Contribution to the Theme Section 'Biologging technologies: new tools for conservation'

Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery

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ABSTRACT: The implementation of appropriate protection measures for endangered species in protected areas requires knowledge of their fine-scale habitat use. In May and June of 2006 and 2007, we used GPS loggers (some linked to the Argos system) and a conventional Argos transmitter to track male and female loggerhead turtles *Caretta caretta* in the vicinity of the breeding area of Laganas Bay within the National Marine Park of Zakynthos, Greece. We obtained (1) 9681 useable locations (mean: 1383 locations ind.$^{-1}$; range: 519 to 2198 locations) from Tracktag GPS loggers attached to 7 females for a mean duration of 34 d (range: 17 to 52 d); (2) 1245 useable locations (mean: 311 locations ind.$^{-1}$; range: 38 to 1110 locations) from 4 males fitted with Fastloc Argos tags for a mean duration of 29 d (range: 3 to 51 d) and (3) 100 locations from 1 male fitted with a conventional Argos satellite tag tracked for 128 d. GPS data indicated that before the onset of nesting, both males and females primarily used an area within 500 m of the shore along a core 9 km stretch of coastline, where existing protective legislation requires strengthening. Our observations suggest that a 76.7 % female-biased operational sex ratio, measured previously from in-water surveys, may represent a realistic sex ratio estimate in the period before nesting starts. In the first month following the onset of nesting, female spatial distribution remained similar, whereas most males departed for distant areas presumably to forage. Our study provides quantitative evidence of the need to improve the management planning and conservation measures to protect sea turtles in a coastal breeding area, and new insights on male turtle migration.

KEY WORDS: Conservation management · Endangered species · Population density · Marine vertebrate · Migratory species · Multiple paternity · Wildlife telemetry

INTRODUCTION

Effective conservation management of wide-ranging marine vertebrates requires quantitative information at both local and regional levels (Hyrenbach et al. 2000). In recent decades, satellite telemetry has facilitated the tracking of wildlife movement over thousands of km.

Invaluable information has been provided on migratory corridors and the essential resources that they link, such as reproductive and foraging grounds (Morreale et al. 1996, Sheppard et al. 2006, Rasmussen et al. 2007, Zbinden et al. 2008). While such corridors are rarely protected, partly due to the fact that they often traverse political borders, the prime resource sites they connect

may meet 'siting' criteria for inclusion within national protected area management schemes (Gardenfors 2001, Campbell 2007, Lawton 2007, Wood & Dragicevic 2007). To formulate effective protective zoning and associated conservation legislation and policies, objective and quantitative evidence is required with respect to habitat preferences of key species and core area use within such sites (Sutherland et al. 2004, Togridou et al. 2006). This is of particular consequence in coastal zones where increasing levels of human settlement, leisure and fishing activities may already be placing pressure on endangered species populations and the natural resources on which they depend (Martien et al. 1999, Zbinden et al. 2007a). However, conventional satellite transmitters provide only fairly coarse spatial resolution and are primarily useful in documenting broad-scale movements (Hays et al. 2001a). Recently, tracking units based on GPS technology have become available to wildlife researchers, with an accuracy of metres (Hulbert & French 2001). For this reason, GPS technology is an increasingly important tool to quantitatively address the conservation management requirements of wide ranging terrestrial and marine species both within and between the reserves designated to protect them (Ryan et al. 2004, Douglas-Hamilton et al. 2005, Schofield et al. 2007).

For the globally endangered sea turtle species, much information is now available on the periodic broad-scale movements of adult females as they migrate between nesting and foraging areas, which is usually derived from Argos satellite transmitters (e.g. Luschi et al. 2003, James et al. 2005b, Broderick et al. 2007, Zbinden et al. 2008). Habitat use within breeding and foraging areas has been inferred using mark-recapture, radio, sonic and/or satellite telemetry (van Dam & Diez 1998, Hopkins-Murphy et al. 2003, Zbinden et al. 2007a), and more recently GPS units (Yasuda & Arai 2005, Schofield et al. 2007). However, there remains a bias towards female-oriented research because they come ashore to nest, providing an easy opportunity to attach tracking equipment. At temperate breeding areas, satellite and sonic telemetry studies of female loggerheads indicate use of areas <15 m deep (Hopkins-Murphy et al. 2003, Zbinden et al. 2007a), and recent GPS tracking indicates possible use of areas as shallow as <4 m (Schofield et al. 2007).

Compared to females, far less is known about male turtle movements (but see Limpus 1993, Plotkin et al. 1996, Hays et al. 2001b, James et al. 2005a, Shaver et al. 2005), due to the necessity, and difficulties, of in-water capture (Ehrhart & Ogren 1999). Existing research indicates that males may occupy areas of up to 40 m depth at breeding grounds (Shaver et al. 2005) and, following a protracted mating period, appear to exhibit similar migration patterns to adult female

conspecifics (for overview see Sakamoto et al. 1997, Godley et al. 2008). To objectively determine whether existing or suggested protection measures at local (i.e. within a national park or reserve), national and regional level is appropriate, high-resolution tracking of all segments of the population actively using the area is needed (Seminoff et al. 2002). Furthermore, in the Mediterranean, sea turtle foraging areas remain largely lacking in protective legislation (Zbinden et al. 2008), hence confirmation of the use of certain areas by both adult males and females following migration from breeding areas may provide evidence supporting the establishment of much needed protection sites.

The island of Zakynthos, Greece, hosts the largest known breeding population of loggerheads in the Mediterranean (Margaritoulis 2005). Several hundred loggerhead turtles enter Laganas Bay at the southern part of Zakynthos to breed from mid April onwards (Schofield et al. 2006), and female turtles generally nest from late May until early August, with an average of 1300 clutches per season (Margaritoulis 2005). Existing marine protection zones were delineated based on nesting beach locations and relative nesting densities (Arapis & Margaritoulis 1996). Since the formation of the National Marine Park of Zakynthos (NMPZ) in 2000, regulation of recreational nearshore activities (particularly organised and incidental turtle watching activities) has been strengthened; however, for new legislation to be passed, accurate information on marine area use by adult male and female turtles is essential. During in-water surveys to assess turtle distribution and behaviour between 2003 and 2005 (Schofield et al. 2006, 2008), we noted a strong bias towards female sightings (n = 80 male, n = 1335 female), and accredited this at the time to differential spatial use by males and females in Laganas Bay. Preliminary research using highly accurate GPS TrackTag loggers indicates that female turtles primarily utilise 18.5 km of nearshore coastline at seabed depths of <5 m (or up to 1 km distance from shore; Schofield et al. 2007). However, it was not known whether males exhibit similar patterns.

