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Sea turtle diving and foraging behaviour around the Greek Island of Kefalonia

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The discovery of a shallow water (<2 m) foraging site off the Greek Island of Kefalonia, where diving and foraging behaviour of male loggerhead turtles (*Caretta caretta*) could be observed simultaneously, was of great interest. The preferred food sources were shown to be the bivalve mollusc *Mytilus galloprovincialis*, the sea grass *Posidonia oceanica*, and the entrails of fish discarded by local fishermen. Whilst foraging, the turtles generally rested on the seabed and employed their forelimbs to clear away detritus from their selected prey. Foraging dives were of short duration (mean ±SE = 2.3 ±0.43 min, N=96) compared to deeper dives reported in the literature presumably, because of the small lung volumes required to attain neutral buoyancy at such shallow depths.

Historically, sea turtle research has been conducted on beaches when the animals come ashore to nest. However, the inherent difficulties involved with observing and following the animals at sea have, until recently, prevented us from gaining a good understanding of their aquatic behaviour.

Over recent years, significant steps have been taken to redress this imbalance with the development of reliable data logging and tracking devices. One such advance includes the use of time–depth recorders (TDRs) which have allowed us to document the diving behaviour of free ranging turtles (Eckert et al., 1989). However, although TDRs have dramatically increased our knowledge, they do not provide detailed information on the type of activity undertaken whilst submerged. For example, a dive profile alone may not reveal whether the turtle is swimming, resting or feeding, whilst at the seabed. The ideal scenario would allow dive data to be analysed in conjunction with accurate behavioural observations. Such a site was discovered off the Greek Island of Kefalonia (38°09′N 20°33′E) which lies to the west of mainland Greece. This study reports the observations made at this site, and discusses the physiological implications of foraging in a shallow water environment.

Observations of sea turtle foraging and diving were made from the vantagepoint of a stone causeway separating the port of Argostoli from Katouvos lagoon. From 1 September through to 16 October 1998, the causeway was monitored for a total of 84 h. This constituted 21 individual survey days, with a mean survey duration of 4 h (SD ±15 min). Additionally, owing to logistical constraints, monitoring of the site was restricted to hours between 0900 and 2000 hours local time (GMT + 2 h). During this period, four male loggerhead turtles (*Caretta caretta*) were identified using external morphological characteristics and the patterns of carapacial epibiota (e.g. *Chelonibia* spp). Sex was determined via the characteristic protrusion of the male's tail beyond the posterior end of the carapace.

Once identified, an individual animal would be continually observed, even when foraging at the seabed, and data collected on foraging technique, dive duration and approximate location. Once visual contact with an individual animal was lost (i.e. it ceased to forage in the direct proximity of the causeway), data collection ceased to prevent erroneous estimations of dive duration. To aid observation, dives were classified as events when the animal became fully submerged and was seen to actively forage on the seabed whereas intervals between breaths, whilst floating at the surface, were discounted from the data set. Finally, all dives were rounded to the closest 30-s increment (e.g. 0.5, 1, 1.5 min, etc.) to aid analysis.

To obtain data relating to depth, the locations of dives were superimposed on British Admiralty chart 2402. As the tidal range within the harbour is known to be minimal (<0.5 m), and owing to the relatively constant depth of the lagoon, it was possible to classify the depth of dives with a high degree of confidence. Such data on the diving behaviour of male turtles are scarce as the animals never return to nesting beaches to permit deployment of electronic devices to monitor their behaviour whilst at sea. As a result, studies of diving physiology and behaviour have primarily been conducted on female sea turtles after a nesting event.

The absence of females from the present 'in-water' study may be attributable to the time of year that it was conducted. For example, during May each year, loggerheads of both sexes congregate in the study site for the purpose of mating. Once mating has taken place, the females move towards the more southerly beaches where they nest until mid-August. Following this, Greek loggerheads are thought to move away from their nesting sites to over-winter in North African waters (Groombridge, 1990). Given that the present study was conducted during September and October, it is feasible that the females may have already moved away from the island. Conversely, observations of males around the causeway long after the end of the nesting season suggests that their presence may not have been related solely to reproduction. Indeed, anecdotal reports from fishermen indicate that males are present at the site all year round which is consistent with the work of Panou et al. (1999) who also made winter observations of turtles around Kefalonia and Ithaca.

