



Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management

Gail Schofield^{a,b,*}, Victoria J. Hobson^a, Martin K.S. Lilley^a, Kostas A. Katselidis^b, Charles M. Bishop^c, Peter Brown^d, Graeme C. Hays^a

^a School of the Environment and Society, Swansea University, Singleton Park, Swansea SA2 8PP, UK

^b National Marine Park of Zakynthos, 1 El. Venizelou Str., GR-29100 Zakynthos, Greece

^c School of Biological Sciences, Bangor University, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK

^d Navsys Ltd, Kirknewton, Edinburgh EH27 8DY, UK

ARTICLE INFO

Article history:

Received 30 April 2009

Received in revised form 11 November 2009

Accepted 12 December 2009

Available online 8 February 2010

Keywords:

Breeding dispersal

Climate change

Habitat selection

Marine protected areas

Marine vertebrate

Phenology

Telemetry

ABSTRACT

We assessed home range size for breeding loggerhead turtles (*Caretta caretta*) near the limit of the species range at the Greek island of Zakynthos in the Mediterranean. Thirteen adult females and seven adult males were tracked using GPS units (loggers and transmitters) during May and June of 2006, 2007 and 2008. Kernel analysis indicated that core home range sizes (50% estimator; range: 2.9–19.7 km²) for both males and females were restricted to a 7.5 km tract of coastline. 15% of GPS locations fell outside of the national park protection zones, while within the protected breeding area 88% of GPS locations occurred in zones of minimal protection. Female home ranges were 64% larger in 2008 than in 2006 and 2007, indicating that several years monitoring may be required for the most effective designation of marine protected areas (MPAs). Ten of the tracked females departed the core breeding area on 15 occasions for periods of 1–15 days travelling distances of 10–100 km, although none nested at alternative breeding sites. The inter-annual variability of breeding area home range size and likelihood of incidence of forays appeared to be correlated with barometric pressure. The movement responses of loggerheads to environmental conditions implicates an ability to switch nesting areas over small scales in response to climate change. However, such behaviour suggests the protection of existing core breeding sites may be inadequate, with policy makers being required to consider the protection of broader areas to encompass potential changes in the habitat needs of this species.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

There is immense interest in movement and space-use by animals, as these are fundamental life-history components and may also be important in the designation of marine protected areas (MPAs) (Bell, 1991; Argardy, 1994; Parnell et al., 2006). Assessment of movement patterns can be used to determine the spatial dynamics and distribution of populations, including habitat selection, home ranges, movement and/or dispersal of individuals (Bowler and Benton, 2005). While home range studies provide quantitative information that may help define protected areas, the factors influencing dispersal and home ranges size must be evaluated for effective conservation management (Borger et al.,

2006; Parnell et al., 2006; Laver and Kelly, 2008). Furthermore, as climate change is already altering, or is predicted to alter, population dynamics and species distributions, conservation strategies must plan to encompass not only existing but possible future sites required by the species under consideration (McMahon and Hays, 2006; Parnell et al., 2006; Hawkes et al., 2007; Giorgi and Lionello, 2008).

Given the importance of home range studies it is perhaps surprising that such studies of sea turtles have primarily concentrated on juvenile movement in neritic foraging habitats (see Seminoff et al., 2002 for overview). While adults are frequently tracked with satellite transmitters and, for example, their movements within the breeding area are described (e.g. Hays et al., 1991; Shaver et al., 2005; Eckert et al., 2006; Georges et al., 2007; Seney and Landry, 2008), these results have rarely been placed in the context of home range estimates. Perhaps the paucity of home range estimates for adults is because the locations recorded with conventional Argos satellite tags may be many kilometres from the true position (Rutz and Hays, 2009), and hence unsuitable for rigorously defining home range size.

* Corresponding author. Address: National Marine Park of Zakynthos, 1 Elefteriou Venizelou Street, Zakynthos GR29100, Greece. Tel.: +30 2695 0 29870, mobile: +30 6944567490; fax: +30 2695023499.

E-mail addresses: g.schof@gmail.com (G. Schofield), v.j.hobson@swansea.ac.uk (V.J. Hobson), M.K.S.LILLEY.385124@swansea.ac.uk (M.K.S. Lilley), kkatselidis@nmp-zak.org (K.A. Katselidis), bss40d@bangor.ac.uk (C.M. Bishop), pbrown@navsys.com (P. Brown), G.Hays@swansea.ac.uk (G.C. Hays).

While GPS tracking has been widely used in terrestrial species for defining home-range (Lawson and Rodgers, 1997; Hulbert and French, 2001), it has proved difficult to implement for diving marine species because of limited time at the surface for acquisition of GPS ephemeris. However, recently developed GPS tracking units that allow very fast acquisition of GPS ephemeris, now have facilitated the tracking of marine species with high resolution (Rutz and Hays, 2009). In the current study we investigated the home range of adult sea turtles at the largest breeding population in the Mediterranean, with a view to providing empirical evidence for key habitats in need of conservation. The Greek island of Zakynthos, in the Mediterranean, hosts one of the most northerly breeding populations for loggerhead sea turtles, and as a result reproductive activity is constrained by a relatively narrow window of optimal ambient conditions (Margaritoulis, 2005; Schofield et al., 2009a). Several hundred individuals migrate each spring to the breeding area of Laganas Bay, at the southern part of Zakynthos, to mate (early April–early June) and subsequently lay around three clutches of eggs (late May–early August). Preliminary observational and GPS tracking has indicated that both males and females tend to preferentially use the nearshore area (Schofield et al., 2006, 2007, 2009b). In the case of females this seems to be to locate warm water patches to enhance egg development from May to mid-June, due to low ambient sea temperatures (c. 13–22 °C) (Schofield et al., 2009a). It has been suggested that the movement of females beyond the core area during the breeding season is anomalous for this population (see Zbinden et al., 2007a). However in the early part of the breeding season at Zakynthos, inter-annual variation in thermal conditions may influence whether females remain or seek alternative breeding sites. An increased frequency of spring storms may reduce the quality of this breeding habitat; alternatively reduced frequency of spring storms may result in earlier nesting as a result of warmer sea temperatures (see Pike et al., 2006; Mazaris et al., 2008).

Climate change predictions in the Mediterranean suggest surface warming of 0.7–4.6 °C (1 °C lower in the sea), reduced precipitation levels by 2–28% and increased variability of extreme weather events such as storms across the 21st century (Giorgi and Lionello, 2008). However there is disagreement over altered storm intensities, frequencies and seasonal distributions (Christensen and Christensen, 2003; Sumner et al., 2003; Beniston et al., 2007). Hence, the aim of our study was to measure the variability in home range size and the potential implications of weather on sea turtle behaviour over a 3 year period. We used GPS tracking units to delineate: (i) core home ranges within and across seasons for breeding males and females (ii) the role of environmental cues for driving female movement beyond the core home ranges within each breeding period (iii) the implications of movement patterns for the selection and delineation of marine conservation areas.