The aim of our study was to investigate the fine scale movement of male and female loggerhead turtles *Caretta caretta* within a major breeding rookery using GPS tracking units. We also assess the departure of males from the breeding grounds and identify the location of distant post-breeding, presumably foraging, sites. We consider how our data might be used to contribute to sea turtle conservation measures, policies and legislation at a local and regional scale. At the local scale, we evaluate the status of protection measures in the NMPZ, while at the regional scale we contribute information for protection across international borders of male sea turtles through linking of breeding and foraging areas.

MATERIALS AND METHODS

Study area. Laganas Bay is situated at the southeastern part of Zakynthos island, Greece (37° 43′ N, 20° 52′ E). The bay is generally shallow, reaching a depth of about 50 m and a marine area of 89.2 km², which forms the Marine Protection Area of the NMPZ. Laganas Bay has a coastline of 27.8 km in length (Fig. 1). Within the bay are 6 discrete nesting beaches (Fig. 1) with a total length of 6.16 km (Margaritoulis 2005).

Tracking units and turtle capture technique. During 2006 and 2007, GPS tracking units were placed on adult male and female loggerheads; GPS transmitters were placed on males due to the low likelihood of resighting for unit retrieval (and hence the need to remotely relay data), while GPS loggers were placed on females, since units could be removed when individuals subsequently nested. In 2006 and 2007, TrackTag™ GPS loggers (Navsys, www.navsys.com) were deployed onto 4 and 5 adult female loggerhead turtles (curved carapace lengths 77 to 89 cm), respectively. The units were attached during the pre-nesting period in May and removed in June (see Schofield et al. 2007 for detailed logger information). In 2 cases (one in each year), loggers malfunctioned due to deployment problems so that no data were collected. In 2007, 4 Fastloc GPS-Argos tags (Sirtrack, www.sirtrack.com) and 1 conventional Kiwisat 101 PTT Argos unit (Sirtrack) were deployed onto males (curved carapace lengths 79 to 91 cm). The Fastloc GPS-Argos transmitters relayed GPS information remotely via the Argos system. The Fastloc tags were on continuously but included a saltwater switch to suppress attempts to transmit or acquire data when the units were submerged. In addition, the Fastloc data was stored on-board, so that all the acquired Fastloc-GPS data could be downloaded directly to a computer in the event of instrument recovery. One coat of antifoulant was painted on all Sirtrack units.

Navsys estimates the accuracy of TrackTag locations to be around 30 m (2dRMS) for 95% of locations recorded using a horizontal and stationary receiver in the UK. Fastloc units have an accuracy of 55 m in 95% of locations recorded and 20 m in 50% of locations recorded (see www.sirtrack.com). The conventional Argos unit accuracy is categorised by location classes (LC): LC 3, LC 2, LC 1 or LC 0 locations, which are classified as within 150, >150 to 350, >350 to 1000 or >1000 m. Locations classified as Classes A and B have been ill defined, but probably indicate poor accuracy (particularly LC B) (Hays et al. 2001a).

A 4 m research boat was used to find turtles at water depths of 1 to 7 m. Turtles were captured at random along the central 12 km stretch of coastal waters over submerged sandbanks only (for safety reasons) using the turtle-rodeo technique (Ehrhart & Ogren 1999), and were swum into a semi-submerged wooden box attached to the side of the boat (Fig. 2a). Following capture, curved carapace length was measured and a GPS logger or transmitter was attached using a standard method previously employed with various transmitters/loggers (Hays et al. 2003). In brief, the carapace was cleaned and then the logger, embedded in quick setting 2-part epoxy resin (Powerfastners) with wooden baffles, was positioned at the anterior to help prevent impacts to the equipment (Fig. 2b,c). The reproductively active status of captured individuals was determined through in-water observation of courtship and mating activity. The attachment of all devices was conducted under licenses from the Greek Ministry of Agriculture. All GPS loggers and one GPS transmitter were retrieved from the animals by 1 of 2 methods: (1) using the rodeo capture technique or (2) by recovery on the beach immediately following nesting.

Data analysis. All GPS transmitter and logger locations were first plotted to allow a quick initial visual inspection. The data were filtered by (1) subjectively removing visually erroneous locations (i.e. on land or spatially different fixes to previous and successive fixes
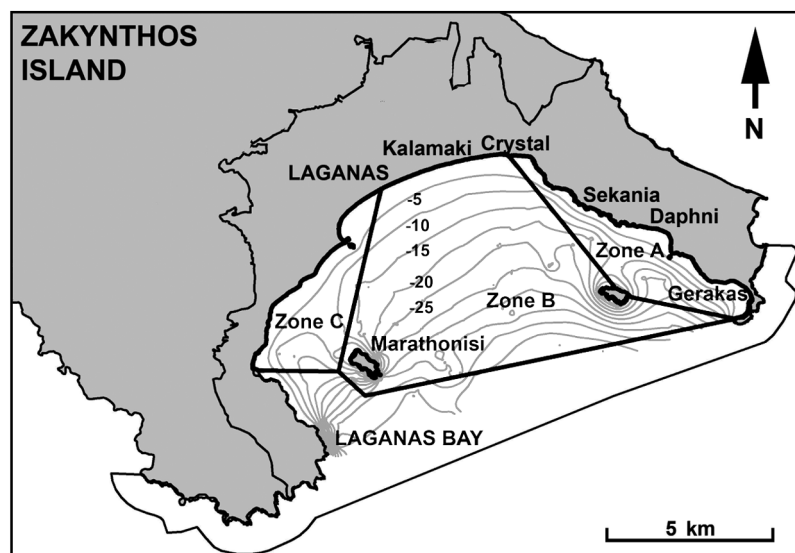

