

## Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef

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Contemporary studies of sea turtle diving behaviour are generally based upon sophisticated techniques such as the attachment of time depth recorders. However, if the risks of misinterpretation are to be minimized, it is essential that electronic data are analysed in the light of first-hand observations. To this aim, we set out to make observations of juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) foraging and resting in a shallow water coral reef habitat around the granitic Seychelles (4°S, 55°E). Data were collected from six study sites characterized by a shallow reef plateau (<5 m) and a flat sandy area at the base of the reef face (<10 m). Observation data were categorized into the following behaviours: (1) stationary foraging; (2) active foraging; (3) resting; and (4) assisted resting. Central to this investigation was the development of a technique for accurately estimating the size of sea turtles *in situ* based upon previously tested techniques for reef fishes. This revealed that through calibration, the curved carapace length (CCL) of marine turtles can be consistently estimated to within 10 cm of their actual size. Although rudimentary, this has advantages for assessing the residency or absence of specific life history stages from particular environments. Indeed, our data supported previous claims that following the reproductive season, adult hawksbills in the region may move away from the nesting beaches to alternative foraging grounds whilst immature turtles (following the pelagic juvenile stage) may opt to reside in areas close to their natal beaches. With regards to habitat utilization, juvenile hawksbills displayed an alternating pattern of short, shallow foraging dives followed by deeper, longer resting dives. These findings are consistent with previous electronic studies of free-range diving in this species and suggest that the maximization of resting duration may be an important factor driving this behaviour.

KEYWORDS: Seychelles, Indian Ocean, sea turtle, diving behaviour, optimal depth, buoyancy control.

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## Introduction

For behavioural ecologists, the ability to observe animals in their natural habitat is fundamental. For large aquatic vertebrates such as marine turtles, cetaceans and phocids this poses a particular problem as the animals are often difficult to locate. Recently, however, significant advances have been made in our understanding of such fauna through the development of sophisticated electronic devices such as satellite transmitters (e.g. Dietz and Heidejorgensen, 1995; Papi *et al.*, 1997) and time depth recorders (e.g. Eckert *et al.*, 1986; Wilson *et al.*, 1996; Le Boeuf *et al.*, 1998). With respect to sea turtles, such developments have revolutionised our understanding of their in-water behaviour with specific reference to diving and migratory patterns (e.g. Eckert *et al.*, 1986; Minamikawa *et al.*, 1997; Hays *et al.*, 2000). Nonetheless, gaps in our knowledge still exist as it is often impossible to identify conclusively specific behaviours on the basis of electronic data alone (Houghton *et al.*, 2000). For example, in a previous study of loggerhead turtles (*Caretta caretta*, Linnaeus 1758) foraging in a shallow lagoon in Greece (Houghton *et al.*, 2000), turtles were observed to rest on the seabed whilst foraging on bivalve molluscs (*Mytilus galloprovincialis*, Lamarck 1819). Had a time depth recorder, or even a motion sensor, been attached to these animals, the resultant profile (i.e. direct descent to the seabed, protracted flat-bottomed phase and direct ascent towards surface with minimal movement at the seabed) would have undoubtedly been classified as resting behaviour (e.g. Type 1 dive: Minamikawa *et al.*, 1997; Type 1a dive: Houghton *et al.*, 2001). For the risk of such errors to be minimized, attention needs to be paid to more rudimentary but direct observations of sea turtles *in situ*. Such data provide an opportunity for researchers to 'ground-truth' electronic data by identifying the type of activities associated with specific dive types. In light of this, a survey of the foraging habitat associated with hawksbill turtles (*Eretmochelys imbricata* Linnaeus, 1766) was undertaken in the granitic islands of the Seychelles during 2000 with two principal objectives: (1) to make first-hand observations of hawksbill turtles within a shallow water (i.e. <20 m) reef habitat, and (2) to relate the findings of this survey to previous electronic studies of diving physiology and behaviours in sea turtles.

