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Ecology of loggerhead marine turtles *Caretta caretta* in a neritic foraging habitat: movements, sex ratios and growth rates

ALan F. Rees · Dimitris Margaritoulis ·
Robert Newman · Thomas E. Riggall ·
Paul Tsaros · Judith A. Zbinden · Brendan J. Godley

Abstract Much is still to be learned about the spatial ecology of foraging marine turtles, especially for juveniles and adult males which have received comparatively little attention. Additionally, there is a paucity of ecological information on growth rates, size and age at maturity, and sex ratios at different life stages; data vital for successful population modelling. Here, we present results of a long-term (2002–2011) study on the movements, residency, growth and sex ratio of loggerhead turtles (*Caretta caretta*) in Amvrakikos Gulf (39°0′N 21°0′E), Greece, using satellite telemetry ($N = 8$) and ongoing capture–mark–recapture (CMR; $N = 300$ individuals). Individuals encountered at sea ranged from large juvenile to adult (46.2–91.5 cm straight carapace length) and demonstrated growth rates within published norms (<2.7 cm yr^{-1}) that slowed with increasing body size. We revealed that an unexpectedly high proportion of animals were male (>44 % of captures above 65 cm straight carapace length), compared to region-wide female-biased hatchling production, indicating sex-biased survival or possible behavioural drivers for likelihood of capture in the region. Satellite tracking confirmed that some turtles establish discrete, protracted periods of residency spanning more than 1 year, whilst others migrated away from the site. These findings are underlined by CMR results with individual capture histories spanning up to 7 years, and only 18 % of individuals being recaptured.

Introduction

Understanding the ecology of marine vertebrates is challenging as a result of the wide spatiotemporal scales over which their life cycles may take place (e.g. Block et al. 2005; Croxall et al. 2005). Accordingly, long-term studies are required to accurately assess demographic and behavioural changes and support efficacy of conservation measures in long-lived species (Abesamis and Russ 2005; Troëng and Rankin 2005; Baird et al. 2008). Technological advances in satellite tracking techniques have allowed global coverage, with studies now encompassing all major marine taxa, from fish (e.g. Holdsworth et al. 2009; Eckert et al. 2002) to sea birds (e.g. Lynnes et al. 2002; Croxall et al. 2005) so that valuable insights into movement patterns and behaviour have been gathered (Heithaus et al. 2007; Andrews et al. 2008; Block et al. 2011). To gain deeper understanding of the ecology of these wide ranging taxa, there has been a progressive move to interdisciplinary studies, incorporating the combinations of telemetry with more traditional identification methods, for example, radio tracking and photograph ID in cetaceans (Scott et al. 1990). A combination of flipper tagging and satellite telemetry has been used to more fully determine spatial distribution of marine turtles (Godley et al. 2003; Troëng et al. 2005a, b) with stable isotope analysis also used to complement these methods (Zbinden et al. 2011).

A. F. Rees (✉) · D. Margaritoulis · R. Newman ·
T. E. Riggall · P. Tsaros
ARCHELON, the Sea Turtle Protection Society of Greece,
Solomou 57, 104 32 Athens, Greece
e-mail: afr203@exeter.ac.uk

A. F. Rees · J. A. Zbinden · B. J. Godley
Marine Turtle Research Group, Centre for Ecology
and Conservation, University of Exeter, Cornwall Campus,
Penryn, Cornwall TR10 9EZ, UK

The loggerhead sea turtle (*Caretta caretta*) is a circum-globally distributed species demonstrating regional population structuring as a result of natal phylopatry (Bowen et al. 1994). Development and maturation take place over several decades (Chaloupka 2003; Casale et al. 2011) during which time juveniles may traverse whole ocean basins before returning to their natal region (Bowen et al. 1995; Bolten et al. 1998; Bowen et al. 2004; Boyle et al. 2009). Traditionally, individuals were thought to exhibit a two-stage ontogenetic life history pattern, with smaller juveniles living and feeding in the epipelagic realm and larger juveniles and adults inhabiting neritic waters feeding on benthic prey (Bolten 2003). However, recent evidence has shown that this shift to neritic habitats is reversible during development (McClellan and Read 2007) and not obligatory for all adults in a population (Hatase et al. 2002; Hawkes et al. 2006; Rees et al. 2010). Additionally, the temporal and spatial scales over which marine turtle life histories occur make comprehensive ecological studies difficult to undertake, and consequently, accurate assessment of vital demographic parameters is difficult to achieve.

Turtle populations are impacted by diverse anthropogenic threats (Lutcavage et al. 1997). Climate change is likely to profoundly affect sea turtles, as temperature influences vital life history characteristics, such as sex determination, breeding phenology and habitat selection (reviewed by Hawkes et al. 2009 and Witt et al. 2010b). Fisheries interactions and coastal development, however, have been identified as causing most concern (Donlan et al. 2010; Hamann et al. 2010). The Mediterranean Sea contains a genetically isolated metapopulation of loggerhead turtles (Encalada et al. 1998; Carreras et al. 2011), and anthropogenic threats prevalent within the region (see Coll et al. 2010) reflect the situation globally.