Fig. 1. Area of the National Marine Park of Zakynthos (NMPZ) encompassing the 6 loggerhead nesting beaches of Laganas Bay (Marathonisi, Kalamaki, Crystal, Sekania, Daphni, Gerakas). Bathymetry (isobars at 5 m sea depth intervals) and the 3 NMPZ protection zones are shown; Zone A (no boating activity), Zone B (boating speed up to 6 kn permitted and no mooring), Zone C (boating up to 6 kn permitted and mooring)

within the same timeframe), (2) using a maximum rate of travel of 5 km h^{-1} between successive locations (Hays et al. 2004), which was selected based on calculations from 3 or more consecutive fixes occurring at 10 to 20 min intervals, and (3) removing data from when the turtles were onshore (nesting and/or aborted nesting attempts). We then calculated the mean GPS location h^{-1} for each turtle (Tremblay et al. 2006). We calculated the daily mean location of each turtle from the hourly datasets, from which the daily distance from shore of different turtles was calculated. We divided the 27.8 km coastline of Laganas Bay into 3 equal sections of coastline, each 9 km long (the eastern, central and western sections), and used hourly datasets to determine general area use. Note that the eastern section of coastline falls in the highly protected no-boating park zone, while the eastern and central sections fall in the low protected zones where boating is permitted. An estimate of migratory distance for the males was calculated by summing up distance travelled between daily locations. For the data from the conventional Argos PTT unit, locations were filtered using a maximum rate of travel of 5 km h^{-1} between successive locations (Hays et al. 2004).

In order to correlate male departure times with respect to the onset of nesting, information on the daily nest number in 2007 was obtained from the NMPZ for all beaches in Laganas Bay. The number of new nests from the previous night was assessed from tracks. The mean date of nesting for 2007, 3 July, was determined by:

$$\text{Mean date of nesting} = \frac{\sum xf}{\sum f}$$

where x is the day of year (i.e. 1 January = Day 1 and 31 December = Day 365) and f is the number of nests.

The nesting 'peak' is the date on which the greatest number of nests was recorded (27 June, Day 178).

The mean date on which the transition between the pre-nesting (phase prior to the first nesting event) and internesting (phase between first and last nesting events) period occurred was calculated from the first nesting event for each female from the GPS datasets (Table 1). This was identified when locations were being consistently recorded at 30 s intervals for a minimum of 30 min, indicating that the turtle was on land. If more than one nesting event was recorded in a 5 d period, the last event was selected as the successful event, with the preceding events being recorded as non-nesting emergences. Subsequent nesting events were also identified in 5 of the tracked turtles, and this information was used to calculate internesting intervals. For correlation with the dataset of the male that remained in the breeding area, we also separated the 2 periods by identifying the date from which nests were recorded daily thereafter. In 2006 and 2007, the first nest was laid on 29 May (Day 149) and 17 May (Day 137), respectively, with regular daily nesting being recorded from 29 May (Day 149) and 1 June (Day 152) onwards, respectively.

Nearshore surveys. For the current study, we revisited the in-water sea turtle distribution and behaviour datasets from 2003, when the most robust surveys were conducted by boat (Schofield et al. 2006, 2008). On 27 fair weather days from 14 April to 31 May 2003, daily line transects were made at seabed depths of 3, 5, 7 and 10 m (i.e. up to 1 km from shore) along a 5.5 km stretch of nearshore coastline within Laganas Bay (for map see Schofield et al. 2006). Boat surveys (405 km total distance, 137 h total duration) were conducted by 2 to 3 observers on a 4 m boat with an outboard engine. Sessions lasted an average of 5 h (minimum 4, maxi-

Table 1. GPS logger and transmitter locations acquired and those remaining after filtration. Dates given as dd/mm/yyyy. CCL: curved carapace length of turtle; CCW: curved carapace width of turtle. No. of operational days and mean points per day are highlighted in bold

