

Microhabitat selection by sea turtles in a dynamic thermal marine environment

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Summary

1. Reproductive fitness is often compromised at the margins of a species' range due to sub-optimal conditions.
2. Set against this backdrop, the Mediterranean's largest loggerhead sea turtle (*Caretta caretta*) rookery at Zakynthos (Greece) presents a conundrum, being at a very high latitude for this species, yet hosting a high concentration of nesting.
3. We used visual surveys combined with global positioning system (GPS) tracking to show that at the start of the breeding season, individuals showed microhabitat selection, with females residing in transient patches of warm water. As the sea warmed in the summer, this selection was no longer evident.
4. As loggerhead turtles are ectothermic, this early season warm-water selection presumably speeds up egg maturation rates before oviposition, thereby allowing more clutches to be incubated when sand conditions are optimal during the summer.
5. Active selection of warm waters may allow turtles to initiate nesting at an earlier date.

Key-words: climate change, distribution, ectotherm, micro-habitat, remote technology

Introduction

Habitat selection, and its impact on reproductive fitness, has long been one of the cornerstones of ecological research (e.g. Loe *et al.* 2006; Parra 2006). Moreover, recent concern over the implications of climate change has heightened interest in how patterns of habitat selection might change in the future (e.g. Braschler & Hill 2007). From the suite of possible environmental parameters, temperature often plays a key role in influencing habitat preferences over a range of spatial scales. For example, over the broad scale (e.g. across ocean basins), temperature may influence the distribution of species and their seasonal movements (McMahon & Hays 2006), while on smaller scales of metres or kilometres, temperature may drive the specific microhabitat selected by individuals. For example, features such as rocks or scrub are used to make adjustments in body temperature for terrestrial species (e.g. frogs, Hamer, Lane & Mahony 2003; baboons, Hill 2004; snakes, Shine *et al.* 2005). Similarly, some aquatic species have been shown to preferentially select sites near water outflows

from power stations where the water is warmer (e.g. manatees, Laist 2005; sea turtles, Lyon *et al.* 2006; alligators, Murphy & Brisbin 1974). Thermal selection has also been demonstrated for freshwater turtles (e.g. Parmenter 1980).

We can liken this ecological problem of thermal selection to animals searching for patchily distributed prey, where individuals are constantly having to make decisions on where to reposition themselves to maximize resource acquisition. For animals searching for prey, the pattern of movement may be fundamentally impacted by whether animals have a good knowledge of what drives the prey distribution within their environment (Sims *et al.* 2005, 2006a). Likewise, when the resource of interest is temperature, rather than prey, we might predict different search patterns depending on the animal's knowledge of its environment as well as its physiological state and ecological needs.

The importance of thermal selection in a dynamic environment may be particularly acute at the limits of species distributions where environmental conditions may be at the margins of suitability, and hence, the implications of thermal habitat selection are greater. Such situations might, therefore, be ideal for testing the existence of fine-scale thermal selection in a dynamic thermal environment.

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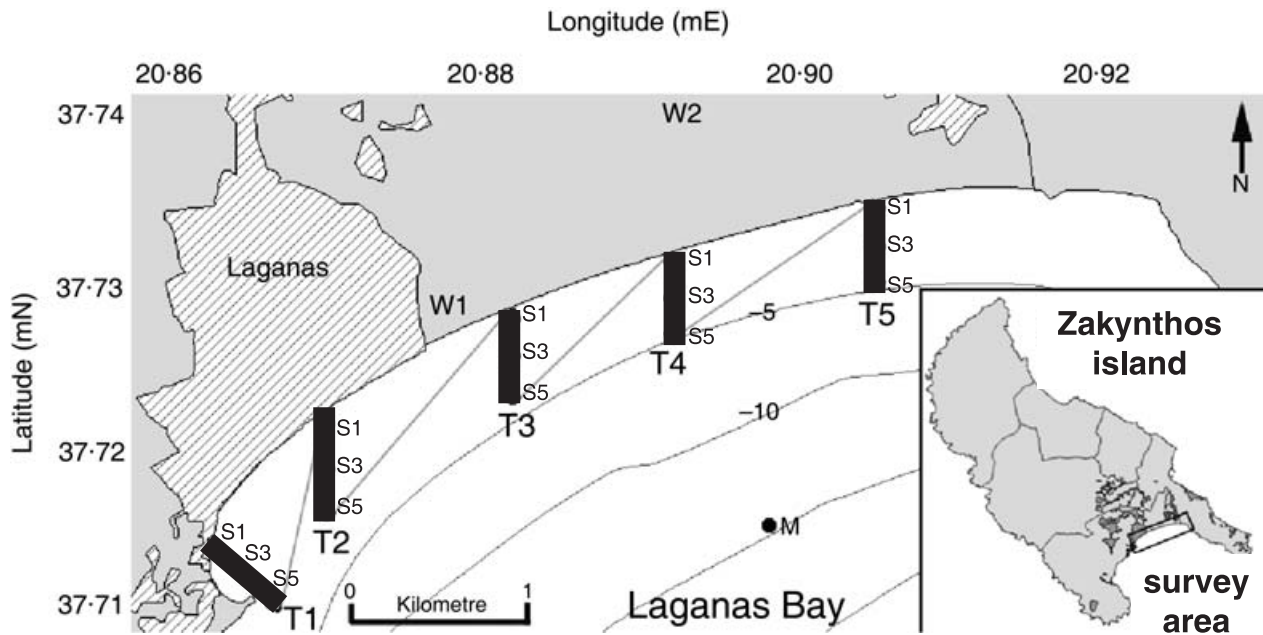