Mediterranean loggerheads mature at the smallest size globally (Tiwari and Bjorndal 2000; Margaritoulis et al. 2003) and grow more quickly than their Atlantic conspecifics that are present but do not breed in the West Mediterranean (Piovano et al. 2011). The distribution of oceanic and open-sea neritic juvenile loggerheads has been examined within the region (Tomas et al. 2001; Cardona et al. 2005; Casale et al. 2007; Revelles et al. 2007), as have the inter-breeding locations of adults (Margaritoulis et al. 2003; Broderick et al. 2007; Schofield et al. 2010; Margaritoulis and Rees 2011; Zbinden et al. 2011) There is, however, a paucity of literature on foraging populations in shallow coastal areas (see White et al. 2010 for the exception), which are likely comprised of the demographically important large juvenile and adult size classes. Furthermore, through temperature-dependent sex determination, highly biased offspring sex ratios may be produced in marine turtle populations (Marcovaldi et al. 1997; Hanson et al. 1998; Wibbels et al. 1999; Booth and Freeman 2006; Chu et al. 2008; Steckenreuter et al. 2010).

These biases are likely to become more extreme in the face of climate change (Mrosovsky et al. 1984; Fuentes et al. 2010; Witt et al. 2010b). Since the anticipated threat of climate change is believed to be particularly pronounced within the Mediterranean Basin (Nicholls et al. 1999; Giorgi and Lionello 2008), there is a need for sex ratio studies of juvenile and adult turtles in foraging habitats.

We report the results of a decade-long study of the Mediterranean loggerhead sea turtle using multiple methods to generate an understanding of the foraging ecology of this species in a shallow, neritic habitat. Using satellite telemetry and capture–mark–recapture, we set out to ascertain the degree of inter- and intra-annual fidelity to capture location. Utilising sexually dimorphic traits, we set out to identify the size at maturation of males from which we could estimate sex ratio of sub-adult and adult-sized individuals in a region where hatchling production is female skewed. Further, the long-term nature of the study allowed us to generate information on growth rates which are poorly reported in the literature.

Materials and methods

Sampling site and data collection

Amvrakikos Gulf, in western Greece ($39°0'$N $21°0'$E), is a virtually enclosed basin covering 405 km^2 with an opening to the Ionian Sea through the Preveza Channel that is 3 km long, 8 m deep and, at its narrowest, 600 m wide (Fig. 1; Kapsimalis et al. 2005). The northern part is formed from the deltas of the Arachthos and Louros rivers, which have created three large lagoons and expansive saltmarsh, reed bed and shallow water habitats. The Gulf has been termed the 'only Mediterranean Sea fjord' (Ferentinos et al. 2010) with a maximum depth of 65 m. Due to low levels of circulation, the deeper regions, encompassing some 50 % of the seafloor, of the gulf are hypoxic or anoxic (Kountoura and Zacharias 2011; Ferentinos et al. 2010). Local knowledge indicated high densities of loggerhead marine turtles were present in the shallow waters around the Arachthos and Vovos estuary system in the north east of Amvrakikos Gulf. The area is specifically characterised by extensive shallow waters <2 m deep; therefore, this region was initially selected as the sampling site (Fig. 1).