2. Material and methods

2.1. Study area

This study was conducted between May and June across a 3 year period (2006–2008), at the loggerhead breeding area of Laganas Bay situated at the south-eastern part of Zakynthos island, Greece (37°43'N, 20°52'E). Laganas Bay is generally shallow, reaching a maximum depth of about 50 m, with sea surface temperatures of 15 °C in March rising to 28 °C in August (Comprehensive Ocean Atmosphere Data Sets (COADS) database, www.cdc.noaa.gov/coads/). Laganas Bay is about 12 km long by 8 km wide, with a coastline of 27.8 km in length, along 13 km of which there is 6.16 km of loggerhead sea turtle nesting beaches.

2.2. Tracking units

In 2006, 2007 and 2008 GPS tracking units were placed on adult male and female loggerheads. 18 female loggerheads (curved carapace lengths 77–89 cm) had TrackTag™ GPS loggers (Navsys Ltd, Edinburgh UK, <http://www.navsys.com>) attached during the pre-nesting period, of which 13 were successfully removed during the inter-nesting period; three of four in 2006; four of five in 2007 and six of nine in 2008. Seven Fastloc GPS-Argos transmitters (Sirtrack, www.sirtrack.com, tags with Firmware version 2.3) were placed on males (due to the unlikelihood of retrieval within the same season) during 2007 (four units) and 2008 (three units) all of which operated until after migration out of the breeding area (i.e. Laganas Bay). Preliminary results of the 2006–2007 tracking data have been published (Schofield et al., 2007, 2009b), with the 2008 year contributing new information to the dataset. The Fastloc transmitters relayed GPS information remotely via the Argos system. In addition the Fastloc data were stored on-board so that in the event of instrument recovery all the acquired Fastloc-GPS data could be downloaded directly to a computer. One coat of antifouling paint (Trilux, International Paints) was painted on all Sirtrack units.

2.3. Turtle capture technique

Turtles were captured at random from a boat using the turtle-rodeo technique (Ehrhart and Ogren, 1999). This activity was conducted at sea depths of 1–7 m along the central 12 km stretch of coastal waters over submerged sandbanks only (for safety reasons). Following capture, turtles were directed into a semi-submerged wooden box attached to the side of the boat. Following capture, the curved carapace length was measured and a GPS unit was attached. In brief, the carapace was cleaned and then the logger embedded in quick setting two-part epoxy resin (Powerfasteners Inc., New Rochelle, NY, USA) with wooden baffles positioned at the anterior to help prevent impacts to the equipment. In-situ observation and photo-identification records (Schofield et al., 2008) of ongoing and previous courtship and mating activity were used to determine the reproductive status of captured individuals. The attachment of all devices was conducted under permits from the National Marine Park of Zakynthos. Units were retrieved (i) using the rodeo capture technique or (ii) by recovery on the beach immediately following nesting.

2.4. GPS data consolidation

Locations from Fastloc and Navsys track devices are generally accurate to within a few tens of metres (Rutz and Hays, 2009). All locations obtained from all GPS units were plotted to allow a quick initial visual inspection. The data were filtered by (i) subjectively removing visually erroneous locations (i.e. on land or spatially different fixes to previous and successive fixes within the same timeframe), (ii) using a maximum rate of travel of 5 km h⁻¹ between successive locations (Hays et al., 2004a), which was selected based on calculations from three or more consecutive fixes occurring at 10–20 min intervals, and (iii) removing data when the turtles were sighted onshore (nesting and/or aborted nesting attempts). The median GPS location per hour and per day for each turtle was then calculated (Tremblay et al., 2006).

2.5. Home range spatial analysis

Home range areas were estimated by the fixed kernel density method (Worton, 1989), using the Home Range Extension (www.spatial ecology.com) for the ArcMap v 9.1 (ERSI, Redlands, California, USA; <http://www.esri.com/software/arcview>). Fixed

kernel home ranges were calculated with least square cross validation as a band width. A 95% and 90% utilisation distribution was used to estimate overall home range used by turtles, while a 50% utilisation distribution was used to establish the core area (Worton, 1989).

The datasets were analysed using median (i) hourly locations and (ii) daily locations to determine whether consistent core areas were produced. The kernel analysis was conducted at two spatial scales (i) using all locations (hourly versus daily) obtained by males and females during the breeding period and (ii) using only locations obtained within the immediate breeding area (i.e. confined to the limits of Laganas Bay). To determine if there was temporal variation in turtle distribution between years, kernel analysis was conducted using (i) all individual turtle locations, and (ii) combined seasonal locations for males and females. To identify the core area in need of protection all datasets were combined for kernel analysis and the relative proportion of datapoints falling in the existing protection zones within Laganas Bay were calculated using the *Home Range Extension for ArcMap v9.1*.

2.6. Environmental data

Weather data were recorded using (i) a WS-2300 weather station (La Crosse Technology Ltd, La Crosse, WI, USA) positioned 100 m inland from Laganas Bay and (ii) the Zakynthos Airport weather station located 1 km inland from Laganas Bay. Information was collected at 30 min intervals with respect to air temperature, dewpoint, humidity, barometric pressure, wind speed and direction, cloud cover, precipitation and storm events. Sea temperature was recorded using six TGP-4017 (Gemini Data Loggers, Chichester, West Sussex, UK) internal probes. The probes were placed at 50 cm below the sea surface, attached to buoys anchored at seabed depths of 3 m, at 5 km intervals around Laganas Bay. The units were set to record at 5 min intervals between April and August in 2007 and 2008.

3. Results

3.1. Tracking data

Excluding deployment and retrieval days, we tracked 13 female turtles equipped with TrackTag GPS loggers in 2006, 2007 and 2008 for a mean 36 days each (range 17–52 days; SD \pm 9.4). The seven males equipped with Fastloc GPS-Argos transmitters in 2007 and 2008 were tracked for a mean 14 days (range 1–37 days; SD \pm 11) when in the breeding area (i.e. in Laganas Bay). Details of turtle morphometrics, attachment & retrieval dates, GPS locations, dates of female forays and nesting, and male departure are presented in *Supplementary Table 1*.

3.2. Daily versus hourly home range calculations

Median daily versus hourly GPS locations were assessed to determine the degree of variation recorded in home range size. There was no significant difference between median daily and hourly GPS locations with respect to 50% (Pearson's correlation $r = 0.93$) and 95% (Pearson's correlation $r = 0.88$) kernel density estimators for home range size. Due to the similarity in median daily and hourly kernel estimates, hourly locations were selected for use to conduct all home range analyses.

3.3. Male home ranges

Home ranges were calculated from GPS locations collected from the date of attachment to the date of departure (or onset of long

distance migration to foraging/wintering areas) for four turtles. Two turtles were resident to Zakynthos; Male 7 travelled from the breeding area to the east coast of Zakynthos on 11/6/2008 where it has remained since (last transmission 18/12/2008) and this date was used; Male 1 did not change locations, so for the purposes of calculating breeding area home range, all GPS locations were used until the mean departure date of all other males ($n = 6$; 22nd May). Male core breeding home range (i.e. 50% kernel estimator) for 2007 and 2008 was a mean 5.2 km² (range: 2.2–9.7 km²; SD \pm 2.14), along a 2 km stretch of coastline. The broadest home range (i.e. 95% kernel estimator) was a mean 21 km² (range: 9.5–31 km²; SD \pm 8.3) along an 8.75 km stretch of coastline (*Fig. 1* and *Supplementary Table 2*).