Fig. 1. The 5-km survey area in Laganas Bay, Zakyntos island, Greece. Hatched lines comprise areas of human development. T1–T5 are the transect lines denoting the 1-, 3- and 5-m sampling stations. W1 and W2 are the beachfront and airport weather stations respectively. Bathymetry lines are set at 5-m sea depth intervals (i.e. –5, –10 etc.). M is the compass midpoint of the survey area for circular statistical analysis.

Loggerhead sea turtles (*Caretta caretta*) are fairly widely distributed across subtropical and temperate latitudes (Dodd 1988). The rookery on Zakyntos island (Greece) in the semi-enclosed Laganas Bay is unusual in that it is relatively large (Margaritoulis 2005) despite being situated at the latitudinal margins of the species' breeding range. When turtles migrate to Zakyntos to mate in March–May, sea surface temperatures are generally cool (c. 13–22 °C) before increasing towards mid-summer. Therefore, the size of the breeding population at Zakyntos, despite these cold conditions, is a conundrum. It might be predicted that turtles display thermal selection to overcome cold conditions, although such thermal selection has not been demonstrated before in sea turtles. Certainly it is widely known that in lakes and semi-enclosed water bodies, the wind direction may cause warm near-surface water to accumulate at the down-wind end of the water mass (e.g. Barnes & Mann 1991). Hence, it is possible that there may be heterogeneous water temperatures at Zakyntos, offering the possibility of thermal selection by sea turtles at this site. Here we examine if sea turtles at this site show thermal selection and consider the possible benefits in terms of increasing egg maturation rates before oviposition, thereby allowing the seasons' first clutch to be laid earlier which may enhance reproductive fitness.

Material and methods

STUDY AREA

Fieldwork took place in Laganas Bay (37.7°N, 20.9°E) on the Greek island of Zakyntos. Ad-hoc surveys at sea using boats and snorkellers conducted between April and July in 2003, 2004 and 2005 indicated that female turtles tended to aggregate along a 5-km

section of coast within the bay (Schofield *et al.* 2007), so we focused our effort on this area.

TRANSECT SURVEYS

Transect surveys were conducted to obtain information on (i) sea surface and seabed temperature, and (ii) sea turtle distribution across Laganas Bay. Five transect lines (T1–T5), each with three temperature stations at 1-, 3- and 5-m sea depths were delineated along a pre-selected 5-km section of near-shore water (Fig. 1). We used a 4-m boat with an outboard engine, with travel speeds of four knots between stations. Each transect line was 0.75 km in length, at a minimum distance of 1 km from adjacent station start points, set on a north–south line, except for the first transect which was set on a northeast–southeast line (due to land form characteristics). The global positioning system (GPS) location of each transect station was recorded using GARMIN eTrex-legend (Olathe, KS, USA). Between 9 May and 13 July 2006, 34 morning and afternoon line transects were conducted, each spanning a 2-h period. Forty-five per cent of transects were conducted between 09:00 and 11:00 h and 55% of transects were conducted between 15:00 and 17:00 h. Seventy-five per cent of transects were conducted in a west–east order, while 25% were conducted in an east–west order to allow for time-dependent variations in temperature/turtle records. At each temperature station, the sea surface and seabed temperatures were recorded for a 3-min interval using Tinytag TGP-4204 (Gemini Data Loggers, Chichester, West Sussex, UK) external probe (rapid response) and TGP-4017 (Gemini Data Loggers, Chichester, West Sussex, UK) internal probe (slower response) loggers respectively. Between stations, the loggers were placed in a bucket of seawater to reduce the time required to adjust to ambient water temperature. Validation experiments showed both types of instrument consistently recorded the temperature to within 0.01 °C of one another. The 3-min measurement period was selected on the basis of the thermal response time of the TGP-4017 logger, that is, after this time there was no change in the measured temperature.

All turtle sightings, whether at the surface or submerged and within 20 m of the boat, were recorded by two observers (i) at each temperature station, (ii) between temperature stations, (iii) on the outgoing (east–west transect order) or return (west–east transect order) journey from port. On sighting a turtle, the time, sea depth, turtle depth and turtle behaviour were recorded. All surveys were conducted in a good sea state, to reduce the impact of conditions on sighting probability.