In June and September 2002 and May 2003, turtles were captured from a boat using a seine net ($N = 16$) primarily for the purpose of deploying satellite transmitters (see below). This region of the Gulf was then selected for subsequent research due to the abundance of turtles observed. Therefore, from 2004 to 2011, between the months of May and September, for periods between 3 and 6 days, animals were captured at this location, using the
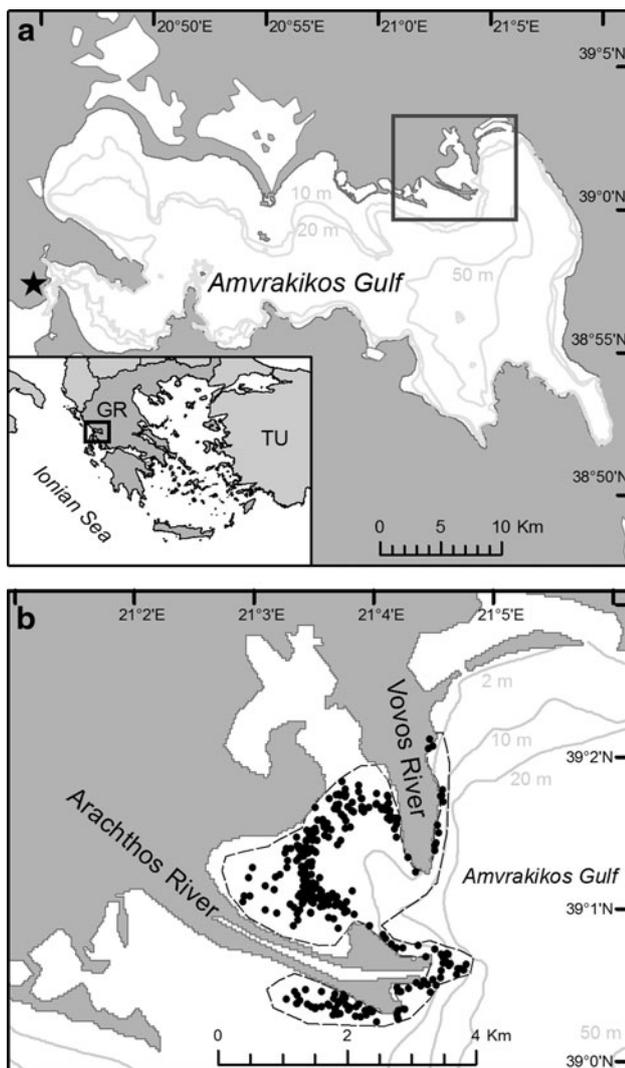
Fig. 1 Location of study area and turtle captures: **a** Amvrakikos Gulf with contextual *inset*. *Rectangle* indicates study area, and the Preveza Channel is indicated with a *star*. *GR* Greece, *TU* Turkey. 10-, 20- and 50-m bathymetric contours are shown. **b** GPS, turtle capture locations in the study area (*N* = 300). *Dashed line* delineates area covered in surveys and the 2-, 10- and 20-m bathymetric contours are shown

sea turtle rodeo technique (Ehrhart and Ogren 1999) from a 4-m inflatable dinghy. Captured turtles were hauled on board for data collection and were generally released within 15 min of capture.

GPS coordinates were recorded for the majority of turtle captures. Curved carapace length (notch to tip) (Bolten 1999; CCL) was measured to the nearest 0.5 cm with a fibreglass tape measure, and straight carapace length (notch to tip) (Bolten 1999; SCL) was measured using wooden or, more commonly, metal callipers (0.5 and 0.1 cm precision, respectively). Tail lengths (TL), from tail tip to inner part of the notch between the supracaudal scutes (Limpus and Limpus 2003), were also recorded using a fibreglass tape measured to the nearest 0.5 cm. Turtles were externally

tagged on two flippers (Balazs 1999) using a combination of uniquely numbered Monel metal (National Band and Tag Company, Kentucky, USA) and plastic (Dalton, Oxfordshire, UK) tags.

In order to determine natural variation and maximum values presented by adult females at probable source populations, TL and SCL measurements were taken from 94 nesting turtles (after completion of egg laying) at the three main nesting areas of Greece (Laganas Bay on Zakynthos Island (*N* = 23), southern Kyparissia Bay on the Peloponnese (*N* = 48) and Rethymno on the Island of Crete (*N* = 23)), in 2011.

Satellite tracking

We tracked six turtles using Kiwisat 101 satellite transmitters (Sirtrack Ltd, Havelock North, New Zealand) using the Argos system (www.argos-system.org) with three tags deployed in 2002 and three in 2003. Captured turtles were taken ashore and retained in a shaded, wooden corral to affix the transmitters and were then released on a beach less than 2.5 km from capture location. The fibreglass and polyester resin attachment method of Balazs et al. (1996) was adopted. Transmitters were duty-cycled to be continuously on for the first 28 days, followed by 24 h. on: 36 h. off to extend battery life, for the rest of the transmitter's functional duration. A separate study involved satellite tracking a further 18 turtles whilst nesting at Laganas Bay, Zakynthos (see Zbinden et al. 2011 for details). Two of these turtles, from 2007, migrated into Amvrakikos Gulf and their movements within the Gulf are opportunistically included here.

Location data for Amvrakikos-tagged turtles were manually retrieved, through Telnet, on a daily basis. Datasets were then uploaded into the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley 2005) for processing and filtering. Data for Zakynthos-tagged turtles were both downloaded by and processed in STAT. Raw Argos data were filtered in the following manner: Location classes 3, 2, 1, A and B were used (Witt et al. 2010a), and locations requiring excessive speed (>5 km h^{-1}) or highly acute turning angles ($<25°$) were omitted. The filtered data were interpolated to provide a single daily location, attributed to noon local time.

Home range kernel estimates were generated for five individuals (4–8), where we obtained sufficient data (over 20 daily locations) within the Gulf. We defined the 75 and 50 % utilisation levels to estimate home range and core areas, respectively, using a 1-km smoothing factor (h) in the fixed kernel density estimator method (Worton 1989) of Hawth's Tools (www.spatialecology.com) for ArcGIS 9.3.1 (ESRI, Redlands, CA, USA; www.esri.com/software/arcgis/index.html).