3.4. Female home ranges

During the early breeding period (i.e. May to late June – following migration of females to the breeding area), female core home range (i.e. 50% kernel estimator) for 2006, 2007 and 2008 was a mean 10.2 km² (range: 6–19 km²; SD \pm 3.8), along a 7.5 km stretch of coastline. The broadest home range (i.e. 95% kernel estimator) was a mean 48 km² (range: 25–85 km²; SD \pm 18) encompassing Laganas Bay. (*Fig. 1* and *Supplementary Table 2*). The core home range size (50% kernel estimator) was similar in all 3 years of the study (12 km², 11 km² and 15 km², respectively in 2006, 2007 and 2008). Furthermore, within the breeding area (i.e. Laganas Bay) the 95% kernel estimator for females in 2008 was 78 km², in contrast to 47 and 50 km² in 2006 and 2007, respectively, which was a 64% increase in bay area use. Also, the broad home range size, including GPS locations outside of the breeding areas (95% kernel estimator), was identical in 2006 and 2007 (59 km² for each respectively), but was significantly different in 2008 (479 km²).

3.5. Female forays and first nesting

Ten of the 13 tracked females conducted a total of 15 forays beyond the core breeding area (i.e. beyond the mouth of Laganas Bay); one turtle made two forays in 2006; two turtles made a total of four forays in 2007, and in 2008 all six turtles made a total of nine forays. Just three forays occurred following the individual's first nesting event, once in each of 2006, 2007 and 2008. Forays lasted from one to 15 days (mean: 5.6 days; SD \pm 5), and of maximum distances of 11.4–99.8 km (mean: 40.6 km; SD \pm 34) (*Table 1* and *Fig. 2*). Of the 15 forays recorded in 2006–2007, just one turtle departed the coast of Zakynthos island to the adjacent breeding ground of Kyparissia. However in 2008, six forays remained in the vicinity of the island while three forays were long distance to the oceanic and coastal areas of the adjacent mainland Peloponnese (some to the nesting area of Kyparissia) and the island of Kefalonia. None of the turtles in any year nested at these alternative breeding sites (confirmed through known date of first and subsequent nesting events based on direct field observations and regular 30 s frequency of GPS transmissions when on land). Synchrony in date of foray departure was recorded by multiple turtles in 2007 and 2008.

The mean date of first nesting of the tracked turtles was the 7th June in 2006, 28th May in 2007 and 14th June in 2008 (*Supplementary Table 1* and *Fig. 3*). There was a significant difference in the date of first nesting between seasons for tracked turtles (ANOVA, $P = 0.05$). Of note, the date of first nesting in 2008 was found to be significantly later than that recorded in 2006 and 2007 (paired Student's *t*-test, $t_{11} = 2.16$, $P < 0.05$, SD \pm 9.68).

3.6. Environmental parameters and turtle departure

The dates that female turtles departed on forays from the core breeding area were assessed in relation to proximate changes in

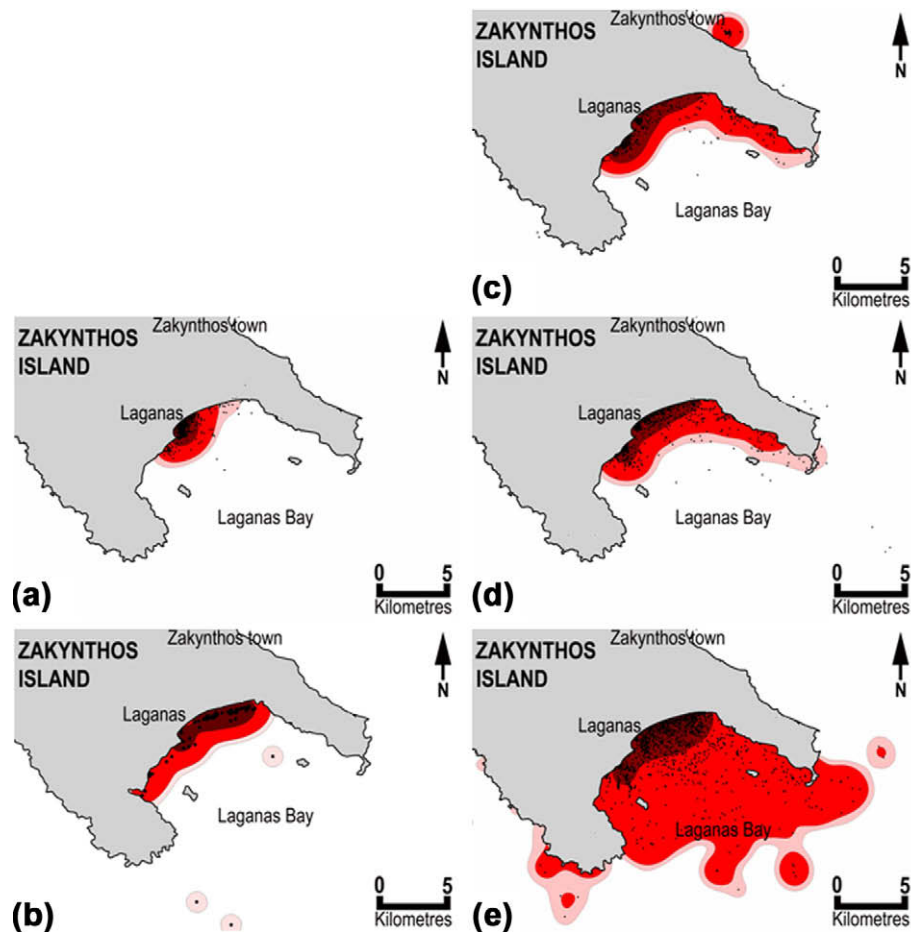


Fig. 1. Map showing 95% (brown), 90% (red) and 50% (pink) kernel estimators within the breeding area of Laganas Bay for: (a) males in 2007 ($n = 4$), (b) males in 2008 ($n = 3$), (c) females in 2006 ($n = 3$), (d) females in 2007 ($n = 4$) and (e) females in 2008 ($n = 6$). Median hourly GPS locations shown as black dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a range of environmental parameters, i.e. sea and air temperature, humidity, barometric pressure, wind velocity, cloud cover, precipitation and/or storm events. Of these, barometric pressure was the only parameter that changed on 100% of occasions when turtles departed the breeding area, although turtles did not necessarily depart following every drop in pressure (Fig. 4). In two of the three survey years, turtle departure from the core breeding area occurred more often than expected by chance when the pressure dropped (G test: 2006 $G_2 = 3$ $P = 0.08$; 2007 $G_2 = 24$ $P < 0.001$; 2008 $G_2 = 50$ $P < 0.001$). Barometric pressure dropped (mean daily drop: 4.75 mbars, range: 0.34–0.37; $SD \pm 12.52$) on a total of 64 days, with pressure dropping by more than 3 mbars on 17 of these days. In 51 instances turtles remained in Laganas Bay but in 13 instances turtles departed the breeding area. The absolute value of the pressure that it drops to may be more relevant than how much it drops on a given day, with departure occurring after drops of >0.1 in./mercury or after accumulative or repetitive drops adding up to >0.1 in./mercury on adjacent days.