ENVIRONMENTAL DATA

Weather data were recorded in three independent ways to try and remove any impact of very local weather conditions on land impacting our interpretation of the weather in Laganas Bay. (i) Wind direction, cloud cover and sea state were recorded approximately at the start and end of each survey by direct observation, (ii) a WS-2300 weather station (La Crosse Technology Ltd, La Crosse, WI, USA) positioned 100 m in land (Fig. 1) was set to record a range of parameters (including air temperature, wind direction and speed) at 30-min intervals (and downloaded bi-weekly onto computer) between 8 May and 31 July 2006, and (iii) hourly data sets were provided by the Zakynthos Airport weather station located 1 km inland from Laganas Bay (Fig. 1) for the period of 1 May to 31 July 2006. Where readings from the WS-2300 and airport weather stations were in agreement, we took the mean of these observations. When they differed appreciably (e.g. due to local topography influencing wind direction), then the weather station record was selected which showed a wind direction that most closely matched that observed visually during the surveys at sea.

ANIMAL-BORNE LOGGERS

Navsys Ltd. TrackTag™ GPS loggers (Colorado Springs, CO, USA; <http://www.navsys.com>) were attached to three female loggerhead sea turtles for a total of 73 complete days (17, 31 and 25 days respectively) between 20 May and 23 June 2006. In addition, we used time-depth recorders (TDRs) that recorded ambient temperature and depth; LOTEK LTD_1100 model TDRs (LOTEK Marine Technologies, St. John's, NF, Canada). These were attached to the three females fitted with GPS loggers plus three others for a total of 140 days (17, 31, 25 and 31, 12, 21 days respectively) between 16 May and 27 June. For GPS and TDR system parameters and attachment-retrieval methodology, see Schofield *et al.* (2007).

Validation trials were conducted to confirm the equivalence of temperature readings made by the different temperature devices. In a controlled experiment, we compared the sea temperature readings of the Tinytag TGP-4204 external probe ($n = 1$), Tinytag TGP-4017 internal probe ($n = 1$) and Lotek TDRs ($n = 6$) used during the research. All equipment readings were simultaneously taken for 10 min at 30-s intervals at the surface, 1-, 3-, 5- and 7-m sea depths. We found that the two Tinytag loggers consistently recorded temperature to within 0.01 °C of one another at the sea surface (the external probe was not used at lower depths). The TDRs recorded temperature on average 0.09 °C lower than the Tinytag TGP-4017 internal probes (range –0.01 to –0.16, SD ± 0.04). These small differences were corrected in the data analysis.

WATER TEMPERATURE FURTHER FROM THE SHORE

We were unable to conduct our own surveys of water temperature far from the shore for logistic reasons. Therefore, we used the *in-situ*

temperature readings made by equipped turtles to assess water temperature further from the shore, since water depth increased in the middle of the bay (Fig. 1).

TURTLE DISTRIBUTION ANALYSES

We investigated whether turtle distribution, recorded both on transect surveys and with GPS tracked turtles, was linked to wind direction. For the surveys in Laganas Bay, we calculated the mean turtle position on transects by assessing their angular distribution around the bay from a central reference point and then applying circular statistics (Fig. 1, ORIANA version 2.00).

To obtain an objective measure of area use for GPS tracked turtles, we initially filtered the GPS fixes (average of 51 fixes turtle⁻¹ day⁻¹) by selecting the central location for each hour for each turtle (Tremblay *et al.* 2006). Subsequently, we calculated the daily mean GPS derived position for each tracked turtle. All GPS locations occurring outside of the Laganas Bay area were removed. All GPS locations in the 3 days before egg laying were removed, as existing literature indicates a pattern of increasing activity as a nesting event approaches (Hays *et al.* 1991; Hays *et al.* 1999) that may be driven by active nesting beach selection rather than immediate environmental parameters.

TURTLE TEMPERATURE ANALYSES

We investigated if individual turtles fitted with TDRs ($n = 6$) experienced warmer water than expected by chance. To do this, we examined the water temperatures measured on transects in Laganas Bay. For each survey (either morning or afternoon), we determined the mean and maximum water temperature measured by the Tinytag temperature devices. During the same sampling period at which each survey was conducted, we determined the mean temperature measured by the TDRs attached to individual turtles.

Results

WIND DIRECTION VERSUS SEA TEMPERATURE

Within the 5-km transect area, there was variability in the sea temperature between different transects, and we found that this variability was strongly correlated with wind direction. For example, when the wind blew from the south-east, the warmest water was found in the north-west part of the bay. Overall, the mean wind direction explained 55% of the variation in the location of the warmest sea temperature recorded on each transect survey ($F_{1,30} = 36.3$, $r^2 = 0.55$, $P < 0.001$) (Fig. 2a). This wind–temperature relationship was even stronger during afternoon surveys ($F_{1,16} = 47.7$, $r^2 = 0.75$, $P < 0.001$) (Fig. 2b).