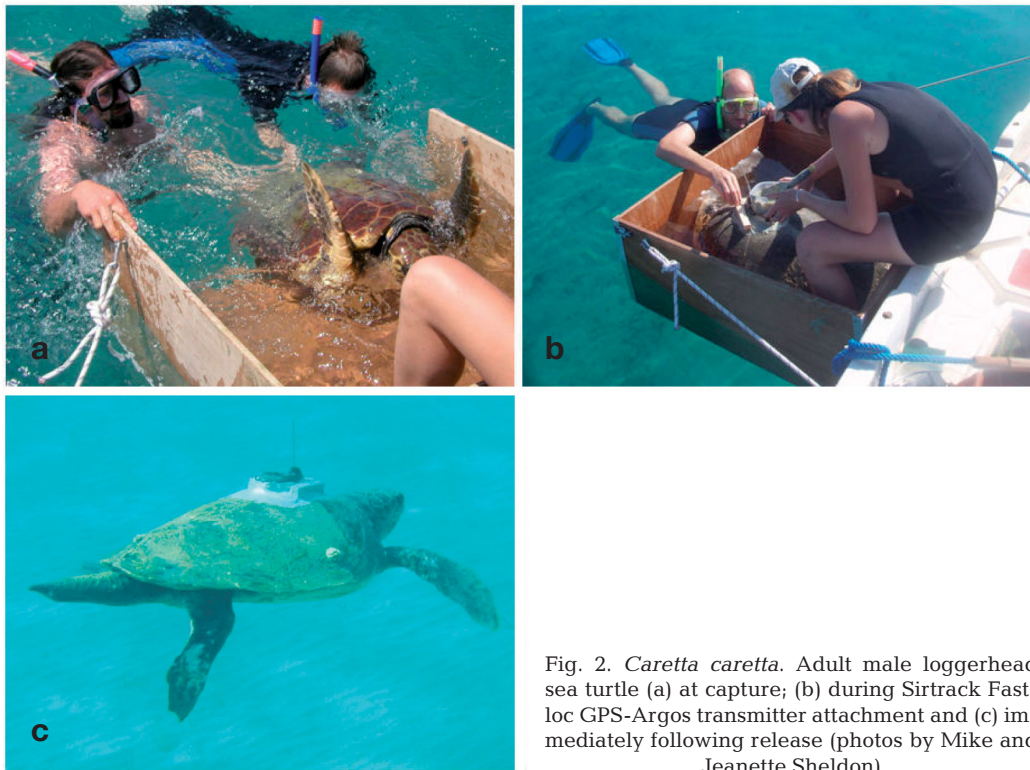| Year	Turtle ID	Device	CCL	CCW (cm)	Date GPS attached	Date GPS stopped	Date of first nesting	Date of departure	No. days operational	Post-filtering locations Total	Mean d^{-1}
2006	Female_1	TrackTag GPS	81	73.5	19/5/2006	6/6/2006	21/5/2006		**17**	519	**31**
2006	Female_2	TrackTag GPS	89	76	23/5/2006	26/6/2006	25/6/2006		**31**	2198	**69**
2006	Female_3	TrackTag GPS	87	72	24/5/2006	18/6/2006	7/6/2006		**25**	818	**33**
2007	Female_4	TrackTag GPS	83	75	4/5/2007	25/6/2007	5/6/2007		**52**	2081	**25**
2007	Female_5	TrackTag GPS	84	77	8/5/2007	11/6/2007	3/6/2007		**34**	909	**27**
2007	Female_6	TrackTag GPS	81	74	9/5/2007	26/6/2007	23/5/2007		**48**	1779	**37**
2007	Female_7	TrackTag GPS	77	66	11/5/2007	12/6/2007	21/5/2007		**35**	1377	**39**
2007	Male_1	Sirtrack GPS	81	72	8/5/2007	26/6/2007		n/a	**49**	1110	**23**
2007	Male_2	Sirtrack GPS	91	81	10/5/2007	30/6/2007		20/5/2007	**51**	53	**1**
2007	Male_3	Sirtrack GPS	81	74	14/5/2007	17/5/2007		14/5/2007	**3**	38	**13**
2007	Male_4	Sirtrack GPS	79	70	10/5/2007	25/5/2007		22/5/2007	**15**	44	**1**
2007	Male_5	Sirtrack satellite	90	83	7/5/2007	12/9/2007		23/5/2007	**128**	100	**0.8**
		Total							**488**	**11026**	**22.5**

Fig. 2. *Caretta caretta.* Adult male loggerhead sea turtle (a) at capture; (b) during Sirtrack Fastloc GPS-Argos transmitter attachment and (c) immediately following release (photos by Mike and Jeanette Sheldon)

mum 7 h) at a maximum boat speed of 4 knots. The survey period covered a range of daylight hours between 09:30 and 19:30 h. GPS locations of turtle sightings were recorded using Garmin E-Trex hand-held units and still photographs were taken underwater when snorkelling at a distance of 2 to 7 m from the target animal, using an Olympus Digital 500 (5.0 megapixel) camera with underwater housing. Animal gender was determined based on tail-length dimorphism (Casale et al. 2005) and presence/absence of external identification-tags (only females are tagged).

We used the natural scalation patterns on the lateral facial region to identify individual turtles with high accuracy (see Schofield et al. 2008).

RESULTS

Tracking data

Excluding deployment and retrieval days, we tracked 3 female turtles equipped with TrackTag GPS loggers in 2006 and 2007 for a mean 34 d each (range 17 to 52 d). The 4 males equipped with Fastloc GPS-Argos transmitters were tracked for a mean 29 d each (range 3 to 51 d). The 1 male equipped with a conventional Argos transmitter was tracked for 128 d (Table 1). The volume of useable locations obtained from the different devices (TrackTag GPS loggers,

unretrieved Fastloc GPS-Argos transmitters, retrieved Fastloc GPS-Argos transmitter and conventional Argos satellite transmitter) are presented in Table 1. The retrieved TrackTag loggers and Fastloc transmitter provided a much greater volume of data compared to that relayed via Argos. As expected, given their greater accuracy, all GPS units provided very detailed information on sea turtle area use, in contrast to the conventional Argos unit from which only the general location of the turtle could be inferred (Fig. 3).

Male and female area use in the breeding area

The data from the GPS units (loggers and transmitters) indicated that both male and female turtles primarily used the marine area close to shore (from hourly positional datasets) (Fig. 3a & video animation in electronic supplement at www.int-res.com/articles/suppl/n010p191_app/). Before and after the onset of nesting, 82% of all 7 female GPS locations in Laganas Bay occurred within 500 m of the shore (Fig. 4a) (approx. depth <5 m). In the pre-nesting period, 92% of all 4 male GPS locations also occurred within 500 m of the shore in Laganas Bay (Fig. 4b).

The GPS units not only indicated this nearshore preference, but also that the tracked males and females appear to prefer certain stretches of coastline within Laganas Bay. We found that, before the onset of nest-
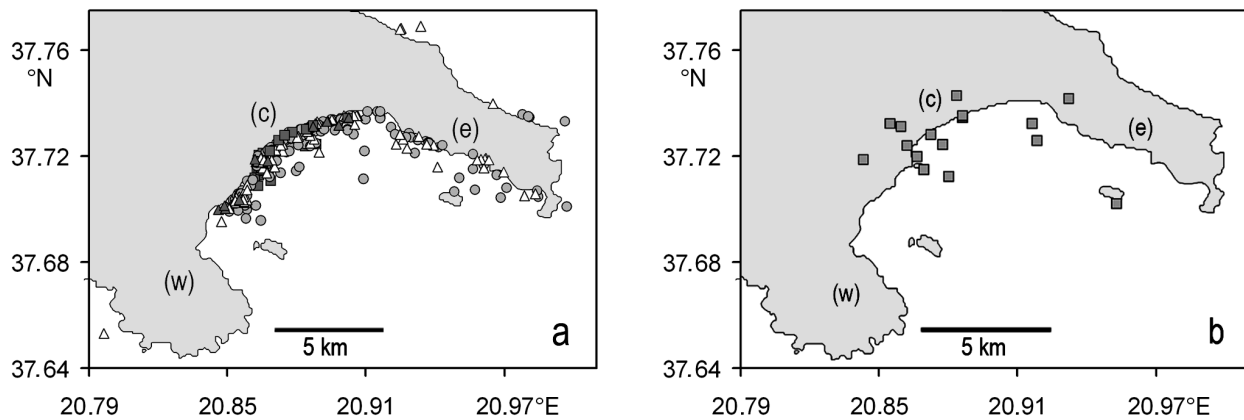
Fig. 3. *Caretta caretta*. Daily mean (a) GPS locations for males (n = 4, 72 locations, squares) and females (2006: n = 3, 109 locations, triangles; 2007: n = 4, 124 locations, circles) in Laganas Bay and (b) male Argos locations (n = 1, 16 locations). We considered Argos fixes falling on land as belonging to the closest point off the coast. Bay divisions: (w) western (c) central, (e) eastern