## Methods

### *Study site and species*

The hawksbill turtle has a circum-global distribution and is closely associated with coral reef habitat (Carr *et al.*, 1966; van Dam and Diez, 1996). It is a typically benthic foraging species preying upon a wide variety of invertebrates (Meylan, 1988; van Dam and Diez, 1996). Furthermore, the species is well adapted for mechanically harsh benthic environments with thick keratinized scutes covering its carapace and characteristically beak-like jaws for snipping prey from within crevices (van Dam and Diez, 1996).

The present study considers the behaviour of hawksbill turtles at a number of sites in the granitic Seychelles which lie in the Indian Ocean to the east of the African continent and north of Madagascar (figure 1). Study sites were located around the main island Mahé (4°45'S, 55°30'E) and a number of small islands within its vicinity (figure 1). Each site was characterized by shallow coral reef habitat interspersed with deeper sandy clearings. In total, data were collected from five sites by a total of six observers: (1) Sainte Anne National Marine Park; (2) Cap Ternay

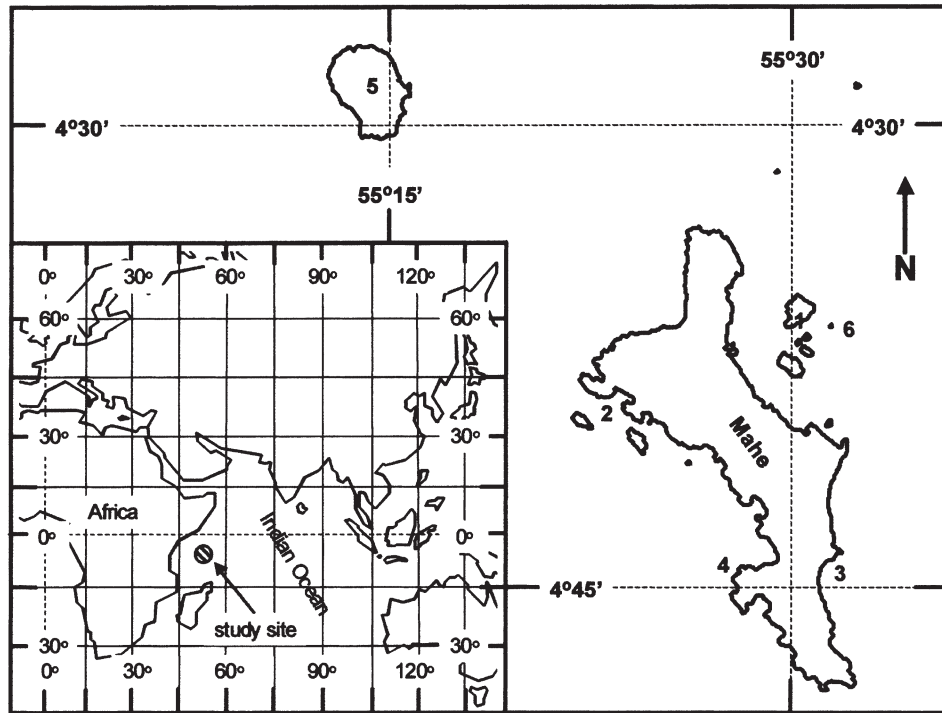


FIG. 1. Map of the Mahé and the inner islands showing the location of the six study sites: (1) Sainte Anne National Marine Park; (2) Cap Ternay National Marine Park; (3) Anse Royale; (4) Anse Soleil; (5) Ile Silhouette National Marine Park; (6) Ile Seché. Inset: the location of the granitic Seychelles in the Indian Ocean.

National Marine Park; (3) Anse Royale; (4) Anse Soleil; (5) Ile Silhouette National Marine Park; and (6) Ile Seché (figure 1). Such fringing reefs are characteristic of the granitic islands of the Seychelles Bank, but they vary greatly in degree of development, both within and between islands. They are most extensive on the two largest islands of Mahé and Praslin, where they occupy 20 and 27 km<sup>2</sup>, respectively (Stoddart, 1984). The reefs along the south-east coast of Mahé, facing the trade winds, are continuous and unbroken, and vary in width from 500 to 750 m (Stoddart, 1984). Along the north-west coast, however, in a more protected situation, the reefs are highly irregular, with deep channels and enclosed hollows up to 15 m deep; they vary in width up to 1500 m. Because of the shallowness of the Seychelles Bank, these fringing reefs have reef fronts only about 20 m high. The reefs of the west coast of Mahé are small and discontinuous, and are mainly found in bays (Anse a la Mouche, Baie Lazare), where they may be interrupted by river mouths (Stoddart, 1984).