TURTLE DISTRIBUTION

A total of 351 turtle sightings were made during 34 surveys in the 5-km study area. On average, 10 individuals were sighted per survey (range 0–38 sightings survey⁻¹). There was strong link between turtle distribution and wind direction. For example, Fig. 3 shows the distribution of turtles on 2 days of contrasting wind direction and shows how when the wind blew from the east, turtles were concentrated in the western

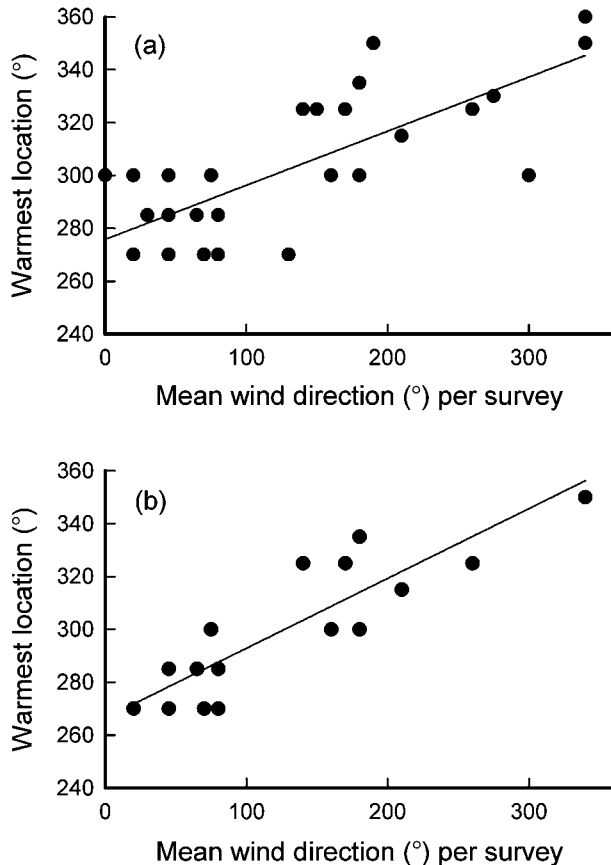


Fig. 2. The relationships between mean wind direction per survey and warmest sea temperature location recorded on transects in the localized 5-km survey area; (a) all records ($F_{1,30} = 36.3$, $r^2 = 0.55$, $P < 0.001$) (b) afternoon records ($F_{1,16} = 47.7$, $r^2 = 0.75$, $P < 0.001$).

part of the bay, while when the wind blew from the south the turtles were seen in the northern part of the bay.

This relationship between wind direction and turtle distribution was always significant but improved when we selected those surveys where more turtles were sighted, presumably because of the inability to accurately assess turtle distribution when few turtles were seen, that is, when the number of turtles sighted increased, the relationship became tighter albeit there were fewer sampling dates that could then be included in the analysis. For example, selecting surveys where there were

> eight turtle sightings ($n = 21$ surveys) showed that 73% of the variation in mean turtle distribution could be explained by wind direction ($F_{1,16} = 43.6$, $r^2 = 0.73$, $P < 0.001$) (Fig. 4a).

This strong correlation between wind direction and turtle location was supported by the data obtained from the three turtles tracked using GPS. For these GPS-tracked turtles, 65% of the variation in their daily mean position in the bay was explained by wind direction ($F_{1,57} = 106$, $r^2 = 0.65$, $P < 0.001$) (Fig. 4b,c).

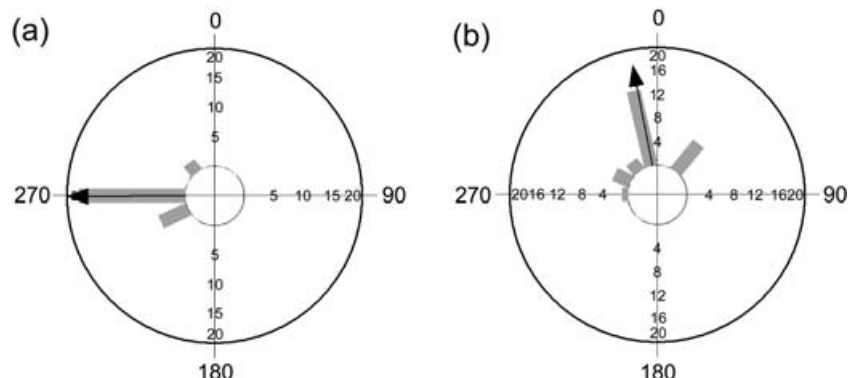
When both mean wind direction and angular position of the warmest water in the bay each day were entered into a stepwise multiple regression (using MINITAB version 8.2) against mean daily turtle location (both with the transect data set and the GPS tracking data set), only wind direction entered the subsequent equation, that is wind direction seemed to have a stronger impact on turtle location than the location of the warmest water.