Biometric data analyses

Individual growth rates were calculated as the difference between carapace length measurements separated by intervals of greater than or equal to 10 months (van Dam 1999), divided by the intervening time period and expressed in cm yr^{-1}. Growth rate was assigned to the mean size between release and subsequent observation as per previous investigations (Chaloupka and Limpus 1997; Casale et al. 2009). A single TL measurement and corresponding SCL is presented per individual. In cases with more than one record per individual, the initial record was used. Several captured turtles bore tags applied whilst nesting at monitored sites in Greece, indicating they were adult females. We carried out the assessment of sex through determining a cut-off point at which extended tail length indicated maleness, blind to the presence of such tags.

All data were checked for normality using the Shapiro–Wilk test, and where normality was not met, nonparametric statistical analyses were undertaken. Additionally, we used GLMs to investigate variation in turtle growth. To normalise growth rate, we log + 1 transformed the data.

Results

We repeatedly observed and captured tens of individuals in water less than 2 m deep (maximum 41 individuals captured in a 6-day field period), which indicates that the study area is a high-use foraging habitat for loggerhead turtles. In a decade of study, comprising 67 days of fieldwork, we have recorded 300 individual loggerhead turtles from 370 captures. Mean size (SCL) at first capture was 67.4 cm and ranged from 46.2 to 91.5 cm (SD = 8.2 cm, $N = 293$) encompassing both juvenile and adult size classes.

Fidelity

Eight individuals were tracked by satellite within the Gulf with median of 57-day duration, (interquartile range 18.25–248 days) ranging from 10 to 548 days (Fig. 2; Online Resource Table 1). Poor quality and infrequent locations from turtles 1–3 indicated they remained in the northern part of the gulf before transmissions ceased (for minimum periods of 10–22 days; Fig. 2a). Two turtles (4 and 5) remained within the study area for 60 and 548 days, respectively (Fig. 2b,c), with turtle 4 subsequently
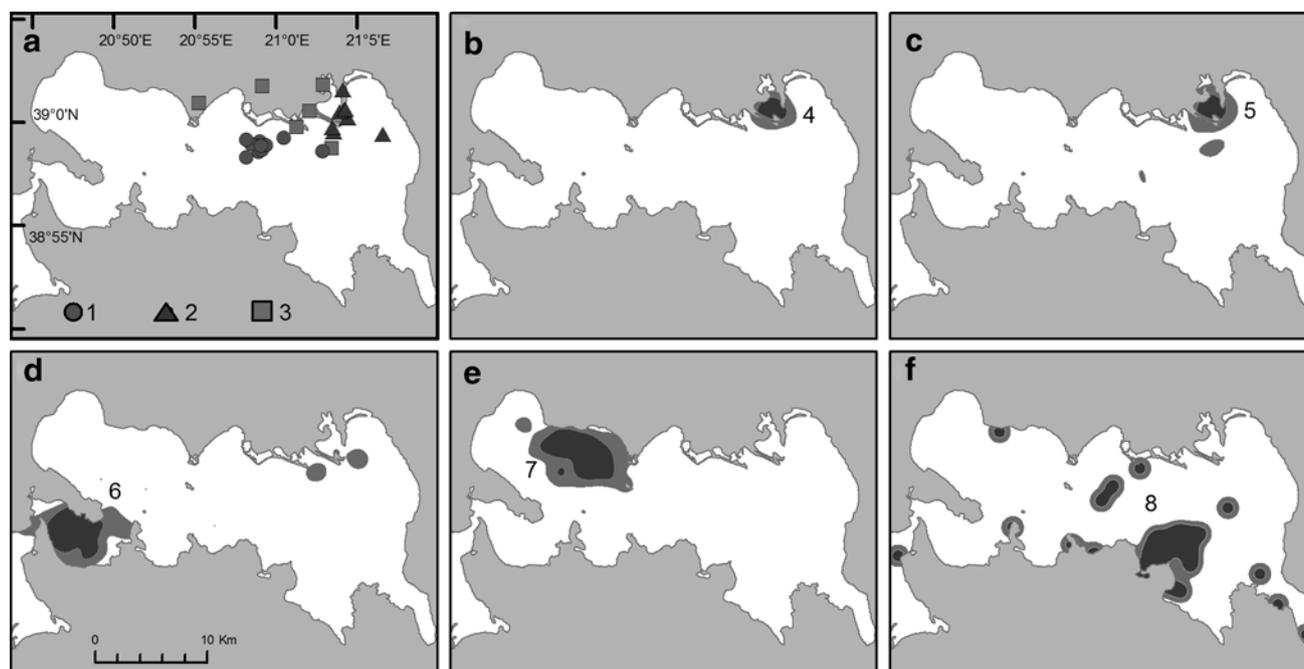