#### *Estimating the size of hawksbill turtles in situ*

One of the principal components of the study was to develop a technique for estimating the size of marine turtles *in situ*, without direct measurement. For this, we adapted a previously tested technique for indirectly estimating the size of reef fishes (Bell *et al.*, 1985; Samoily, 1992; Samoily and Carlos, 1992). This required the construction of four mock-up carapaces of varying sizes (40, 50, 60 and 70 cm curved carapace length (CCL)) to validate estimates of size made underwater. We

achieved this by randomly numbering each carapace and submerging it to a depth of 10 m (figure 2). Observers equipped with SCUBA equipment were then asked to estimate the size of each carapace in turn from a distance no closer than 4 m. This minimum distance was adopted as it represented a realistic range at which hawksbill turtles could be viewed without altering their behaviour. The numbers on the carapaces were then changed and the exercise repeated. By comparing these data with the actual curved length of each mock-up it was possible to determine the inherent error for each observer, which was later applied to actual estimates of sea turtle sizes.

#### *Behavioural observations*

Observations of marine turtles were made from the surface using standard snorkelling (water depth <6 m) and SCUBA equipment (water depth >6 m). Survey sites were monitored on an opportunistic basis for a maximum of 2 h per day. If a turtle was encountered during monitoring, observations of behaviour were made until close visual contact with the animal was lost. Study animals were approached until ~4 m from the observer, thus standardizing the distance at which size estimates were made. The following data were recorded: (1) date and time of day; (2) location; (3) type of behaviour observed; (4) depth at which the observed behaviour occurred (noting movements between sites of different depth for different activities). This was achieved using a calibrated depth gauge (Scuba Pro) and dive computer (UWATEC) for both snorkelling and SCUBA data; (5) dive duration (when possible).

#### *Classification of observed behaviours*

Behaviours were classified as one of the following: (1) stationary foraging—SF (ingestion of prey whilst resting on the seabed); (2) active foraging—AF (location and ingestion of prey items at the seabed whilst maintaining position in the water column); (3) resting—R (remaining stationary on the seabed without foraging); (4) assisted resting—AR (remaining stationary at the seabed whilst using an external structure such as a cave or table coral).

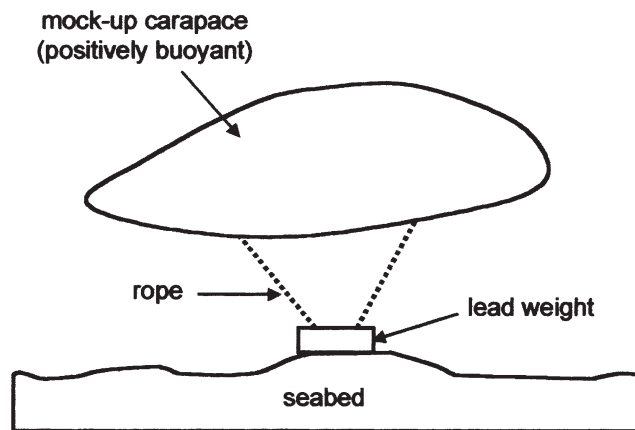


FIG. 2. Side view of mock-up carapace attached to the seabed during the calibration experiment.

## Results

### *Estimating the size of hawksbill turtles in situ*

The relationship between actual and estimated sizes of the four mock-up carapaces can be seen in figure 3. The ability of observers to repeatedly estimate the size of a given carapace on different occasions is expressed as standard deviation in table 1. In general, observers tended to slightly overestimate the size of the carapaces which was adjusted for using the equation derived for each observer (table 1). Following the calibration experiment it was decided that estimates of curved carapace length should be made to the nearest 10 cm increment (e.g. 40 cm, 50 cm, 60 cm etc).

