Gouvello et al. [2020]). Stressors can influence individuals directly, or indirectly by impacting resource availability (Rees et al. [2016]; Bjorndal et al. [2017]). In the Tunisian shelf, Patel et al. ([2015]) report high primary productivity due to eutrophication. In the Levantine basin, another loggerhead foraging area, high salinity, high temperature, and low productivity have been identified as the main factors reducing sizes of fish and cetaceans (Sonin et al. [2007]; Sharir et al. [2011]). At present, we have no information on turtles foraging in the Levantine basin, but similar patterns could be expected to affect turtles in that region, since environmental pressures can drive maturation at a younger age (see Marn et al. [2019] and references therein). Combination of our results with data from Casale et al. ([2009a]), resulted in a non-monotonic growth curve. Non-monotonic growth function and/or polyphasic size-at-age growth function have been reported for almost

all hard-shelled sea turtles irrespective of foraging area or diet differences: loggerhead (Chaloupka [1998]; Snover et al. [2010]), green (Seminoff et al. [2002]; Balazs and Chaloupka [2004]), Kemp's ridleys (Chaloupka and Zug [1997]), hawksbill turtles (Chaloupka and Limpus [1997]; Diez and van Dam [2002]), but not in flatback sea turtles which frequent neritic habitat throughout their lives (Turner Tomaszewicz et al. [2022]). A growth spurt may be caused by shifting from epipelagic to benthic preys (Snover et al. [2010]; Avens et al. [2013]). A monotonic growth curve may be observed when the size range prior or correspondent to the shift to a neritic diet is absent or underrepresented (e.g., Bjorndal and Bolten [2009]). Alternatively, a non-monotonic curve may describe growth trajectories of discrete shifters (sensu Ramirez et al. [2017]) or a lower growth rate preceding the shift may occur when turtles have a plastic behavior (i.e., alternating between oceanic and neritic habitat). It is plausible that a shift from pelagic to benthic feeding could increase growth rates (Peckham et al. [2011]). A pelagic diet may be insufficient to sustain the rates observed in the first years of life, as was reported from combined skeletal growth mark and stable isotope analyses (Snover et al. [2010]; Avens et al. [2013]). This low-quality foraging could itself trigger recruitment to benthic habitats (Werner and Gilliam [1984]). Dietary studies from West (Tomas et al. [2006]) and Central Mediterranean (Casale et al. [2008]) and North Adriatic (Lazar et al. [2008]) showed that loggerhead turtles 25–30 cm CCL already recruit to neritic habitats and predominantly feed upon benthic prey (vs recruitment at > 40 cm CCL in the Atlantic; Bjorndal et al. [2000b]; Avens et al. [2013]). This early ontogenetic shift, with a short duration of the epipelagic phase, seems to be reflected in increased growth rates of juveniles 25–40 cm CCL (Fig. [3]) and may reflect the switch to more energetically valuable prey.

Different methods used in this and previous studies in the Mediterranean (Casale et al. [2009b], [2011a], [b]; Guarino et al. [2020]; Şirin and Başkale [2021]) yielded similar age estimates, reinforcing that they can be used interchangeably. In comparison with the other methods, CMR provides direct measurements, but re-encounters are infrequent and information may be lost due to tag loss, thus data may be challenging to acquire over long time periods. Moreover, because CMR typically spans long time periods and involves several organizations there is an additional source of uncertainty because measurements are taken by several different people. Length Frequency Analysis (LFA) and skeletochronology allow collection of larger sample sizes over a shorter time period, but measurements are indirect and get more imprecise as larger

size classes are involved due to slower growth rates and bone remodeling (Zug et al. 1986). Neither CMR or LFA are able to detect growth spurts, which can affect estimates of life-stage duration (Murakawa and Snover 2018).

The environmental heterogeneity of loggerhead foraging grounds located in relatively close proximity to one another in the Mediterranean basin represents a good opportunity to investigate the factors affecting growth rate patterns in sea turtles. More growth studies applying a variety of methods in other areas across the Mediterranean, and especially in the Aegean Sea, Levantine Basin and North Africa shelf, would be desirable to increase our knowledge on the demography of sea turtles and improve models for conservation planning. Because environmental factors seem to influence growth rates, monitoring changes in these rates over time can be used to keep track of both the status of the population and the status of the foraging habitats. This is especially important in areas where there is a high human impact and in areas with great potential to experience impacts from climate change.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. The authors have no conflicts of interest to declare.

Ethical approval The study did not involve human participants. It analyzed sea turtle data previously collected by different organizations with the adequate authorizations of their countries.

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