Fig. 2 Site fidelity and movement of loggerhead turtles within Amvrakikos Gulf described by satellite telemetry. **a** Three turtles (1–3) tagged in 2002 with maximum duration of usable data of 22 days; filtered locations shown. **b** Turtle 4 that departed the gulf after 60 days of transmissions. **c** Turtle 5 that remained in the Gulf for over 540 days. **d** Male turtle 6 (SCL = 71.5 cm) that transmitted for 70 days. **e** Adult female turtle 7, tracked in the gulf for 266 days. **f** Adult female turtle 8, tracked in the Gulf for 194 days. Polygons show 50 % (*dark*) and 75 % (*pale*) occupancy levels. See Online Resource Table 1 for further details of the satellite-tracked turtles

departing the gulf for Syria and Turkey (track not shown). Turtle 6 resided near the entrance to the gulf for the majority of its 70-day tracking duration (Fig. 2d). Turtles 7 and 8 (tagged whilst nesting on Zakynthos) never entered the sampling area, although they established long-term foraging locations in the northwest and south-central parts of the Gulf, respectively (Fig. 2e,f), and were tracked for 266 and 194 days in these locations. Median 50 % core area foraging habitat was 18.2 km^2, ranging from 4.9 to 54.7 km^2. No relationship was found between core area size and residency duration (Spearman's rank correlation, $r_s = 0.300$, $N = 5$, $P = 0.624$), indicating individuals rapidly established foraging habitat limits.

In total, 54 turtles (18 %) were recaptured during the study with recapture intervals ranging from 1 to 1986 days. We recorded individuals present at the study site for up to 7 years including recaptures in the intervening time period (Online Resource Fig. 1). The maximum distance between the most disparate capture locations, which defines our sampling range, was 3.6 km. Mean distance for within-year recaptures (range 1–144 days) was 1.05 km from 13 individuals (SD = 0.65, 0.25–1.99 km) including one turtle that was caught three times in a year, for which the distance between the first and last capture was used. Mean distance for multi-year recaptures (range = 328–1875 days) was 0.82 km from 14 individuals (SD = 0.61, 0.08–2.18 km). A further five turtles were recaptured at marked locations three times over several years. Mean maximum distance between recaptures for these turtles was 1.54 km (SD = 0.49, 1.04–2.09 km).

Growth rates

This fidelity evidenced by some individuals and their consequent recaptures permits estimations of growth rates. Of the multi-sampled turtles, 33 individuals were recaptured with intervals of ≥10 months and were successfully measured on both occasions. Maximum growth rate derived from these recapture data was 2.7 cm yr^{-1} at 49.9 cm SCL. No significant difference in growth rate was found between sexes ($F_{1,18} = 0.1313$, $P = 0.72$) nor for size ($F_{1,18} = 2.24$, $P = 0.15$) with turtles of estimated sex (SCL >65 cm). However, growth rate was significantly higher in smaller turtles when included in the model ($F_{1,32} = 7.37$, $P = 0.01$, Fig. 3). This significance was generated by the smallest turtle that had the fastest growth rate. No significant relationship between size and length existed when this data point was removed ($F_{1,31} = 2.87$, $P = 0.10$).

Sexual dimorphism

Tail length measurements (TL) of known adult females (measured after nesting in Greece) ranged from −3 to 7 cm
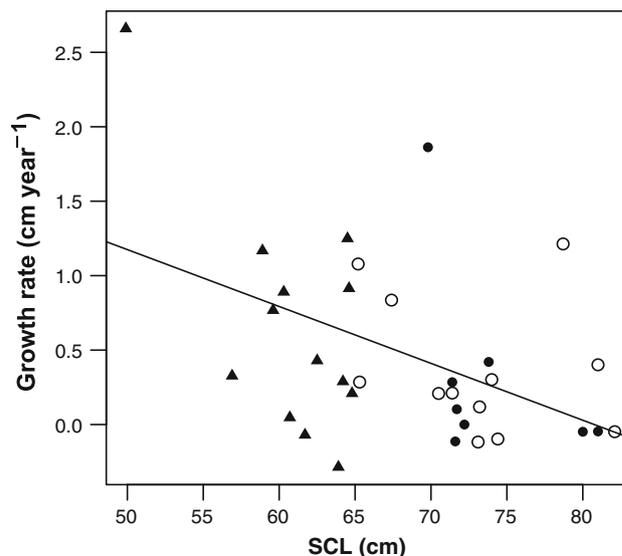

Fig. 3 Annualised growth rates in terms of carapace length (SCL). See text for methods of selecting growth data. Maximum growth rate was recorded for the smallest individual and growth rate decreased to approximately zero for larger turtles ($N = 33$). *Triangles* = unsexed individuals. *Open circles* = (probable) females. *Filled circles* = males. *Line* indicates regression through all data points, showing decrease in growth rate with increasing size