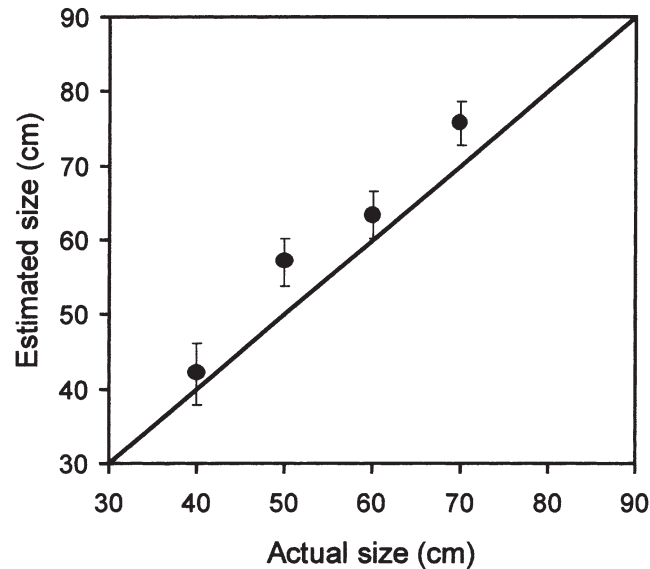


FIG. 3. Comparison of actual and estimated sizes of the four mock-up carapaces ( $\pm 1$  SD). Data shown represent a combination of all observers ( $N=6$ ). Line of equivalence (i.e. actual size = estimated size) is shown.

Table 1. Comparison of size of four mock-up carapaces with mean estimated sizes ( $\pm 1$  SD) for the six experimental observers. Below are the linear equations derived from the validation experiment used to correct data.

Mock-up size (cm)	Mean estimated size, Obs 1 (cm)	Mean estimated size, Obs 2 (cm)	Mean estimated size, Obs 3 (cm)	Mean estimated size, Obs 4 (cm)	Mean estimated size, Obs 5 (cm)	Mean estimated size, Obs 6 (cm)	Mean estimated size, all observers (cm) ( $\pm 1$ SD)
40	43 (2.5)	47 (2.0)	38 (3.5)	43 (1.1)	45 (0.4)	36 (2.8)	42.0 (4.2)
50	55 (3.4)	56 (1.8)	58 (1.2)	60 (1.3)	58 (1.8)	55 (1.2)	57.0 (2.0)
60	65 (2.1)	63 (1.9)	67 (1.8)	62 (0.9)	58 (2.3)	65 (1.8)	63.3 (3.1)
70	71 (2.6)	74 (3.0)	76 (2.8)	79 (0.8)	76 (1.4)	78 (0.4)	75.6 (2.9)
Correction equation:	$Y = 0.94x + 6.8$	$Y = 0.88x + 11.6$	$Y = 1.2x - 7.9$	$Y = 1.1x + 0.5$	$Y = 0.93x + 8.1$	$Y = 1.36x + 16.3$	$Y = 1.0733x + 0.4667$
	$Y = \text{actual CCL};$						
	$x = \text{estimated CCL}$						

Between 8 March 2000 and 1 April 2000 a combined total of 51 in-water sightings of hawksbill turtles were made in 120 h of monitoring. The estimated mean carapace length (after size corrections had been applied) was 51.0 cm (SD 6.38) with a modal size class of between 50.0 and 59.9 cm (figure 4). The range of sizes varied from 38 to 61 cm (after corrections had been applied). These carapace dimensions were substantially smaller than those of adult females observed on nesting beaches around the granitic Seychelles (e.g. Diamond, 1976), suggesting that the animals were immature (figure 4).

#### *Behavioural data*

The mean depth ( $\pm 1$  SD) for each behaviour is shown in figure 5, together with range and sample size in table 2a.