ing, 100 % of male GPS locations and 77 % of female GPS locations occurred along the central section of coastline. Only one GPS-tracked male remained in Laganas Bay following the onset of the nesting season and appeared to restrict all its activity to the central section of coastline before and after the onset of nesting. Of the 7 tracked females, activity was confined within Laganas Bay before the onset of nesting (99 % of GPS locations), with some movement out of Laganas Bay occurring after the nesting season had started in June (79 % of GPS locations in Laganas Bay).

After the onset of nesting, females continued to preferentially frequent the central section of coastline (54 % of GPS locations). Before and after the onset of nesting, 21 % of female GPS locations occurred along the eastern section of coastline (containing 3 nesting beaches together representing 70 % of rookery nesting effort), which appeared to be associated with nesting activity, with turtles in general moving to this section of coastline 3 to 5 d before nesting. Just 0.2 % of female GPS locations occurred along the western section of the coastline.

Female movement in the vicinity of the breeding area

Of the 7 females tracked using GPS loggers, 4 remained in Laganas Bay before and after the onset of nesting. Three turtles exited Laganas Bay on 6 occasions. In 2006, one turtle exited Laganas Bay on 2 occasions, frequenting the island's west coast for one day during the pre-nesting period and the east coast for 4 d following the first nesting event. In 2007, 1 turtle exited Laganas Bay on one occasion during the internesting period and occupied the east coast for 4 d. One turtle exited Laganas Bay on 3 occasions prior to the first nesting and swam to the east coast for 1 d on each occasion. The day following the first nesting (indicated by the GPS data), the same turtle travelled 96 km to Kyparissia Bay in the Peloponnese over a 15 d period (Fig. 5); travelling for 4 d directly to the Peloponnese, remaining there for 8 d and returning over 3 d. The turtle nested again on Zakynthos 5 d later, with an internesting interval of 20 d. It is unlikely that the turtle nested when in Kyparissia, as no locations were continuously recorded at 30 s intervals to indicate the
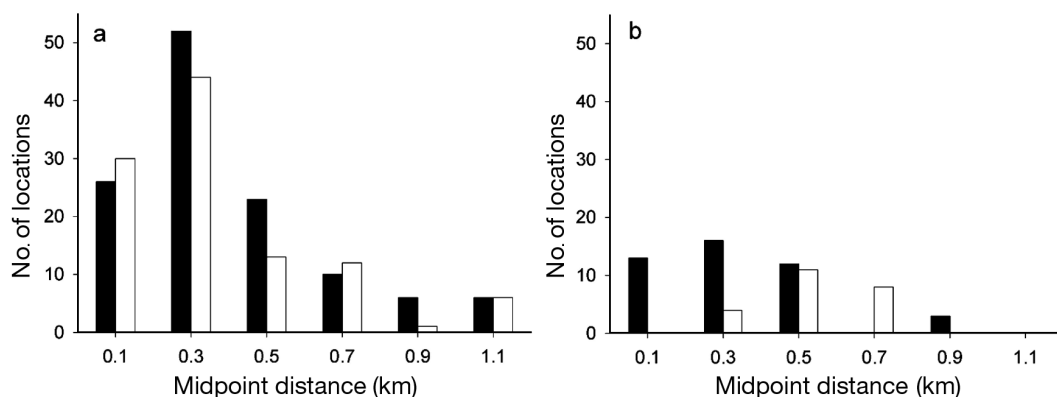

Fig. 4. *Caretta caretta*. Distance from shore before (black bars) and after (white bars) the onset of the nesting season for (a) females (n = 7) and (b) males (n = 4 before and n = 1 after) obtained from hourly positional datasets
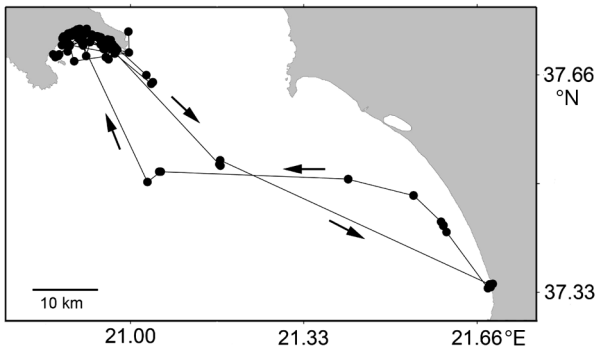
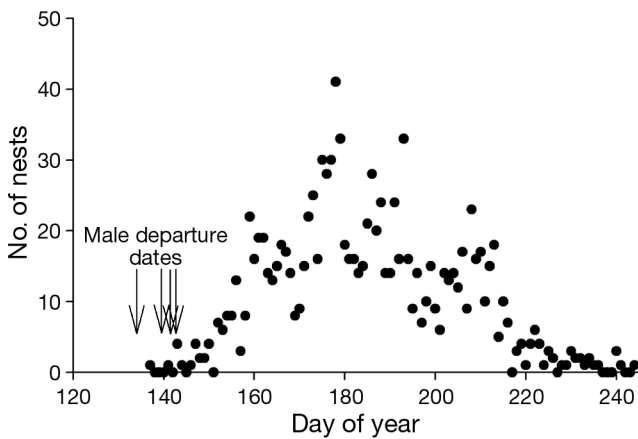Fig. 5. *Caretta caretta*. Internesting migration from Zakynthos to the Peloponnese by 1 female during 2007

Fig. 6. *Caretta caretta*. Number of nests each day of year 2007. Days of departure of the 4 tracked male turtles are indicated with arrows (nesting data obtained from NMPZ archives)

turtle was out of the water, and we also documented a mean internesting interval of 17 d (SD ± 3.3) in 5 of the tracked turtles.