Direct observations on foraging suggested that it centred on the extensive beds of bivalve molluscs (*Mytilus galloprovincialis*) that are found along the walls of the causeway. Whilst feeding on the bivalve molluscs, the sea turtles used their front flippers extensively. Initially, the flippers were used in a sweeping manner to clear away sediment from their selected prey, after which molluscs were torn away from their substrate by means of the sea turtle's jaws and then held between its front flippers. Similar observations were made by Davenport & Clough (1985) who noted the use of pseudoclaws on the front flippers of

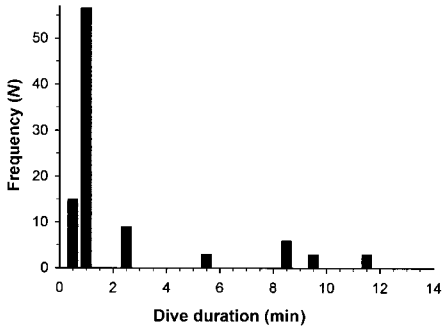

Figure 1. Frequency distribution of all adult male sea turtle dives observed from the causeway during the entire survey period (N=96).

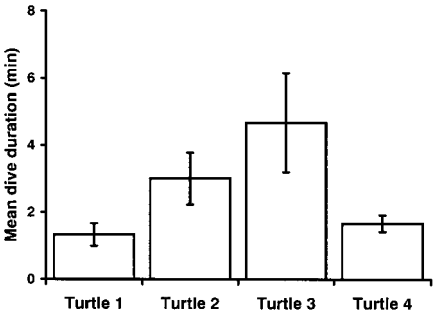

Figure 2. Mean dive duration, for the four adult male loggerheads over the entire survey period (±1SE) (turtle 1, N=19; turtle 2, N=28; turtle 3, N=34; turtle 4, N=15).

hatchling loggerheads to manipulate prey items, before again turning their head sideways to tear at the prey with their jaws. Although pseudoclaws decrease as the turtle grows (Davenport & Clough, 1985), the current observations suggest that the use of fore flippers in feeding may continue throughout an animal's life which is consistent with reports of sweeping fore flipper movements by loggerheads foraging in Moreton Bay, Australia (Limpus et al., 1994).

In addition to bivalve molluscs, the male turtles were also seen to feed extensively on the beds of sea grass (*Posidonia oceanica*), and on the entrails of fish discarded by local fishermen. To feed upon such benthic food sources, turtles have to be able to remain at the seabed for prolonged periods of time. Data collected at the causeway (depth $\leqslant$2 m, N=96 dives) revealed that the maximum duration for an individual dive was 11 min (N=3) with the shortest dive being only 30 s (N=15). When the data for all sightings were combined, the overall mode was found to be 1 min (N=57) (Figure 1) with a mean dive time of 2.3 ±0.4 min (N=96). The duration of dives for individual animals can also be seen in Figure 2.

For benthic foraging to be beneficial, the energy expended reaching and remaining at the required depth must be outweighed by the energy gained through ingestion and assimilation. Milsom (1975) and Minamikawa et al. (1997) showed that loggerhead turtles control their buoyancy by changing the volume of air inspired before diving to the depth where they intend to stay. The lung volume is highest at the sea surface, and decreases with increasing water pressure (Minamikawa et al., 1997). Correspondingly, when foraging in shallow water, turtles must be able to reach the seabed without having to constantly fight against their own buoyancy. Sightings of turtles resting on, or crawling over, the seabed suggest that individuals achieved this by becoming 'neutrally' or slightly 'negatively' buoyant.

Since lung volume, and hence O_2 store, will increase for deeper dives, duration would be expected to increase with dive depth. This is consistent with Minamakawa et al. (1997) who found a positive correlation between maximum depth and duration for resting dives with a flat profile at the maximum depth for female loggerheads. Such 'flat-bottomed' dives were observed in the present study and, as such, comparisons were made with the previous work to see if the relationship between depth and duration for such dives was consistent. This was achieved by digitizing figure 5A in Minamakawa et al. (1997), and determining the relationship between depth and duration. This was then used to make predictions of dive duration at depths representative of the causeway (i.e. 1–2 m). The results of this were broadly consistent with the Kefalonian data, although the predicted dive durations were found to be longer than the observed times. For example, for a 2 m flat-bottomed dive the predicted duration was 9.2 min, whereas the actual mean duration was a mere 2.3 ±0.4 min. This implies that the metabolic rate of the Kefalonian turtles was higher than in the previous study, possibly as a result of their observed energetic foraging (as opposed to resting), or as a consequence of sexual differences in study animals.

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