However, analysis of individual GPS tracks showed that turtles were not simply always located directly downwind, but rather they made movements parallel to the shore moving across the wind direction (Fig. 5). This suggests that the turtles were not simply passively advected but rather actively controlled their position.

SEA TEMPERATURE AND TURTLE DISTRIBUTION

In total, we obtained 93 instances of TDR records where there was an accompanying temperature survey along the near-shore transects. The mean TDR temperature was significantly warmer than the near-shore temperature (mean difference $+1.70$ °C, $t = 17.33$, $P < 0.001$) (Fig. 6). Furthermore, the mean TDR temperature was also warmer than the maximum near-shore temperature measured at the same time along the transects (mean difference $+0.25$ °C, $t = 3.2$, $P = 0.002$). The elevation of the TDR temperatures above mean near-shore temperatures was significantly higher during afternoon surveys (mean difference $+1.97$ °C, $n = 56$) than during morning surveys (mean difference $+1.28$ °C, $n = 37$) ($t_{90} = 4.0$, $P = 0.0001$). Furthermore, the elevation of TDR temperatures above mean near-shore temperatures tended to decline as the season progressed ($F_{1,54} = 23.8$, $r^2 = 0.31$, $P < 0.0001$) and ambient water temperatures approached 26 °C (Fig. 7). This suggests that turtle response to environmental

Fig. 3. Turtle distribution on days with different wind direction; (a) turtle distribution during a survey with north-east wind conditions with aggregations forming at transect 1 and (b) turtle distribution during a survey with south south-east wind conditions with aggregations forming between transects 3 and 4. Shaded bars show number of turtles recorded along each transect. Arrow on each plot indicates mean turtle location.



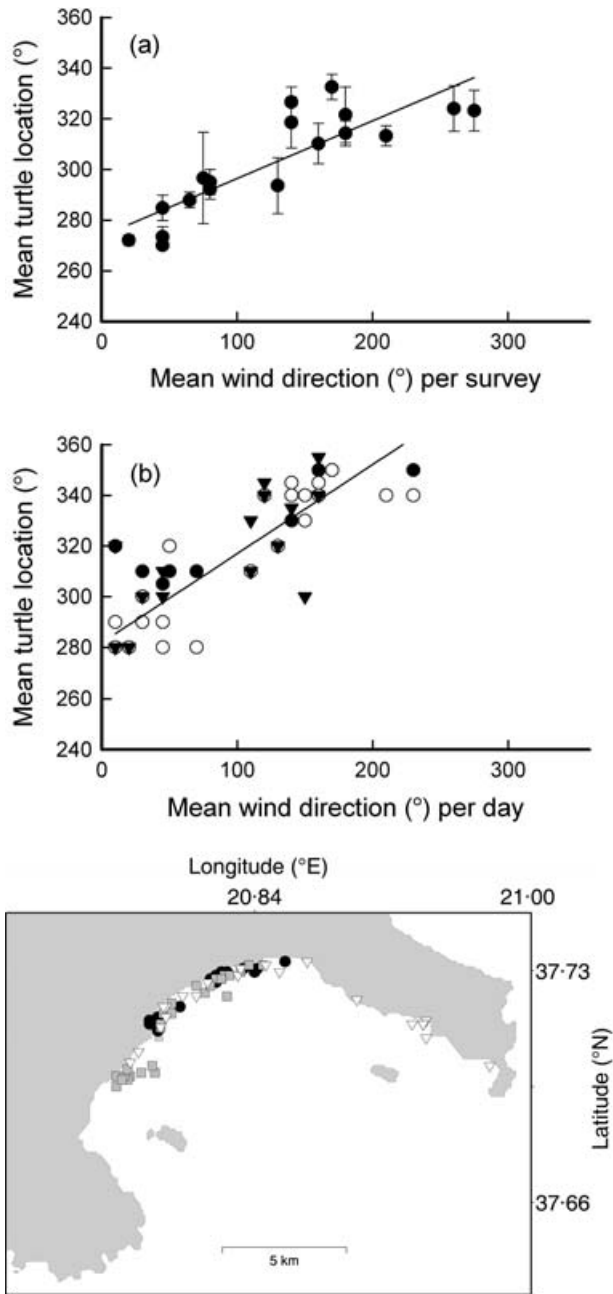


Fig. 4. The relationships between the mean turtle location and mean wind direction for (a) surveys recording > eight turtle sightings in the 5-km study area ($F_{1,16} = 43.6$, $r^2 = 0.73$, $P < 0.001$) with standard deviation bars and (b) mean derived GPS position per day of tracked turtles within Laganas Bay ($F_{1,57} = 106$, $r^2 = 0.65$, $P < 0.001$); GPS1 black circles, GPS2 open circles, GPS3 triangles. In (c) the hourly GPS locations of the three tracked turtles are shown; GPS1 circles, GPS2 squares and GPS3 triangles.

conditions lessened as the season progressed and sea temperature increased.