The most interesting finding was the pronounced dichotomy between foraging (both stationary and active) and resting sites in terms of depth. For example, juvenile hawksbills were often seen foraging in a shallow reef habitat <3 m depth. Once foraging had finished, the turtles would ascend to the surface to breathe then descend along the reef face to a deeper sandy-bottomed site (typically 6–9 m) where they would rest for up to 30 min at a time. Following this, the turtles would ascend to the surface again, then commence foraging at the original shallower site (figure 6). Figure 7 compares the depth of foraging and resting dives during such a sequence of events for 11 turtles and shows that resting dives were consistently deeper than active and stationary foraging dives (R vs AF:  $t_{19} = 8.6$ ,  $P < 0.001$ ; R vs SF:  $t_{19} = 6.4$ ,  $P < 0.001$ ). Furthermore, the depth of resting dives was also found to be significantly deeper than assisted resting dives (R vs AR:  $t_{19} = 8.5$ ,  $P < 0.001$ ).

Finally, the mean duration ( $\pm 1$  SD), range and sample size for dive duration is shown in table 2b. From this, both active and stationary foraging dives were found

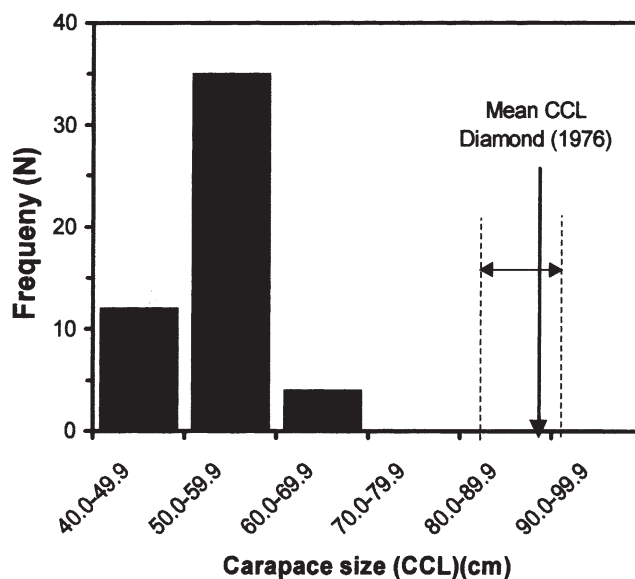


FIG. 4. Frequency distribution showing estimated sizes of hawksbill turtles (after corrections) observed at the six study sites between 8 March 2000 and 1 April 2000. Additionally marked is the mean size ( $N=9$ ) and range of nesting hawksbills at Cousin Island, Seychelles (Diamond, 1976).

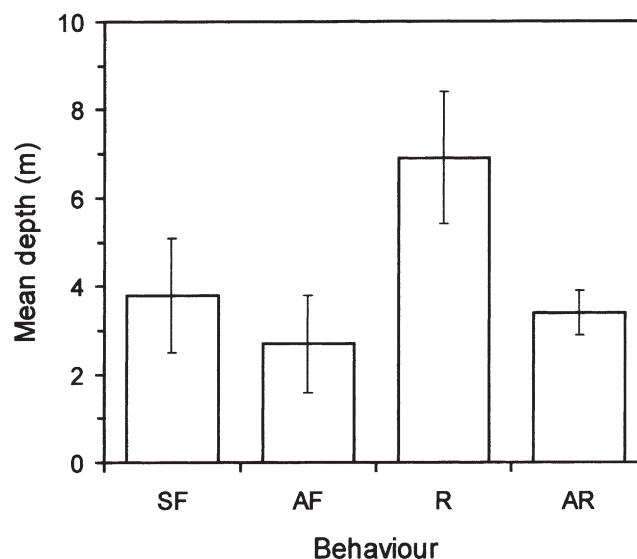


FIG. 5. Mean depth ( $\pm 1$  SD) for different behaviours at the six study sites combined. SF, stationary foraging; AF, active foraging; R, resting; AR, assisted resting.

Table 2a. Mean depth ( $\pm 1$  SD), range and sample size of depth data collected for each behaviour.