(mean = 2 cm, SD = 2.1 cm, $N = 94$). More than 95 % of adult females had TL measurements of less than 6 cm. No significant relationship between carapace length (SCL) and TL was found for adult females (Pearson's product correlation, $r_{92} = 0.194$, $P = 0.062$; Fig. 4a). TL measurements for turtles captured within Amvrakikos Gulf ranged from −5 to 28.5 cm ($N = 274$) (Fig. 4b). It can be inferred, from our data and from published studies (Casale et al. 2005; Limpus and Limpus 2003), that individuals with TL ≥ 6 cm are highly likely to be males. In our sample, the onset of tail elongation occurred between 60 and 65 cm SCL (Table 1; Fig. 4b) and from around 75 cm SCL individuals fell into two distinct tail length categories (Fig. 4b).

Sex ratios

Based on extended tail length, the minimum percentage of males (MPM) per 5 cm size category progressively increases from SCL 60 cm, reaching 100 % in the two largest classes (Table 1). Using the common minimum size of nesting females (65 cm SCL; Fig. 4a), which coincides with the increased proportion of identifiably male turtles, we calculated the MPM captured during each field period. Grouped, monthly sample sizes ranged from 13 to 65 captures, and the corresponding MPM ranged from 31 to 55 % with May and July having values of 40 % or more (Online Resource Table 2); however, monthly variation in sex ratio did not vary significantly (Kruskal–Wallis test, $H_4 = 5.176$,
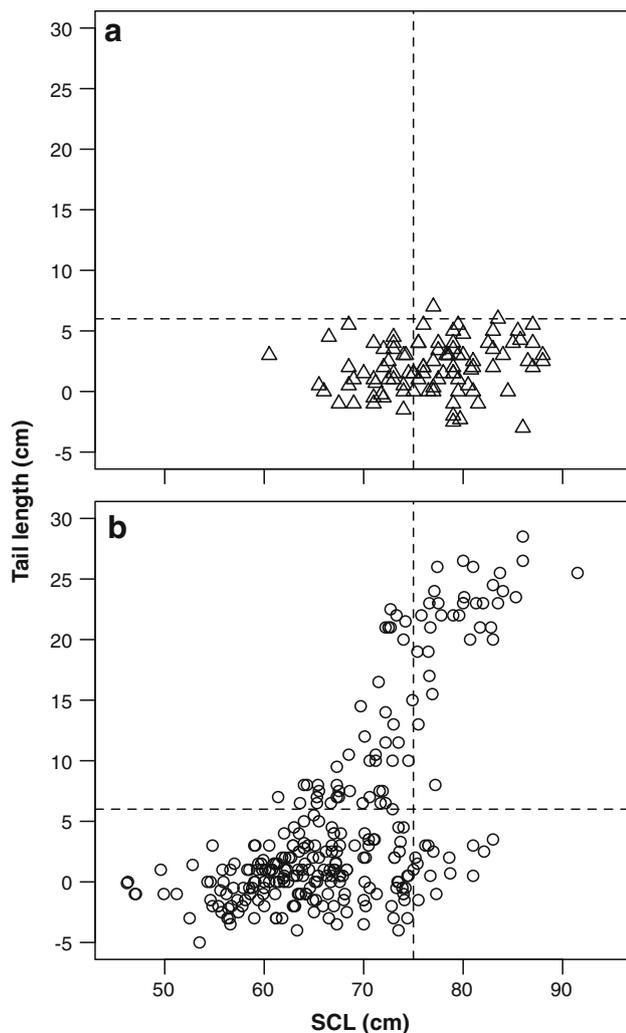
Fig. 4 Tail length plotted against carapace length (SCL). **a** Known adult female turtles, sampled from nesting areas (*N* = 94), showing their distribution from which our maximum TL for females was derived. **b** Amvrakikos turtles (*N* = 274) show onset of tail elongation at 60–65 cm SCL and separation of the sexes, based on tail length, by 75 cm—indicated by the *dashed vertical line*. The *dashed horizontal line* on both *plots* represents the cut-off point where longer tails indicate the turtles are male (6 cm)

Table 1 Minimum percentage of males in different size classes determined from sexually dimorphic tail length and based on one observation per individual

SCL (cm)	TL <6 cm	TL ≥6 cm (≡ male)	Min. % male
>45–50	4	0	0
>50–55	7	0	0
>55–60	36	0	0
>60–65[a]	63	4	6
>65–70	45	12	21
>70–75	31	25	45
>75–80[b]	12	16	57
>80–85	4	15	79
>85–90	0	3	100
>90–95	0	1	100

SCL straight carapace length, *TL* tail length

[a] Size class with the onset of tail elongation and the size at which maleness can be ascribed

[b] Minimum size class in which sex can be definitively assigned based on tail length, as it falls within two distinct groups (see Fig. 4b)