3.7. Turtle home range versus existing protective legislation

Overall, while all male GPS mean hourly locations fell within the National Marine Park of Zakynthos protection zones, 15% of female locations occurred outside of the protected area (Fig. 5). In fact, males never departed the breeding area, with home ranges being on average 46–54% smaller than that of females based on 50% and 95% Kernel estimates respectively. Analysis of mean

hourly GPS locations within the National Marine Park of Zakynthos protection zones indicated that 12% of points ($n = 424$) fell in zone A, 53% of points fell in zone B ($n = 1814$) and 35% of points ($n = 1211$) fell in zone C. 99% of male turtle locations occurred in zones B (46%) and C (53%). Yearly female locations ranged from 8% to 20% in zone A, 39–73% in zone B and 20–42% in zone C.

4. Discussion

Our study described the variation in home range size between male and female loggerhead sea turtles at a breeding area across several seasons, and identified meteorological cues that may trigger possible ranging movement by females beyond the immediate breeding area.

Marine protected areas (MPAs) should envelope habitats required by a species, however the level of species mobility, influence of environmental parameters and habitat availability may result in the change of critical habitat size, shape and location (Parnell et al., 2006). The GPS data collected in this study showed that while the breeding home range size of individual turtles was highly variable, both male and female turtles share a stable core 5 km nearshore range across seasons. The combined 50% kernel contours for all tracked turtles across the 3 year study period were within a 20 km² home range area, which contrasted to up to 1000 km² recorded for breeding Kemp's Ridleys in Texas (Shaver et al., 2005; Seney and Landry, 2008), and up to 6000 km² for breeding Atlantic

Table 1

(a) Table detailing female forays from the breeding site (dates, duration and distances), (b) Summary table of foray information.

Year	Turtle id	If foray occurred	Foray frequency	Dates		Days on foray		Max. distance travelled		Locations	
				No. of forays	No. females that forayed	Mean	Max	Min	Max	Min	Max
(a)	Female_01	No	0	n/a							
2006	Female_02	No	0	n/a							
2006	Female_03	Yes	2	4/6–5/6; 10/6–14/6	1	4	14.7; 11.4	West coast Zakynthos; East coast Zakynthos			
2007	Female_04	Yes	3	10/5–11/5; 31/5–1/6; 6/6–21/6	1; 1; 15	15.6; 27.5; 96.5	East coast Zakynthos; East coast Zakynthos; Peleponnesse				
2007	Female_05	No	0	n/a							
2007	Female_06	Yes	1	12/6–15/6	3	16.4	East coast Zakynthos				
2007	Female_07	No	0	n/a							
2008	Female_08	Yes	3	21/5; 30/5; 15/6	1; 1; 1	11; 11; 12	Central Ionian sea				
2008	Female_09	Yes	1	8/5–12/5	4	32	West Ionian sea				
2008	Female_10	Yes	1	5/5–15/5	10	65	Peleponnesse-Kefalonia				
2008	Female_11	Yes	1	8/5–12/5	4	13	Central Ionian sea				
2008	Female_12	Yes	1	8/5–10/5	2	10	Central Ionian sea				
2008	Female_13	Yes	2	11/5–15/5/2008; 23/5–5/6/2008	4; 13	27; 100	Central Ionian sea; Peleponnesse				
Year	Total No. females	No females that forayed	No. of forays	Mean	Max	Min	Max	Mean	SD	Max	Mean first Nesting date
(b)	3	1	2.5	4	1	4	13.1	n/a	n/a	14.7	7/6/2006
2006	4	2	5	15	1	15	39	8.5	56.6	96.5	28/5/2006
2007	6	6	4.3	13	4	13	31.2	4.3	31.2	99.8	13/6/2006
Overall	13	10	4.2	15	1	15	30.8	4.6	30.6	99.8	30.6

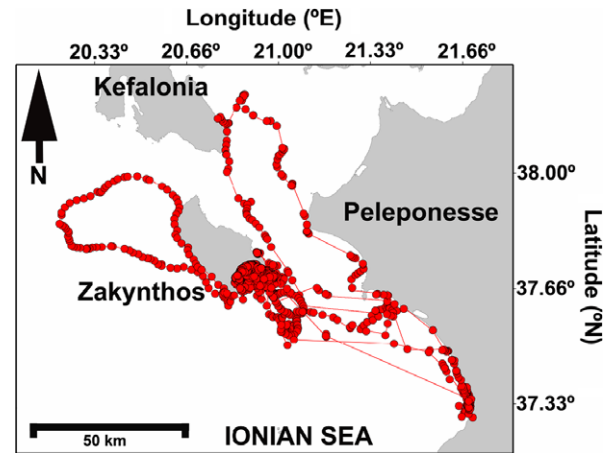


Fig. 2. Tracks of 10 female loggerheads equipped with GPS loggers following their arrival at the breeding area of Zakynthos, between 2006 and 2008 in May and early June. The tracks illustrate the extent of occasional excursions away from the core breeding area of the south coast of Zakynthos. On these excursions turtles travelled in a range of directions (broadly west, north and east).

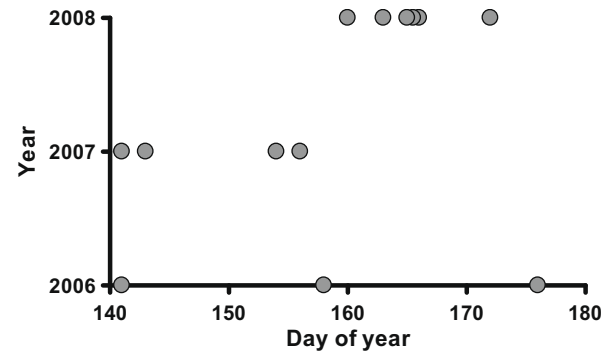


Fig. 3. The timing of the first nesting event of female turtles tracked between 2006 and 2008. There was significant inter-annual variability with turtles nesting later in 2008.

leatherbacks (James et al., 2005a; Eckert et al., 2006). It is possible that the different ranges may reflect the size of adjacent available nesting beaches or reflect species specific needs. For example foraging to supplement stored energy reserves during the inter-nesting period as has been recorded in leatherbacks (Georges et al., 2007; Byrne et al., 2009), as well as greens (Hays et al., 2002) and loggerheads (Hochscheid et al., 1999) in the Mediterranean. In all studies, a strong overlap in home range area between individuals was recorded at the breeding site, which contrasted to the disparity of home ranges at distant foraging grounds along extensive coastal and oceanic areas (Hochscheid et al., 1999; Houghton et al., 2002; Hays et al., 2004b; James et al., 2005b; Casale et al., 2007; Zbinden et al., 2008). Hence, breeding areas, where large numbers of individuals aggregate, may be most viable for protective management through the establishment of marine protected areas. However these populations remain vulnerable to by-catch and mortality as the majority of their lives is spent outside of these comparatively safe zones (Ferraro et al., 2004; Lewison et al., 2004; James et al., 2005b; Georges et al., 2007; Peckham et al., 2007; Byrne et al., 2009).