Activity	Mean depth (m)	Range of depths (m)	Sample size ( $N$ )
Stationary foraging (SF)	3.8 (1.3)	3–6	24
Active foraging (AF)	2.6 (1.1)	1–5	17
Resting (R)	6.9 (1.5)	4–9	20
Assisted resting (AR)	3.4 (0.5)	3–4	8

Table 2b. Mean duration ( $\pm 1$  SD), range and sample size of depth data collected for each behaviour.

Activity	Mean duration (min)	Range of duration (min)	Sample size ( $N$ )
Stationary foraging (SF)	16.8 (1.7)	15–19	9
Active foraging (AF)	14.3 (1.6)	13–15	11
Resting (R)	23.8 (5.6)	17–31	10
Assisted resting (AR)	21.3 (4.2)	18–26	8

to be significantly shorter than resting dives (R vs AF:  $t_{10} = 2.3$ ,  $P < 0.05$ ; R vs SF:  $t_{11} = 2.5$ ,  $P < 0.05$ ) although no difference could be detected between active and stationary foraging dives (AF vs SF:  $P > 0.05$ ) or resting and assisted resting dives (R vs AR:  $P > 0.05$ ).

### Discussion

The effective interpretation of electronic data in behavioural studies is linked to a prior knowledge of the species in question. For example, if a speed sensor were applied to a terrestrial predator, how would sudden bursts of speed be interpreted if observations of hunting behaviour had not been made previously? Consequently,

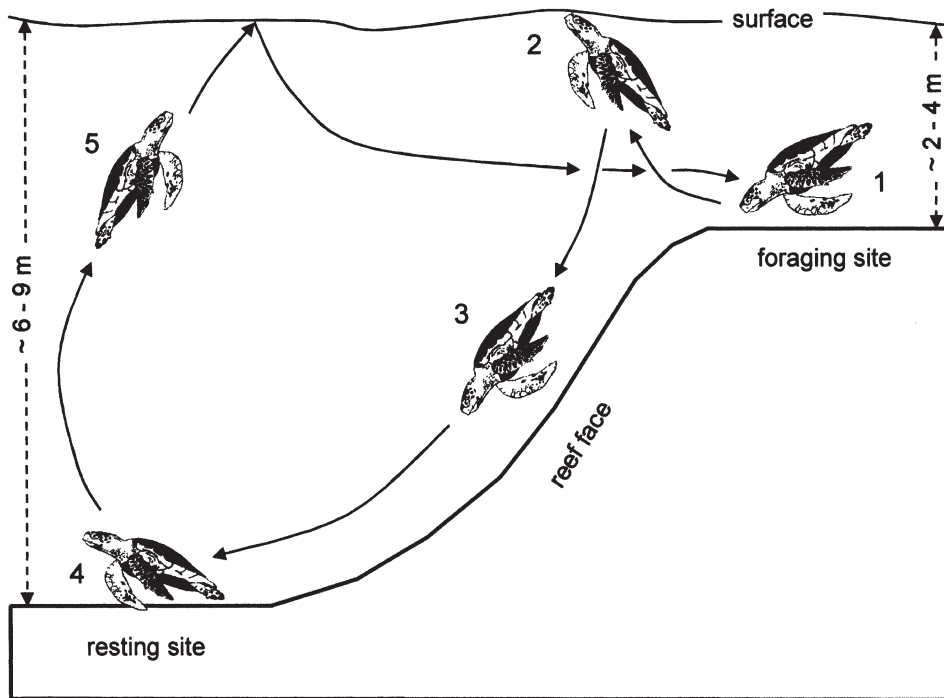


FIG. 6. Schematic showing the movement of hawksbill turtles between foraging and resting sites: (1) foraging on reef flat; (2) ascending to the surface once foraging has ended; (3) descending down reef face; (4) resting site (typically sandy bottomed); (5) ascending to surface following period of rest and return to foraging site.

in terms of diving behaviour there is an ever-increasing requirement for first-hand observations of sea turtles *in situ*. With regards to this, the technique for indirectly estimating body size in sea turtles proved extremely valuable, as has been shown previously for studies of reef fishes (e.g. Bell *et al.*, 1985; Samoily, 1992; Samoily and Carlos, 1992). Furthermore, although such a technique is inherently less accurate than direct measurement, it has distinct advantages for assessing the residency or absence of specific life history stages from particular environments.