(Broderick et al. 2002) and so localised foraging areas in which turtles may be numbered in hundreds, such as Amvrakikos Gulf, comprise regionally important habitats. Focal foraging areas for adult female loggerheads in the Mediterranean have previously been revealed through flipper and satellite tagging nesting females. The African coastline and Adriatic Sea are highlighted as key foraging areas for turtles breeding in Greece and Cyprus (Zbinden et al. 2011; Broderick et al. 2007), though there is evidence that at least one breeding aggregation also preferentially utilises the Aegean Sea (Margaritoulis and Rees 2011). Most mixed sex and size class studies, from which turtle abundance have been estimated, have relied on fisheries bycatch to sample turtles (see Casale et al. 2012 for a summary). In our study, the first of its kind in Greece, through identifying 300 individual turtles, with limited recaptures, in only 67 days of fieldwork spread over a decade, we confirmed that Amvrakikos Gulf is a hotspot for loggerhead turtles. We have only recorded large juvenile and adult turtles that appear to have undergone the ontogenetic shift from being epipelagic to benthic foragers. This shift, though reversible (McClellan and Read 2007), occurs in Atlantic and North East Pacific loggerheads from around 46 cm (Bjorndal et al. 2000; Seminoff et al. 2004) with loggerheads from Australia and South Africa recruiting into neritic habitats at larger sizes (Limpus and Limpus 2003; Hughes 1974). Within the Mediterranean, a relaxed life history model has been suggested, with individuals slowly shifting from epipelagic to benthic foraging from around 26 cm carapace length (Laurent et al. 1998; Casale et al. 2008). Our results are aligned with those from the Atlantic with only turtles greater than 46 cm in length

P = 0.270). Overall MPM was 44 % (*N* = 216). The proportion of males increased if the threshold was raised to 75 cm SCL (which permits full sex discrimination based on tail length) and ranged from 40 to 90 %, with an overall of 64 % males calculated from 72 captures (Online Resource Table 2). This increase is to be expected, as there was a higher MPM in larger turtles (Table 1).

Discussion

The annual number of nesting loggerheads in the Mediterranean region has been estimated as less than 2800

being recorded, although we cannot rule out the possibility of smaller turtles occurring elsewhere within the gulf. The apparent exclusive presence of adult and large-sized juvenile loggerhead turtles in the Gulf may be a result of the geographical constraints of location; this imparts a certain importance to the region, as modelling has shown that reduced survivorship in these size classes will have most effect on breeding population viability (Crouse et al. 1987; Heppell et al. 1999).

Multi-year fidelity, by loggerheads, to foraging areas has been previously demonstrated (Limpus and Limpus 2003; Broderick et al. 2007; Schofield et al. 2010; White et al. 2010). From tag recaptures, we report a pattern of long-term fidelity (up to 7 years), and from telemetry, we have confirmed year-round presence of turtles in the Gulf. Fidelity to a foraging habitat is thought to persist for juveniles through to maturity (Limpus and Limpus 2001). Though not conclusive for changes in maturity status, we have recorded male turtles going through puberty, based on rapidly increasing tail length, and females that were originally tagged in the study location subsequently witnessed on nesting beaches before being re-sighted in the Gulf (details not presented); thus, the growing body of data from this study indicates that, for at least some individuals, turtles of the Mediterranean also maintain fidelity to foraging locations through maturation.

Core area utilisation was broadly in line with other studies, in that coastal, neritic core foraging areas cover tens of square kilometres (Broderick et al. 2007; Schofield et al. 2010), whereas core areas for turtles in open water habitats are orders of magnitude larger (Schofield et al. 2010; Hawkes et al. 2011). We also reveal that Mediterranean loggerheads establish spatial structuring within extensive suitable foraging habitat. Non- and poorly overlapping home ranges of study animals tracked for extended periods indicate that individuals establish distinct foraging areas, often not at the study site. Behaviour of another adult male that was tracked into the Gulf in successive years (Schofield et al. 2010) further supports this observation as it established two localised foraging areas, using one in 1 year and both in the other, with neither incorporating the study area. This, aligned with the fact that only 18 % of turtles have as yet been recaptured in the small area of our intensive survey efforts, would indicate that many turtles have only a transient association with the study site, as demonstrated by the majority of the tracked turtles establishing foraging areas elsewhere (Schofield et al. 2010; present study). Similar results have been recorded in the NW Atlantic where some individuals show strong fidelity to localised foraging areas (Avens et al. 2003), whereas the majority of individuals are recorded as transients (Sasso et al. 2006), confirming widespread behavioural plasticity in foraging habitat use.