Effective long-term conservation management must not only ensure the protection of existing favourable breeding areas but predict future habitat needs (King et al., 2001; Cotton et al., 2005; Perry et al., 2005; Hawkes et al., 2007; Chaloupka et al.,

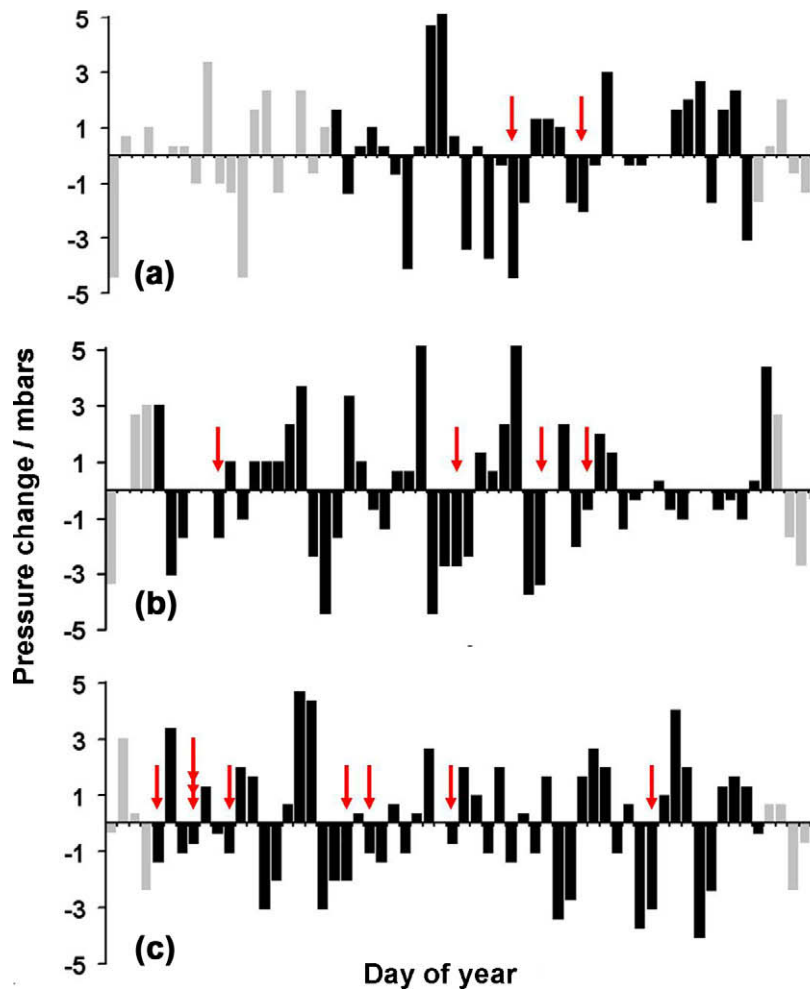


Fig. 4. The change in barometric pressure each day between 1st May and 30th June (each bar represents 1 day) in (a) 2006 (b) 2007 and (c) 2008 and the days on which turtles departed (red arrows). Black bars = pressure change during period of tracking; grey bars = pressure change records outside of tracking period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

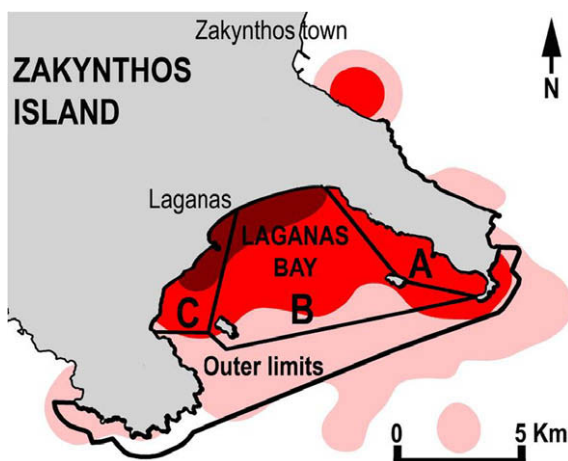


Fig. 5. The 95% (brown), 90% (red) and 50% (pink) home range kernel estimators (using median hourly GPS locations) of all male ($n = 7$) and female loggerheads ($n = 13$) in May and June of 2006–2008 in the National Marine Park of Zakynthos in relation to the protection zones (zone A = no boating zone; zone B = boating at six knots and no mooring; zone C = boating at six knots and mooring). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2008). Our data showed that male home ranges were half the size of that recorded for females, with males never departing the core breeding area until migration to wintering/foraging areas. Males may maintain their position close to the breeding beaches to maximise their encounter rates with females (Schofield et al., 2006) and secure more mating opportunities, as has been speculated for leatherback males (James et al., 2005a). In contrast, once females have been impregnated (Lee and Hays, 2004), they may benefit little from further mating. Short and long distance forays during the nesting period may provide a means for females to replenish stored energy reserves through foraging, as has been inferred from dive data for green and loggerhead turtles in the Mediterranean (Hochscheid et al., 1999; Houghton et al., 2002) and leatherbacks in the Atlantic (Georges et al., 2007; Byrne et al., 2009). However a 3 year direct in-water observation study of the Zakynthos loggerhead population during the nesting period suggested that females in this population minimally invest in foraging activity (Schofield et al., 2006). On the other hand, speculative forays may serve to maximise female reproductive success through locating and nesting at the best available sites. Therefore, if conditions deteriorate females may have better success by nesting at alternative sites.

The regularity with which females conduct forays outside of the core breeding area to other parts of Zakynthos island and to adjacent breeding areas on mainland Peleponese and Kefalonia island

is of conservation interest. While low levels of nesting activity have regularly been recorded along the east coast of Zakynthos, the beach and marine areas are not subject to any protection and are subject to high-impact watersports activities from which turtles are at risk of propeller damage. The breeding areas of the Peleponnesse and Kefalonia are considered distinct, with occasional records of interchange of females indicated by external flipper tags (Margaritoulis, 1998). The loggerhead population of a single breeding site is often managed as a self-contained entity, however if movement of turtles between breeding sites is a regular occurrence, pro-active conservation actions may require implementation at a larger scale to ensure the sustainability of loggerhead populations (Sala et al., 2002; Sheppard et al., 2006; Seney and Landry, 2008).

In general, the relatively small stable core marine area used by the Zakynthos breeding population presents a manageable unit for protection. The 3 year dataset of male and female area use within the breeding area of Laganas Bay indicates that 88% of GPS locations fell in the two lesser protected zones where recreational and targeted turtle-watching activity is permitted. The impact of recreational activities is not known, however we presume the turtles may be subjected to a degree of disturbance from boats and swimmers as has been recorded in dolphins (Lusseau, 2004, 2006). Future studies are required to assess if this disturbance is important and whether this nearshore area requires strengthened regulation, particularly during the period when thermal conditions are suboptimal (see Schofield et al., 2009a).