WATER TEMPERATURE FURTHER FROM THE SHORE

Turtles very rarely dived deep, with < 0.5% of their total time spent deeper than 6 m. However, for three of the six equipped

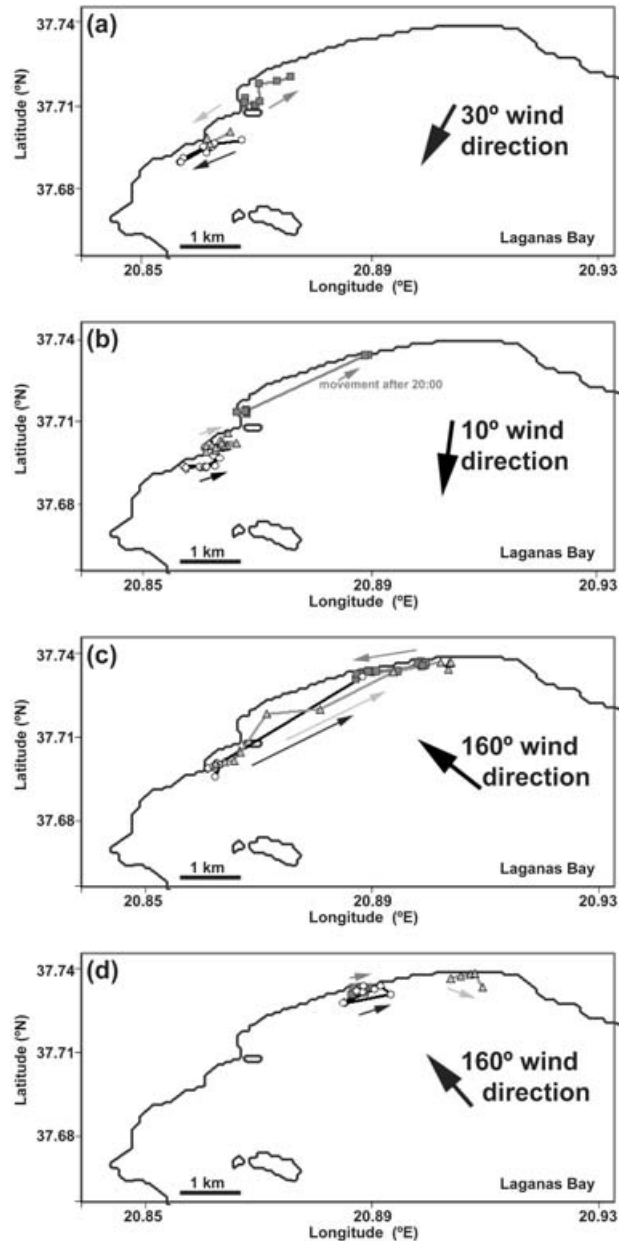


Fig. 5. Movement of three turtle equipped with GPS loggers between 26 May 2006 and 29 May 2006. Each panel shows the movement of each turtle on 1 day and the mean wind direction measured using two independent weather stations (see methodology). The panels show how when the wind blew from the north-east on 26 May (panel a), the turtle aggregated further to the south-west of the bay, but note they were not located directly downwind indicating they were not simply passively advected but rather actively controlled their position. Between 27 May (panel b) and 28 May (panel c), the wind turned around to blow from the south-east and all three turtles moved to the north-east part of the bay. But note again that they did not simply aggregate directly downwind indicating that they were not simply passively advected but rather actively controlled their position.

turtles, we recorded a total of five dives to deeper than 10 m during May. We compared the temperature at depth versus the temperature experienced shallower than 5 m in the 30 mins before and after these deep dives. Water temperature

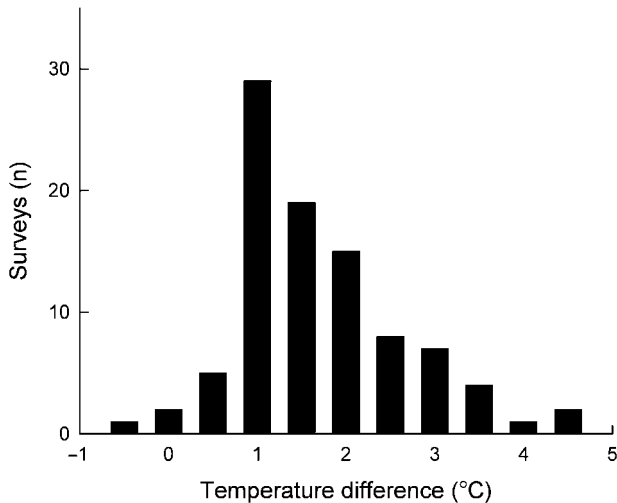


Fig. 6. The differences recorded between the temperature experienced by tagged turtles (measured with a TDR) and the mean near-shore water temperature measured during each boat survey. Positive values indicate that the temperature experienced by a turtle was warmer than the mean near-shore water temperature.