Male movement following the onset of the nesting season

Males departed from the breeding grounds of Laganas Bay between 14 and 23 May (Table 1), which averaged 3 d after the first recorded nest (17 May, Day 137), 12 d before the start of regular nesting activity (1 June, Day 152), 38 d before the nesting peak (27 June, Day 178) and 44 d before the mean date of peak nesting (3 July, Day 183) (Fig. 6).

Four of the males departed in different directions; 2 departed in a south-easterly direction, one in a south-westerly direction and one in a north-westerly direction (Fig. 7a). One male remained in Laganas Bay and was last sighted on 27 August (when the Fastloc GPS-Argos transmitter was retrieved), still inhabiting the same nearshore section.

Two males were tracked to their presumed foraging areas (Fig. 7b). The male with the Fastloc GPS-Argos transmitter swam to a foraging area between the islands of Olib and Silba in Croatia, 721 km north of the nesting area. It travelled a total distance of 762 km over 21 d and was recorded to arrive at the presumed foraging grounds on 12 June, remaining there until 30 June when transmissions terminated. The male equipped with the conventional Argos transmitter swam to a foraging area in the Bay of Izmir in Turkey, 597 km north east of the nesting area. The turtle travelled a
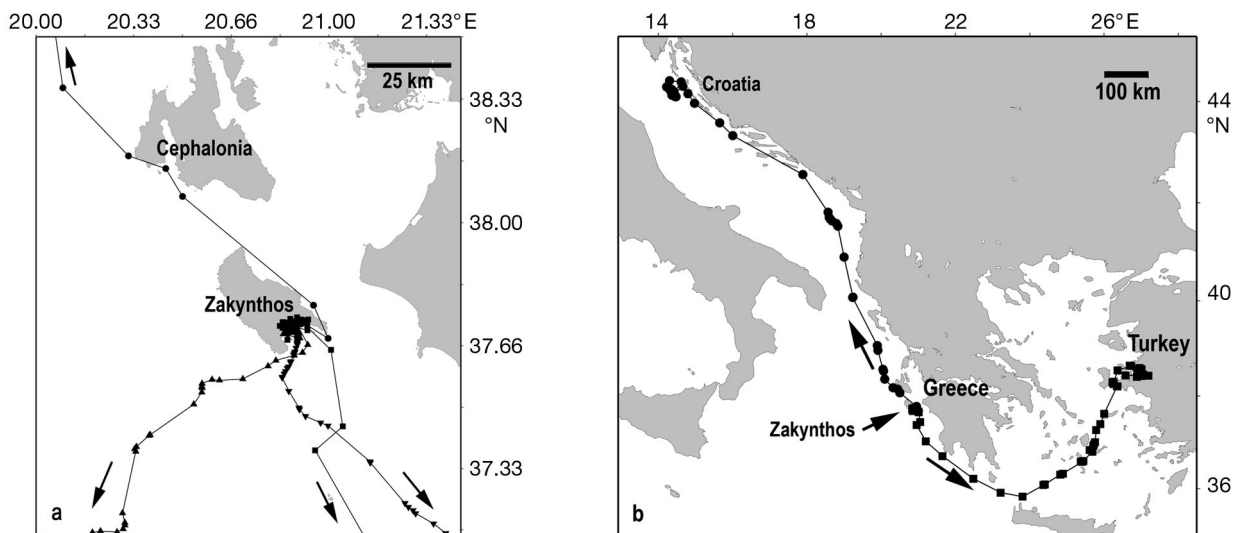

Fig. 7. (a) Disparate departure directions of the 4 males that migrated away from Zakynthos. (b) Long distance migration of 2 male turtles from the breeding area of Zakynthos; 1 GPS transmitter track to the islands of Olib and Silba in Croatia and 1 satellite transmitter track to the Bay of Izmir in Turkey

total distance of 927 km (calculated from daily mean locations) to reach the presumed foraging area over an 18 d period, was recorded to arrive on 10 June and was still transmitting from the same vicinity on 12 September.

Interestingly, the male that remained in Laganas Bay changed its spatial area use in the periods before and after the onset of nesting activity from mainly within 500 m to more than 500 m from shore (Fig. 4b).

Population parameters

In the current study, we combine the results of the in-water surveys with turtle GPS locations information to calculate an operational sex ratio for the breeding area. We crudely estimated the mean female seasonal breeding population size to be 463 individuals by dividing the mean number of nests recorded between 1984 and 2002 (1293.7 nests; Margaritoulis 2005) with an estimated mean clutch frequency of 3 (based on information from Jensen et al. 2006, Zbinden et al. 2007a).