To date home range studies of juvenile and adult sea turtles have been conducted using radio and sonic telemetry (Mendonca, 1983; Schmid et al., 2002; Seminoff et al., 2002; Hopkins-Murphy et al., 2003), Argos satellite telemetry (Renaud and Carpenter, 1994; Shaver et al., 2005; Eckert et al., 2006; Georges et al., 2007; Peckham et al., 2007; Seney and Landry, 2008) and experimental GPS telemetry (Yasuda and Arai, 2005). Often the technique used can impact the results obtained. For example, while relatively accurate, the number of locations obtained by sonic and radio tracking can depend on survey area size, degree of effort, field conditions, signal reception and the behaviour of the animal. For example, in a worst case scenario, the animal might disappear beyond signal range and hence the true extent of its home range would not be obtained. While achieving global coverage, conventional Argos satellite telemetry can potentially overestimate home range size due to location inaccuracies. For example, in an extreme example a stationary animal would still appear to “move” appreciably due to location inaccuracies derived by Argos. GPS loggers and transmitters overcome both these limitations producing frequent and highly accurate fixes across 24-h periods (Yasuda and Arai, 2005; Schofield et al., 2007, 2009b). It is still important to try and ensure an even temporal pattern of locations and for this reason we explored the use of both the median location within each hour and median daily locations. Both approaches gave very similar results, indicating that in our case the exact temporal resolution (hourly versus daily) was relatively unimportant in dictating home range estimates. This finding suggests our home range estimates are robust.

The attachment of GPS loggers to females prior to the onset of nesting provided an opportunity to investigate the dates of first clutches by individuals across several seasons. There have been widely documented advances in the timing of seasonal activities (or phenology) of plants and animals (see Walther et al., 2002; Crick, 2004). Birds have been subject to extensive study, with shifts in arrival and departure dates at breeding and foraging areas being monitored globally (see Crick, 2004). As ectotherms, sea turtles are thermally sensitive, and earlier egg-laying of a magnitude of 10–17 days based on long-term datasets has been recorded in relation to warmer sea temperatures (Weishampel et al., 2004; Pike et al.,

2006; Mazaris et al., 2008), with an estimated shift of 1 day per year. In our 3 year study we noted that individual turtles tend to initiate nesting across a broad time frame; May 21 to June 25. Noticeable differences in the timing of first nesting was recorded in 2007 ($n = 4$; nesting between 21 May and 5 June) versus 2008 ($n = 6$; nesting between 8 June and 20 June), which may reflect the variation of ambient sea surface temperatures between seasons (Mazaris et al., 2004) and/or meteorological parameters identified in this study. Within a given season, variation in the onset of nesting (2006: 36 days; 2007: 16 days; 2008: 13 days) may also be attributed to (i) timing of arrival at the breeding area, or (ii) individual ability to locate water warmer than the ambient to enhance egg development (Schofield et al., 2009a).

Our data indicated that forays by females from the core breeding area may be partially triggered by meteorological cues. Animals rely on daily and seasonal environmental cues to guide their behaviour and critical life history processes (Pike, 2008). Hence to survive, animals must be able to respond to unpredictable changes to their environment (Wingfield, 2003). Many vertebrates have been shown to alter their movement patterns in response to changes in weather patterns (e.g. fish, Guy et al., 1992; snakes, Brown and Shine, 2002; birds, Shamoun-Baranes et al., 2006). Changes in atmospheric pressure (as little as 5 hPa) may serve as a signal of approaching environmental change to which animals respond to avoid storms (e.g. sharks, Heupel et al., 2003; flounder, Sackett et al., 2007) or initiate migration (e.g. spider-mites, Li and Margolies, 1994; eels, Okamura et al., 2002; birds, Shamoun-Baranes et al., 2006). While a recent sea turtle study indicated that successful nesting was found to occur during periods of high barometric pressure (Pike, 2008), our study found that all recorded forays from the breeding area were preceded by a noticeable drop in barometric pressure. As the population we studied occurs near the edge of the loggerhead breeding range, where temperature conditions during May and June have been shown to be suboptimal (Schofield et al., 2009a), turtles in this population may be sensitive to cues in barometric pressure to ensure heightened reproductive fitness. Response was probably in correlation with other co-variables, as turtles did not necessarily depart from breeding area with every recorded drop in barometric pressure. This may also indicate a variable response in individuals to cues and within-population variation in organism fitness. Hence while barometric pressure may serve as a cue of deteriorating habitat conditions to the turtles, the decision to “stay or go” may be based on a combination of previous experience, physiological condition and additional environmental parameters (Dieckmann et al., 1999; Forero et al., 1999; Serrano et al., 2001; Brown and Shine, 2002).

At the beginning of the breeding season, two alternative scenarios may take place. In the first, female turtles still being in suboptimal thermal conditions in May, would respond to variable barometric pressure and unpredictability of storms with an increase in frequency of forays beyond the core breeding area in search of more stable sites at which to nest. Turtles remaining at, or returning to, the breeding area might be subject to a delayed onset in nesting, however new nesting sites may be founded. High multiple paternity levels recorded at Zakynthos (Zbinden et al., 2007b) could potentially facilitate the colonisation of new nesting beaches by only a few gravid females (Moore and Ball, 2002) due to the high genetic diversity carried by a single clutch. In the second scenario, increased variability in barometric pressure may no longer serve as a reliable cue, hence females might benefit by suppressing the dispersal response (Wingfield, 2005), thus reducing stress and conserving vital energy as soon as the conditions become optimal in June. This would result in increased philopatry to one breeding area, increasing the vulnerability of the population to any sudden shifts in climate change, as has been detected in long-term studies in fish (McFarlane et al., 2000; King et al., 2001).

Our study demonstrated the value of high resolution GPS tracking of animal movements over several years to (i) objectively delineate home range sizes, and (ii) identify how environmental conditions drive movements. The ability of turtles to respond to local-scale variations in environmental conditions, when breeding conditions are suboptimal, may heighten reproductive fitness and potentially facilitate recruitment to new breeding areas. Our results demonstrate the importance for long-term studies to determine appropriate protection zoning, as well as the necessity to consider the protection of possible alternative breeding habitats. GPS tracking of sea turtles is likely to become far more widespread now that GPS units are commercially available (Rutz and Hays, 2009). As comparable high resolution tracking is assimilated across populations and species, we can expect more comparative analysis of what factors drive home range size in sea turtles.

Acknowledgements

The authors thank the National Marine Park of Zakynthos (NMPZ) for permission to conduct this research. Financial and logistical support was provided by the Boyd Lyon Sea Turtle Fund, Peoples Trust for Endangered Species, the British Chelonia Group, TrackTag™, NERC Connect B Grant NERC/D/S/1999/00078 (award to CMB), Swansea University and the NMPZ. We thank Martyn Baker, Kostas Gounelis, Giannis Liveris, Nikos Margaritis, Giorgos Mitrouskas, David Oakley and Mike Sheldon for in-water capture assistance. We thank NMPZ and Archelon personnel for logger retrieval assistance. We acknowledge use of the Maptool program (www.seaturtle.org).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2009.12.011](https://doi.org/10.1016/j.biocon.2009.12.011).