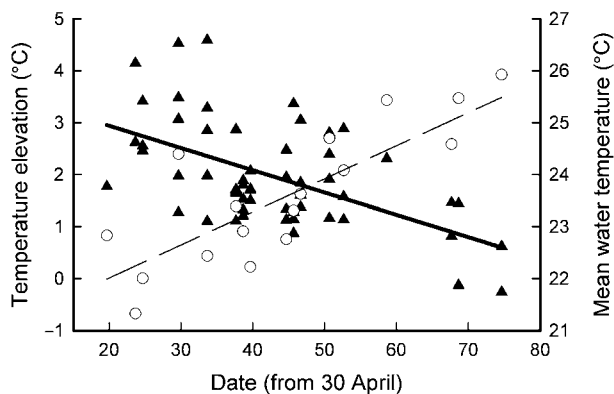


Fig. 7. The elevation of temperatures (left axis, triangles) experienced by tagged turtles (measured with a TDR) above the mean near-shore water temperature during afternoon surveys versus the date. As the season progressed, this temperature elevation declined: temperature elevation ($^{\circ}\text{C}$) = $3.8 - 0.0428$ date (days since 30 April) ($F_{1,54} = 23.8$, $r^2 = 0.31$, $P < 0.0001$). Also shown (right axis, circles) is the mean survey area temperature, showing the seasonal warming of the water.

measured when turtles were deeper than 10 m (i.e. > 1 km from the shore) was, on average, 2.34°C less than water temperature when they were shallower than 5 m.

THE POTENTIAL ENERGETIC BENEFITS OF ADOPTING THERMAL SELECTION

We used empirical data on the relationship between inter-nesting intervals and water temperature to estimate the potential reduction in time to laying the first clutch caused by early season thermal selection by loggerhead turtles. In a comparative study across different nesting populations (Hays *et al.* 2002) it

was shown that: $\log(\text{interesting interval in days}) = 2.25 - 0.043 \text{ temperature } (^{\circ}\text{C})$. At water temperatures of 22, 25, and 27°C , the typical intervals between successive clutches are 20.1, 15.0 and 12.3 days. So at the start of the season when mean water temperatures are around 22°C (or less in deeper water), if turtles select water that is 5°C warmer than average, they might be expected to reduce their time to laying their first clutch by almost 8 days, and by 5 days if they select water 3°C warmer than average.

Discussion

Data loggers and transmitters are starting to transform our understanding of patterns of habitat utilization for hard-to-study species. For example, acoustic tracking of dogfish has shown how individuals tend to rest in deeper cooler water and hunt in warmer shallower water to maximize their net energy gain (Sims *et al.* 2006b). Miniature dive loggers attached to American mink have revealed contrasting patterns of behaviour between individuals, with some being more terrestrial versus others that are more aquatic (Hays *et al.* 2007). Similarly, high-resolution tracking with GPS loggers is allowing the detailed pattern movement for a range of terrestrial and aerial species to be determined (Hamer *et al.* 2007; Wegge, Finne & Rolstad 2007), whereas technical constraints have, to date, largely limited the use of GPS tracking for species that spend most of their time submerged. We showed that the pattern of movement exhibited by GPS tracked turtles reflected the distribution of individuals revealed in boat surveys and that both of these patterns of distribution covaried with wind direction. As has been widely reported in lakes (Barnes & Mann 1991), we found that wind direction influenced the location of warm water patches close to the shoreline. Furthermore, this link was tighter in the afternoon, presumably when the water had been subject to solar heating during the earlier part of the day (Hattori & Warburton 2003; Pulgar, Bozinovic & Ojeda 2005). The location of warm water patches provided the potential for thermal selection by loggerhead turtles and the consequence was that they experienced warmer water than if they were randomly distributed in the near-shore waters. Furthermore, while our information on the water temperature at greater depths within the bay was limited, the records from turtles equipped with temperature loggers suggested that the temperatures at depth further from shore were over 2°C cooler than the shallower temperatures, that is, the actual water temperatures experienced by turtles at the end of May were probably around 5°C above those they would have experienced if they rested at > 10 m, which is the typical resting depth of turtles in tropical nesting sites (Hays, Metcalfe & Walne 2004). While the important role of temperature in driving habitat selection is well established for a broad range of species, including a number of freshwater turtles (e.g. Tamplin 2006), the novelty of our study is that we have shown how selection occurs even in a very dynamic thermal environment.