The frequency distribution of observed turtle sizes shown in figure 4 has important implications in terms of developmental habitat. For example, in January 1998 Mortimer and Balazs (1999) attached satellite transmitters to five hawksbill turtles nesting at Cousin Island (4°20'S, 55°40'E) to assess post-nesting movements away from the nesting beach. Following the deposition of the final clutch, each turtle travelled continually for 3–5 days away from the nesting site covering distances of up to 20–175 km (Ellis and Balazs, 1998). Once the respective animals reached their destination on the Seychelles Bank, movement became limited to a radius of 15 km over the ensuing months. From this, and previous tagging studies, it was concluded that hawksbills nesting in the Seychelles are likely to spend their entire lives in the territorial waters of the island group. Correspondingly, studies in other isolated islands, such as Hawaii, have also suggested similar short-range post-nesting migrations (Ellis *et al.*, 2000). Such behaviour may explain the absence of adult hawksbills from the present study. Indeed, given that each of the six study sites was located close to sites of known hawksbill nesting (M. Callow, personal observation), the



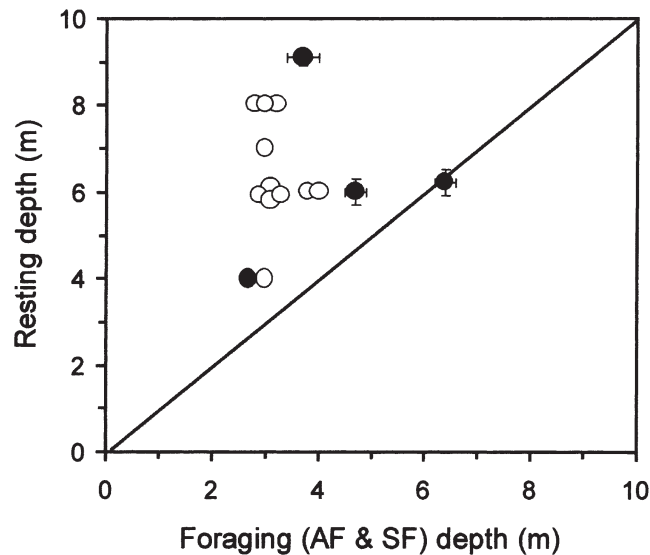


FIG. 7. Comparison of foraging depth (active and stationary combined) with the depth of the resting site (post-foraging) (open circle). Line of equivalence (i.e. foraging depth = resting depth). Data represent occasions when the turtle was observed to swim repeatedly between foraging and resting sites ( $N=11$ ) and not when observed at either site independently. Superimposed are mean dive depth data ( $\pm 1$  SD) for juvenile hawksbills taken from table 3 in van Dam and Diez (1996) (closed circle).

predominance of juvenile turtles during the non-nesting season suggested that turtles which nest on Mahé and its surrounding islands may emulate those on Cousin Island (Ellis and Balazs, 1998) by moving to alternative foraging grounds at the end of the breeding season. Arguably, through such movements, juvenile and adult turtles may avoid competition for resources, although additional data would be required to test this. Nonetheless, the idea of resource limitation around the Seychelles is particularly pertinent for hawksbill turtles following the coral bleaching events of 1997/1998 that greatly depleted the marine flora and fauna of the region (Hoegh-Gulberg, 1999; Robinson *et al.*, 2000; Souter *et al.*, 2000; Spencer *et al.*, 2000; Wilkinson, 2000). An alternative explanation for post-nesting migration away from the study sites relates to studies of diet composition. For example, following recruitment to the benthic environment hawksbill turtles may undergo a period of omnivorous feeding before they adopt the specialized spongivory of larger juveniles and adults (Bjorndal, 1997). This ontogenetic shift in foraging habitat may influence the distribution of hawksbill turtles in the region with individuals moving to alternative foraging sites on the Seychelles Bank following maturation.