Growth rates for wild sea turtles require recapture of potentially wide ranging individuals over long periods of time and hence are difficult to obtain. New data on growth rates therefore may contribute to our understanding of marine turtle demographics. The rates derived from our study lie within published norms for loggerheads (Online Resource Table 3), indicating that the gulf is a suitable developmental and long-term foraging site. Large size (possibly adult) individuals captured at the study site showed growth at near zero as found in other studies (e.g. Broderick et al. 2003; Limpus and Limpus 2003). However, this contradicts other results from the Mediterranean where the larger-sized animals still exhibited growth in excess of 1 cm year^{-1} (Casale et al. 2009; Piovano et al. 2011). These fast-growing larger turtles were hypothesised, by Casale et al. (2009), to be of Atlantic origin and from stocks that mature at a larger size, but the more recent work of Piovano et al. (2011) has indicated that, in this size range, Mediterranean loggerheads actually grow almost twice as fast as their Atlantic conspecifics. The present study still requires more data for the smaller size classes present to create a more robust growth curve for turtles foraging in Amvrakikos Gulf and only when this is achieved will we be able to provide an estimate of age at maturity and duration of the juvenile neritic foraging stages, which are vital parameters for modelling turtle life histories.

The simple, non-invasive sexing of larger turtles through use of tail lengths has great utility in studies that lead to better understanding of population demographics. As stated, our results using TL to sex individuals compare well with others (Casale et al. 2005 (Mediterranean), Limpus and Limpus 2003 (Australia) and Ishihara and Kamezaki 2011 (Japan)), but have additional validation over the other Mediterranean study in that we obtained tail and carapace length measurements from a large sample of turtles of known sex and maturity status (adult females) and thus we were able to determine with more certainty the tail length threshold which, when exceeded, is indicative of maleness (i.e. 6 cm).

A female-biased sex ratio of hatchling production has been reported for loggerheads at its major nesting areas in the Mediterranean (reviewed in Witt et al. 2010b), and although methodology and timescales of studies differ, this bias is accepted to be globally predominant (Wibbels 2003). Conversely, studies have generated conflicting estimates for at-sea sex ratios of larger loggerhead turtles in the Mediterranean; from female biased to balanced ratios (Casale et al. 2005; White et al. 2010; Casale et al. 2006; Lazar et al. 2008). Our study has revealed a male bias, increasing with size, with 69 % of individuals over 75 cm SCL determined to be male. It may be that males preferentially settle in this location or that sex-specific mortality

rates differ through the development and maturity. However, further investigations including the use of genetic techniques to identify contributions from different source populations from which hatchling sex ratios have been or can be estimated need to be undertaken to explain this.

The sex ratios we generated provided some intriguing revelations concerning lack of seasonality. Within the Mediterranean, loggerhead turtle nesting is mostly confined to the summer months of June through to early August (Margaritoulis et al. 2003) and hence the sex ratios in adult foraging areas might be expected to follow a predictable pattern, namely April should show reduced numbers of adult male and female turtles in foraging grounds as they migrate to their breeding areas with a higher proportion of males departing the foraging area as they undergo breeding migrations more frequently than females (Hays et al. 2010). Males return to their foraging areas in May/June, whilst females continue their breeding season that end in August and it is then they return to foraging areas (Schofield et al. 2009). A full complement of adults should therefore be present in foraging grounds in September after the completion of the breeding season. However, our results do not support this scenario as no significant differences in sex ratio per month were identified. This may be due to the small sample size of monthly captures, leading to a type II statistical error, in which case more intensive sampling efforts need to be made, from the relatively small proportion of adult females that leave the Gulf each summer to breed or from more complicated behaviour patterns. Adult female loggerheads typically undertake breeding migrations to the nesting grounds every 2–3 years, with interbreeding intervals varying per individual (Broderick et al. 2002); consequently, no more than 50 % of the adult females in a region would normally depart their foraging habitats to breed. If those individuals that lay only one or two clutches in a season return immediately to their foraging areas, this could mask evidence for reduced presence of adult female turtles due to breeding migrations during all sampling periods except May.

In conclusion, we have, over time, identified hundreds of turtles, with an unusually high proportion of males that reside and transit through a small area of Amvrakikos Gulf. These turtles evidently select the region for the latter part of their maturation and adult life stages. Amvrakikos Gulf is a known ecologically important area hosting internationally important breeding populations of Dalmatian pelicans (Pelecanus crispus) and other protected bird species (Zogaris et al. 2003) and it is also inhabited by a resident population of bottlenose dolphins (Tursiops truncatus; Bearzi et al. 2008). The additional recognition of sea turtles as long-term residents in the Gulf will increase its importance, and existing management plans and schemes should

incorporate sea turtle protection. Although, through combining the use of diverse research techniques, we have progressed in identifying the intrinsic significance of the loggerhead turtle population in Amvrakikos Gulf, several important ecological/conservation research questions remain unanswered; especially, how many turtles are present in the entire Gulf and which rookeries (and in what proportions) are represented in the foraging assemblage? Research on these topics, which will provide evidence on connectivity with nesting grounds across the region, is already underway.

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