In 2003, photographic records were collected from a total of 460 loggerhead sightings during 27 surveys in April and May. From these records, we identified 38 unique males and 127 unique females, with an average resighting rate of 3 times per individual across surveys. From this information, we calculated a 76.7% female bias (1 male to 3.3 females) in the operational sex ratio. We also recorded the average sex ratio in each field survey and found a significant temporal change across the survey period, from 66.7% male bias (2 males to 1 female) in April to a 90% female bias (1 male to 9 females) in late May ($F_{1,22} = 71.3$, $r^2 = 0.75$, p < 0.001) (Fig. 8).
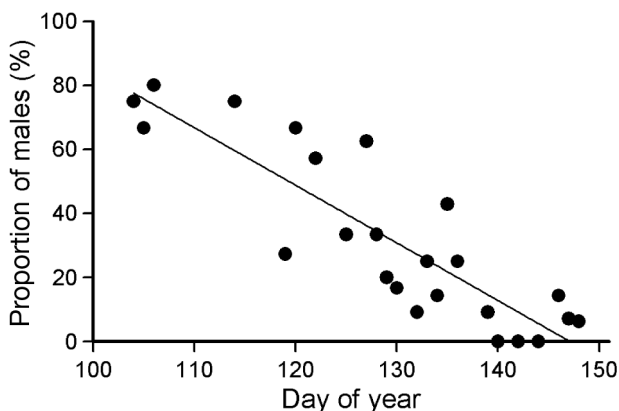

Fig. 8. *Caretta caretta.* Proportion of males present in the nearshore waters of Laganas Bay, showing a significant decline between 14 April and 31 May in 2003 ($F_{1,22} = 71.3$, $r^2 = 0.75$, p < 0.001)

DISCUSSION

The fine-scale movements recorded for both male and female loggerhead turtles in the present study provide information on critical habitat use to guide management decisions fundamental to their conservation. Our data strongly suggest that, before the onset of nesting, both males and females use the same nearshore area, along a specific 9 km stretch of coastline and primarily within 500 m of shore (or within 5 m sea depths) in Laganas Bay. This supports previous observations that females use sea depths up to 15 m when in the breeding area (Hopkins-Murphy et al. 2003); however, our results indicate a much narrower area use by males than the previously recorded sea depths of up to 40 m (Shaver et al. 2005). One of the tracked males remained in the breeding area, with a noticeable shift in sea depth use to deeper water following the onset of nesting. This shift may have reflected a change in the status of a resident, i.e. from breeding to foraging, and may explain the greater depth range recorded for males in other breeding areas (see Shaver et al. 2005).

Our observations suggest that it is unlikely that females are successfully using the nearshore habitat as a refuge from males following mating (Booth & Peters 1972, Whittow & Balazs 1982). For example, females maintained the same pattern of nearshore habitat use in the first month following the onset of nesting, despite the fact that most males had migrated out of the breeding area by this time. Males may be found close to shore because they follow the females to maximise their mating opportunities. By restricting their area use, females may conserve energy expenditure during the reproductive season, when they may lay several clutches over several months (Hays et al. 1999, Wallace et al. 2005). Furthermore, turtles utilising the nearshore area of Laganas Bay have been found to experience water temperatures around 5°C above that in waters >10 m depth (Schofield et al. 2009), which would decrease the duration between nesting events (Sato et al. 1998, Hays et al. 2002), thereby allowing a greater number of clutches to be laid when incubation conditions are optimal. Future studies might examine the behaviour of females later in the season to see if their interesting behaviour changes, for example with seasonally increasing water temperatures (Hays et al. 2002).

In 2006, one of the 3 tracked female turtles utilised waters outside of Laganas Bay (Schofield et al. 2007). The behaviour of this individual was not discussed due to the small sample size and the probability of this being anomalous for this population (see Zbinden et al. 2007a). However, the results of the 2006 and 2007 tracking data combined indicated that several of the

tracked females moved at spatial scales beyond the main breeding area, which is consistent with previous suggestions that loggerheads may show poorer beach fidelity (Stoneburner 1982, Hays & Sutherland 1991, Katselidis et al. 2004) than some other sea turtle species (Mortimer & Portier 1989). The discrepancy in observations between Zbinden et al. (2007a) and our study, both in the same breeding area, may be attributed to the former recording movement in late June to August and the latter recording movement in May to late June, possibly indicating a change in behavioural patterns across the nesting period. The level of internesting movement may depend on the habitat needs of each species, such as foraging in leatherbacks (Georges et al. 2007) or possibly prospecting alternative nesting sites in loggerheads. This suggestion is supported by the fact that nesting activity does occur on the east coast of Zakynthos and Peloponnese where the turtles were recorded in our study. If these broad-scale movements occur regularly within the population, then current protective measures of the Zakynthos breeding area may require re-evaluation.

The use of GPS tracking in the present study defined the fine-scale habitat use by both males and females of the sea turtle breeding population and, therefore, the critical site at which heightened protection measures are required (Sutherland et al. 2004, Wood & Dragicevic 2007). Our research was conducted in collaboration with the NMPZ to evaluate the effectiveness of existing protective zoning. Of management interest, GPS tracking of females in 2006 and 2007 indicated preferential nearshore area use outside of the core marine protected area, with similar patterns being recorded in tracked males. Our findings support the experimental introduction of the national park 'ecotourism zone' in 2006 to reduce disturbance to turtles through stricter boating regulations (Lusseau 2004) and expansion to include the prime section of coastline used by both sexes. However, governmental legislative action is required to reform existing zones, which is difficult to secure (Togridou et al. 2006, Campbell 2007, Lawton 2007). Our study also indicated the possible presence of resident turtles, hence research to determine winter area use around Zakynthos is important to improve protection measures, particularly with respect to the fishery industry bycatch (Martien et al. 1999). GPS tracking facilitates the fine-scale analysis of wildlife movement patterns and we strongly recommend its use in the delineation of protection zones to ensure that the habitat requirements of the species in question are met (Martien et al. 1999, Sutherland et al. 2004, James et al. 2005b).

Establishing the number of adult males and females is important, as empirical evidence for highly skewed female adult sex ratios may necessitate an increased conservation focus on males. Furthermore, climate change may impact turtle population dynamics, hence an understanding of sex ratios at different life stages is vital to ensure effective protection. At the Zakynthos rookery, we inferred a highly female-biased adult sex ratio using our photo-identification and GPS tracking information. The GPS tracks from our 11 male and female turtles indicated that 100% of male and 77% of female hourly locations occurred along the central 9 km of coastline during May. The consistency of nearshore use by tracked individuals in this study strongly suggests that this is a general feature of the population as a whole, therefore the Zakynthos operational sex ratio recorded in 2003 may be representative of the population. However, as with many biotelemetry studies, our sample sizes were fairly small and further tracking with larger sample sizes would clearly be useful. To obtain a preliminary estimate of population size, we crudely combined the 2003 sex ratios with the mean female operational population size. We predicted an operational population size of about 593 individuals: 130 males and 463 females. This calculation clearly contains a number of assumptions—further work is needed to refine estimates of relative males and female numbers as well as to establish the variance of these estimates.