Several lines of evidence suggest that turtle repositioning is unlikely to be the result of passive drift. First, adult turtles are

strong swimmers and therefore dictate their own position in the breeding season, even if currents or winds are strong. For example, at Ascension Island, breeding female green turtles position themselves around the 20-m isobath despite locally strong winds and currents (Hays *et al.* 1999). Second, loggerhead turtles spend most of the time submerged, either in water or resting on the bottom (Houghton *et al.* 2002), so they are unlikely to be strongly impacted by winds. Third, the thermal selection by the turtles seemed to change as the breeding season progresses, with the biggest elevation above mean bay temperature, that is, the strongest thermal selection, seeming to occur at the start of the season when water temperatures were coolest. Regardless of the exact mechanism at work, it was clear that the turtles repositioned themselves with respect to wind direction and this has not been reported at a breeding site previously. This finding poses two distinct types of question: what are the benefits of thermal selection by loggerhead turtles at this site and how is the thermal selection actually achieved?

Due to their large size, and resulting thermal inertia, adult loggerhead turtles may have a core temperature a few °C above ambient, although their body temperature is still largely driven by the ambient water temperature (Spotila, O'Connor & Paladino 1997). In general, Q_{10} values (the metabolic rate at $T + 10$ °C divided by the metabolic rate at T °C) for loggerhead turtles are around 2.4 to 5.4 (Hochscheid, Bentivegna & Speakman 2004). So loggerhead turtles in warmer water will have increased metabolic rates and hence their production of clutches would be expected to be quicker, albeit that the instantaneous rate at which energy reserves are used will be faster. We used the empirical relationship between interesting intervals and water temperature to estimate that by selecting warm water, time to laying the first clutch might be reduced by as much as 5 days. Greece is near the latitudinal limit for loggerhead turtles and there is a marked seasonal variation in air temperature. The consequence of this variation is that there is a fairly tight window of optimal sand temperatures for egg development limited to between June and September (Margaritoulis 2005). In more tropical nesting areas, this window of optimal conditions is much broader (Godley *et al.* 2002), and hence, it is a female's energy reserves rather than the length of the available nesting season that constrains her reproductive output. Typical incubation durations for sea turtle eggs are around 50–60 days (Margaritoulis 2005). Hence, clutches laid late in the season, (e.g. August) are at risk of being unable to complete development within the window of optimal conditions. By laying their first clutch of eggs as soon as possible in May, loggerhead turtles will thereby maximize the number of clutches they can lay within a season that experience optimum development temperatures even close to hatching. Furthermore, reducing the time required to lay the first clutch will mean that turtles are able to minimize the time that they spend away from their foraging grounds.

It is well known that in many species, reproduction is timed seasonally to maximize offspring survival. For example, many species of mesozooplankton in temperate waters time

egg production so that developing larvae are in the water when their phytoplankton prey is maximally abundant during the spring bloom (Irigoien *et al.* 1998). Similar examples exist in other environments. For example, for birds migrating to high-latitude breeding sites, the chicks need to fledge and be ready for the return migration before local conditions or migration conditions deteriorate too much (Cooke, Findlay & Rockwell 1984). Again, this situation may favour an early seasonal start for reproduction. The early season thermal selection shown by loggerhead turtles in Greece therefore seems to form part of a general strategy of animals to time their reproduction to those times when offspring survival is maximized.

Although we have demonstrated that turtles experience warmer water than expected by chance early in the breeding season in Greece, we have not established how this thermal selection is attained. The search strategies employed by animals is a hotly debated topic, particularly with reference to finding patches of prey (Edwards *et al.* 2007; Sims, Righton & Pitchford 2007). These same considerations apply equally to loggerhead turtles finding patches of warm water. Turtles might be able to perceive wind direction and use this as a cue to locate patches of warm water. In this case, experience would play a role in their ability to locate warm water patches. Alternatively, it might be that there is a component of more random search by turtles along the shore to find warm water patches. Tracking individuals in combination with simultaneous mapping of the thermal environment and wind direction might be used to disentangle these possibilities. Furthermore, various quantitative movement models (e.g. Sims *et al.* 2000; Bailey & Thompson 2006), primarily developed for objectively examining tracking data to infer where animals forage, might be usefully employed to examine tracking data to establish the search rule used by turtles to find warm water. In addition, biophysical models that integrate metabolic rate, body temperature, water temperature, and dive behaviour may shed further light on the benefits of thermal selection by sea turtles.

In summary, we have shown how an endangered ectotherm, the loggerhead sea turtle, near the limits of its breeding range, repositions itself daily to take advantage of thermal hotspots within a highly dynamic thermal environment. How turtles achieve this selection is not known, but it most probably contributes to the success of this species near its cold water range limits.

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