References

- Argardy, M.T., 1994. Advances in marine conservation: the role of marine protected areas. *Trends in Ecology & Evolution* 9, 267–270.
- Bell, W.J., 1991. *The Behavioural Ecology of Finding Resources*. Chapman & Hall, London.
- Beniston, M., Stephenson, D.B., Christensen, O.B., Ferro, C.A.T., Gfrei, C., Goyette, S., Halsnaes, K., Holt, T., Jyhla, K., Koffi, B., Palutikof, J., Scholl, R., Semmler, T., Woth, K., 2007. Current and future extreme climatic events in Europe: observations and modeling studies conducted within the EU PRUDENCE project. *Climatic Change* 81, 71–95.
- Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatial ecology.com/htools>.
- Borger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75, 1393–1405.
- Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80, 205–225.
- Brown, G.P., Shine, R., 2002. Influence of weather conditions on activity of tropical snakes. *Austral Ecology* 27, 596–605.
- Byrne, R., Fish, J., Doyle, T.K., Houghton, J.D.R., 2009. Tracking leatherback turtles (*Dermodochelys coriacea*) during consecutive inter-nesting intervals: further support for direct transmitter attachment. *Journal of Experimental Marine Biology and Ecology* 377, 68–75.
- Casale, P., Freggi, D., Basso, R., Vallini, C., Argano, R., 2007. A model of area fidelity, nomadism, and distribution patterns of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea. *Marine Biology* 152, 1039–1049.
- Chaloupka, M., Kamezaki, N., Limpus, C., 2008. Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? *Journal of Experimental Marine Biology and Ecology* 356, 136–143.
- Christensen, J.H., Christensen, O.B., 2003. Climate modeling: severe summertime flooding in Europe. *Nature* 421, 805–806.
- Cotton, P.A., Sims, D.W., Fanshawe, S., Chadwick, M., 2005. The effects of climate variability on zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. *Fisheries Oceanography* 14, 151–155.
- Crick, H.Q.P., 2004. The impact of climate change on birds. *Ibis* 146, 48–56.
- Dieckmann, U., O'Hara, B., Weisser, W., 1999. The evolutionary ecology of dispersal. *Trends in Ecology and Evolution* 14, 88–90.
- Eckert, S.A., Bagley, D.A., Kubis, S., Ehrhart, L.M., Johnson, M.L., Stewart, K., DeFrieze, D., 2006. Internesting and post nesting movements and foraging habitats of leatherback turtles (*Dermodochelys coriacea*) nesting in Florida. *Chelonian Conservation and Biology* 5, 239–248.
- Ehrhart, L.M., Ogren, L.H., 1999. Studies in foraging habitats: capturing and handling turtles. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), *Research and Management Techniques for the Conservation of Sea Turtles*, vol. 4. IUCN/SSC Marine Turtle Specialist Group Publication. pp. 1–4.
- Ferraroli, S., Georges, J.Y., Gaspar, P., Le Maho, Y., 2004. Where leatherback turtles meet fisheries. *Nature* 429, 521–522.
- Forero, M.G., Donazar, J.A., Vblas, J., Hiraldo, F., 1999. Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology* 80, 1298–1310.
- Georges, J., Fossette, S., Billes, A., Ferraroli, S., Fretey, J., Grémillet, D., Le Maho, Y., Myers, A.E., Tanaka, H., Hays, G.C., 2007. Meta-analysis of movements in Atlantic leatherback turtles during the nesting season: conservation implications. *Marine Ecology Progress Series* 338, 225–232.
- Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. *Global and Planetary Change* 63, 90–104.
- Guy, C.S., Neumann, R.M., Willis, D.W., 1992. Movement patterns of adult black crappie, *Poxomis nigromaculatus*, in Brant Lake, South Dakota. *Journal of Freshwater Ecology* 7, 137–147.
- Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2007. Investigating the potential impacts of climate change on a marine turtle population. *Global Change Biology* 13, 923–932.
- Hays, G.C., Webb, P.L., Hayes, J.P., Priede, I.G., French, J., 1991. Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* 71, 743–746.
- Hays, G.C., Glen, F., Broderick, A.C., Godley, B.J., Metcalfe, J.D., 2002. Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between 2 green turtle (*Chelonia mydas*) populations. *Marine Biology* 141, 985–990.
- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., Lovell, P., 2004a. First records of oceanic dive profiles for leatherback turtles, *Dermodochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Animal Behaviour* 67, 733–743.
- Hays, G.C., Houghton, J.D.R., Myers, A.E., 2004b. Pan-Atlantic leatherback turtle movements. *Nature* 429, 522.
- Heupel, M.R., Simpfendorfer, C.A., Heuter, R.E., 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *Journal of Fish Biology* 63, 1357–1363.
- Hochscheid, S., Godley, B.J., Broderick, A.C., Wilson, R.P., 1999. Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Marine Ecology Progress Series* 185, 101–112.
- Hopkins-Murphy, S.R., Owens, D.W., Murphy, T.M., 2003. Chapter 5: ecology of immature loggerheads on foraging grounds and adults in interesting habitat in the Eastern United States. In: Bolton, A.B., Witherington, B.E. (Eds.), *Loggerhead Sea Turtles*. Smithsonian Institution, Washington and London, pp. 79–82.
- Houghton, J.D.R., Broderick, A.C., Godley, B.J., Metcalfe, J.D., Hays, G.C., 2002. Diving behaviour during the internesting interval for loggerhead sea turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series* 227, 63–70.
- Hulbert, I.A.R., French, J., 2001. The accuracy of GPS for wildlife telemetry and habitat mapping. *Journal of Applied Ecology* 28, 869–878.
- James, M.C., Eckert, S.A., Myers, R.A., 2005a. Migratory and reproductive movements of male leatherback turtles (*Dermodochelys coriacea*). *Marine Biology* 147, 845–853.
- James, M.C., Ottensmeyer, A., Myers, R.A., 2005b. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecology Letters* 8, 195–201.
- King, J.R., McFarlane, G.A., Beamish, R.J., 2001. Incorporating the dynamics of marine systems into the stock assessment and management of sablefish. *Progress in Oceanography* 49, 619–639.
- Laver, P.N., Kelly, M.J., 2008. A critical review of home range studies. *Journal of Wildlife Management* 72, 290–298.
- Lawson, E.J.G., Rodgers, A.R., 1997. Differences in home-range size computed in commonly used. *Software Programs* 25 (3), 721–729.
- Lee, P.L.M., Hays, G.C., 2004. Polyandry in a marine turtle: females make the best of a bad job. *Proceedings of the National Academy of Science* 101, 6530–6535.
- Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19, 598–604.
- Li, J., Margolies, D.C., 1994. Barometric-pressure influences initiation of aerial dispersal in the 2-spotted spider-mite. *Journal of the Kansas Entomological Society* 67, 386–393.
- Lusseau, D., 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioural information. *Ecology and Society* 9, 2.
- Lusseau, D., 2006. The short-term behavioural reactions of bottlenose dolphins to interactions with boats in doubtful sound, New Zealand. *Marine Mammal Science* 22, 802–818.
- Margaritoulis, D., 1998. Interchange of nesting loggerheads among Greek beaches. In: Epperly, S.P., Braun, J. (Eds.), *Proceedings of the Seventeenth Annual Sea Turtle Symposium*. NOAA Technical Memorandum NMPS-SEFC-415, Orlando, Florida, pp. 225–227.
- Margaritoulis, D., 2005. Nesting activity and reproductive output of Loggerhead Sea Turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos,