Highly skewed female sex ratios of 60 to 99% have already been documented for loggerhead hatchlings in the Mediterranean (see Zbinden et al. 2007b) and other populations around the world (Mrosovsky & Provancha 1989, Marcovaldi et al. 1997). Studies of juveniles indicate that skewed ratios may be balanced by males originating from elsewhere (Henwood 1987), though this may be a result of sex-related dispersal (Casale et al. 2006). Estimates of total population numbers and sex ratios depend on recruitment rates and the return rates of both males and females; females are believed to return biannually (Hays & Sutherland 1991) and data from Australia suggest annual return rates in males (Chaloupka & Limpus 2001). If this is the case, an 85% female bias may exist in the total adult population, which is similar to the 75% female bias in hatchling sex ratios on Zakynthos predicted by Zbinden et al. (2007b). However, robust measurements of remigration intervals for both males and females from a single population are scant, and this topic needs further study. If the difference in remigration intervals between males and females is even more marked than the 1 and 2 yr, respectively, that we have assumed, then the consequences are that the female bias in the adult sex ratio may be even more extreme than 85%. Laganas Bay is not thought to contain large numbers of juvenile turtles. Certainly no small juveniles were seen during surveys. In theory, very large juveniles might be assigned as females, but the lack of smaller juve-

niles suggests that this possibility is unlikely and therefore would not impact our conclusions in any important way.

We found that sea turtle density in the breeding area may be high, since our GPS data show that sea turtles primarily aggregate along 9 km^2 (9 km long by 1 km out to sea) of coastline, rather than uniformly using the 89 km^2 area of Laganas Bay. Based on our preliminary population estimate we calculated that, if sea turtle densities were uniform across Laganas Bay, there would be 5.3 ind. km^{-2}. However, our GPS data suggested that, if 100% males and 77% females utilise 9 km^2 nearshore area during May, we may have densities of 54 ind. km^{-2}. Hence, this high use area should be the first priority for the management plan and legislation of the NMPZ. It should be noted that, for the purposes of these calculations, we used a clutch frequency of 3; however, this number is highly variable within loggerhead populations and requires confirmation (Dodd 1988). Estimating the number of turtles from the total number of clutches laid each year is crucially dependent on the estimate used for the mean number of clutches per individual. Establishing the number of adult males and females is important, as empirical evidence for highly skewed female adult sex ratios may necessitate an increased conservation focus on males. However, estimates of mean clutch frequency for sea turtles are problematic because of the logistic difficulties of observing females every time they nest. Hence, estimates of mean clutch frequency may need to be refined in the future as better data become available using new methods (e.g. Cronin & McConnell 2008). The high density of turtles at Zakynthos may explain the unusually high multiple paternity recorded at the Zakynthos rookery (Zbinden et al. 2007c) despite it being a small loggerhead population relative to other rookeries exhibiting high levels of multiple paternity (Jensen et al. 2006, Lee 2008).

In support of the literature, we observed a male bias in the adult population at the start of the nesting season, yet most tracked males departed prior to the onset of nesting (Plotkin et al. 1996, Godley et al. 2002, James et al. 2005a). Both males and females undertake long migrations to breeding areas. Female turtles only need to mate once as they have the capacity to store sperm to fertilise subsequent clutches and so may resist multiple mating (Booth & Peters 1972, Lee & Hays 2004). Therefore, there is a trade-off for male turtles when away from the foraging area; to maximise paternity rates, they must arrive at the breeding area early enough to mate with unmated females, but not so early that they waste energy waiting for females to arrive. Males that remain at the breeding ground all year would save on the energetic cost of migration and have the potential to mate with more females, espe-

cially in populations where female arrival is variable. While some individuals may forage year-round on Zakynthos, prey availability may not be adequate to sustain the population, resulting in different adult dispersal strategies as indicated by Shaver et al. (2005), with most males migrating out of the breeding area prior to the onset of nesting. Presumably, these males were departing from the breeding area when most females had mated and were no longer receptive (Plotkin et al. 1996, Hays et al. 2001b, Godley et al. 2002, James et al. 2005b).

Adult male turtles monitored by satellite have been recorded to travel large distances from breeding grounds (Sakamoto et al. 1997, Hays et al. 2001b, James et al. 2005a). One of the few studies to follow both sexes tracked adult leatherbacks in the North Atlantic, where similar long-distance movements for the sexes were seen (James et al. 2005b). Our results suggest that males have broadly similar dispersal and migratory patterns to those recorded in post-nesting females (Zbinden et al. 2008), with disparate distant (presumed foraging) grounds. Two of the males in our study were tracked to distant presumed foraging areas in Turkey and Croatia, identified due to the tracking locations being concentrated in one area. Following the widely held paradigm for the life history of loggerhead turtles, we assume these distant areas were foraging and/or overwintering areas (see Lohmann et al. 2008). By combining tracking data of sex and age classes with local empirical studies it may be possible to identify other foraging sites in need of national and trans-boundary conservation management action (Gardenfors 2001, Campbell 2007, Wood & Dragicevic 2007).

Our study supports the value of GPS tracking for the understanding of spatial area use of marine vertebrates such as sea turtles at both local and regional scales. At the local scale, GPS tracking contributes to the evaluation of conservation measures, policies and legislation, while at the large scale, it can be applied to create integrated networks of protected areas encompassing breeding, migratory and foraging areas at national, trans-boundary and global levels. Our study indicated that, while retrievable GPS units produce a much larger volume of data, GPS transmitters provide the opportunity to track the fine-scale movement of more elusive components of the population (i.e. males) within the protected area and at post-migratory foraging grounds. This is of particular importance because of the low male sex ratios recorded in the Zakynthos population, which appears to continue throughout development. In conclusion, fine-scale GPS tracking of wildlife movement patterns may contribute towards enhancing national and international efforts to identify, delineate and develop new and effective protected areas.

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