In terms of habitat utilization, the movement of juvenile hawksbills between foraging and resting sites was of great interest. Specifically, the turtles appeared to select resting sites of greater depth than the shallow reef fringes where they were foraging. This pattern of alternating bouts of short, shallow foraging dives and longer deeper resting dives has previously been reported for juvenile hawksbills in a Caribbean cliff-wall habitat (van Dam and Diez, 1996). For example, the overall mean foraging depth for the four study animals was 4.7 m, while resting dives had a mean depth of 6.8 m (van Dam and Diez, 1996). The mean depth of resting and foraging dives for each turtle has been superimposed on to figure 7, suggesting that

both data sets are broadly consistent. One possible explanation of this behaviour can be made following studies of buoyancy control in sea turtles. For example, 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 (Houghton *et al.*, 2000). Milsom (1975) and Minamikawa *et al.* (1997) suggested that buoyancy in sea turtles is regulated by adjusting the volume of air inspired before diving to a pre-selected depth. Lung volume is greatest when the animal is at the surface, and decreases with increasing water pressure (Minamikawa *et al.*, 1997; Houghton *et al.*, 2000). Correspondingly, for hawksbill turtles to forage in a shallow coral reef habitat they must be able to feed upon selected items without constantly fighting against their own buoyancy. Sightings of turtles resting upon the reef whilst foraging or floating just above the substratum suggest that individuals achieved this by becoming neutrally or slightly positively buoyant. This, combined with the higher level of activity, may explain the decreased duration of foraging dives compared to resting dives as oxygen stores would be more rapidly depleted. Conversely, the greater depth and lower activity level of resting dives may allow the turtles to remain submerged for longer, thus decreasing the energy expenditure of ascending and descending through the water column. Despite this, care must be taken not to interpret these findings as a general model for the species with 'shallow' foraging sites and 'deep' resting sites as the depths of particular behaviours were strongly influenced by the topography of the reef. Indeed, the salient point to emerge is not that foraging and resting occur at different depths, but rather that the turtles selected specific resting sites as opposed to merely resting where they foraged. Subsequently, one might argue that when foraging occurs at depths shallower than the point of neutral buoyancy (with lungs full of air), the respective animal may opt for a deeper resting site that allows it to dive with more air in its lungs. Conversely, if foraging were to occur at a depth equal to, or greater than, the point at which neutral buoyancy was attained (again with lungs full of air), the depth of resting and foraging dives may overlap as there would be no requirement to move to a deeper resting site. The idea that turtles may select specific resting sites/depths may also be reflected in the decreased depth of assisted resting dives compared to dives when the animal is resting on the seabed. For example, it is feasible that hawksbill turtles may employ physical structures such as the roof of a cave or a coral outcrop to counteract the positively buoyant affect of inhaled air. As such, turtles may be able to rest in reduced water depth with a full lung of air thus increasing the duration and effectiveness of the resting dive. Finally, in a broader context, the selection of deeper resting sites may go some way to explain the movements of green turtles (*Chelonia mydas*, Linnaeus 1758) between daytime foraging and night-time resting sites at sites in the Bahamas and St Croix, respectively (e.g. Bjorndal, 1980; Ogden *et al.*, 1983).

To summarise, our results suggest that estimations of carapace dimensions can be made *in situ*. Although rudimentary, this has advantages for assessing the residency or absence of specific life history stages from particular environments. With respect to this, our data support the idea that following the reproductive season, adult hawksbills in the granitic Seychelles may move away from the nesting beaches to alternative foraging grounds. Immature hawksbills, however, may opt to reside in areas close to their natal beaches following the pelagic hatchling phase perhaps as a means of reducing resource competition. Whilst in the neritic environment, juvenile hawksbills displayed an alternating pattern of short, shallow foraging dives

followed by deeper, longer resting dives. These findings are consistent with previous electronic studies of free-range diving in this species and suggests that the maximization of resting duration may be an important factor driving this behaviour.

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