- Greece. The largest rookery in the Mediterranean. *Chelonian Conservation and Biology* 4, 916–929.
- Mazaris, A.D., Kornaraki, W., Matsinos, Y.G., Margaritoulis, D., 2004. Modelling the effect of sea surface temperature on sea turtle nesting. *Natural Resource Modelling* 17, 445–465.
- Mazaris, A.D., Kallimanis, A.S., Sgardelis, S.P., Pantis, J.D., 2008. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *Journal of Experimental Marine Biology and Ecology* 367, 219–226.
- McFarlane, G.A., King, J.R., Beamish, R.J., 2000. Have there been recent changes in climate? Ask the fish. *Progress in Oceanography* 47, 147–169.
- McMahon, C.R., Hays, G.C., 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biology* 12, 1330–1338.
- Mendonça, M.T., 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia* 1983, 1013–1023.
- Moore, M.K., Ball, R.M., 2002. Multiple paternity in loggerhead turtle (*Caretta caretta*) nests on Melbourne Beach, Florida: a microsatellite analysis. *Molecular Ecology* 11, 281–288.
- Okamura, A., Yamada, Y., Tanaka, S., Horie, N., Utoh, T., Mikawa, N., Akazawa, A., Oka, H.P., 2002. Atmospheric depression as the final trigger for the seaward migration of the Japanese eel *Anguilla japonica*. *Marine Ecology Progress Series* 234, 281–288.
- Parnell, P.E., Dayton, P.K., Lennert-Cody, C.E., Rasmussen, L.L., 2006. Marine reserve design: optimal size, habitats, species affinities, diversity and ocean microclimate. *Ecological Applications* 16, 945–962.
- Peckham, S.H., Maldonado Diaz, D., Walli, A., Ruiz, G., Crowder, L.B., Nichols, W.J., 2007. Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS One* 10, e1041.
- Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915.
- Pike, D.A., 2008. Environmental correlates of nesting in loggerhead turtles, *Caretta caretta*. *Animal Behaviour* 76, 603–610.
- Pike, D.A., Antworth, R.L., Stiner, J.C., 2006. Earlier nesting contributes to shorter nesting seasons for the Loggerhead sea turtle, *Caretta caretta*. *Journal of Herpetology* 40, 91–94.
- Renaud, M.L., Carpenter, J.A., 1994. Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bulletin of Marine Science* 55, 1–15.
- Rutz, C., Hays, G.C., 2009. New frontiers in biologging science. *Biological Letters*. doi:10.1098/rsbl.2009.0089.
- Sackett, D.K., Able, K.W., Grothues, T.M., 2007. Dynamics of summer flounder, *Paralichthys dentatus*, seasonal migrations based on ultrasonic telemetry. *Estuarine, Coastal and Shelf Science* 74, 119–130.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., Dayton, P.K., 2002. A general model for designing networks of marine reserves. *Science* 298, 1991–1993.
- Schmid, J.R., Bolten, A.B., Bjørndal, K.A., Lindberg, W.J., 2002. Activity patterns of Kemp's ridley turtles, *Lepidochelys kempii*, in the coastal waters of the Cedar Keys, Florida. *Marine Biology* 140, 215–228.
- Schofield, G., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2006. Behaviour analysis of the loggerhead sea turtle (*Caretta caretta*) from direct in-water observation. *Endangered Species Research* 2, 71–79.
- Schofield, G., Bishop, C.M., MacLean, G., Brown, P., Baker, M., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2007. Novel GPS tracking of sea turtles as a tool for conservation management. *Journal of Experimental Marine Biology and Ecology* 347, 58–68.
- Schofield, G., Katselidis, K.A., Pantis, J.D., 2008. Assessment of photo-identification and GIS as a technique to collect in-water information about loggerhead sea turtles in Laganas Bay, Zakynthos Greece. In: *Proceedings of the Twenty-fourth Annual Symposium on Sea Turtle Biology & Conservation* US Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC.
- Schofield, G., Bishop, C.M., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2009a. Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology* 78, 14–22.
- Schofield, G., Lilley, M.K.S., Bishop, C.M., Brown, P., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., G.C., H., 2009b. Conservation hotspots: intense space use by breeding male and female loggerheads at the Mediterranean's largest rookery. *Endangered Species Research* doi:10.3354/esr00137.
- Seminoff, J.A., Resendiz, A., Nichols, W.J., 2002. Home range size of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series* 242, 253–265.
- Seney, E.E., Landry, A.M., 2008. Movements of Kemp's ridley sea turtles nesting on the upper Texas coast: implications for management. *Endangered Species Research* 4, 73–84.
- Serrano, D., Tella, J.L., Frero, M.G., Donazar, J.A., 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology*.
- Shamoun-Baranes, J., van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y., Leshem, Y., 2006. Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecology and Biogeography* 16, 541–552.
- Shaver, D.J., Schroeder, B.A., Byles, R.A., Buchfield, P.M., Pena, J., Marquez, R., Martinez, H.J., 2005. Movements and home ranges of adult male Kemp's ridley sea turtles (*Lepidochelys kempii*) in the Gulf of Mexico investigated by satellite telemetry. *Chelonian Conservation and Biology* 4, 817–827.
- Sheppard, J.K., Preen, A.R., Marsh, H., Lawler, I.R., Whiting, S.D., Jones, R.E., 2006. Movement heterogeneity of dugongs, *Dugong dugon* (Mueller), over large spatial scales. *Journal of Experimental Marine Biology and Ecology* 334, 64–83.
- Sumner, G.N., Romero, R., Homar, V., Ramis, C., Alonso, S., Zorita, E., 2003. An estimate of the effects of climate change on the rainfall of Mediterranean Spain by the late twenty first century. *Climate Dynamics* 20, 789–805.
- Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, P.E., McDonald, B.I., Weise, M.J., Bost, C.A., Weimerskirch, H., Crocker, D.E., Goebel, M.E., Costa, D.P., 2006. Interpolation of animal tracking data in a fluid environment. *Journal of Experimental Biology* 209, 128–140.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guilberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Weishampel, J.F., Bagley, D.A., Ehrhart, L.M., 2004. Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biology* 10.
- Wingfield, J.C., 2003. Control of behavioural strategies for capricious environments. *Animal Behaviour* 66, 807–816.
- Wingfield, J.C., 2005. The concept of allostasis: coping with a capricious environment. *Journal of Mammalogy* 86, 248–254.
- Worton, B., 1989. Kernel methods for estimating the utilisation distribution in home-range studies. *Ecology* 70, 164–168.
- Yasuda, T., Arai, N., 2005. Fine scale tracking of marine turtles using GPS-Argos PTTs. *Zoological Science* 22, 547–553.
- Zbinden, J.A., Aebischer, A., Margaritoulis, D., Arlettaz, R., 2007a. Insights into the management of sea turtle interesting area through satellite telemetry. *Biological Conservation* 137, 157–162.
- Zbinden, J.A., Llargiadèr, C.R., Leippert, F., Margaritoulis, D., Arlettaz, R., 2007b. High frequency of multiple paternity in the largest rookery of Mediterranean loggerhead sea turtles. *Molecular Ecology* 16, 3703–3711.
- Zbinden, J.A., Aebischer, A., Margaritoulis, D., Arlettaz, R., 2008. Important areas at sea for adult loggerhead sea turtles in the Mediterranean sea: satellite tracking corroborates findings from potentially biased sources. *Marine Biology* 153, 899–906.