

Diet Composition of Hawksbill Turtles (*Eretmochelys imbricata*) in the Republic of Seychelles

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Abstract — Effective conservation of the critically endangered hawksbill turtle (*Eretmochelys imbricata*) in the western Indian Ocean is hindered by a lack of basic ecological information about its diet and habitat requirements. This study utilised stomach samples from dead turtles and oesophageal lavage, together with in-water observations of foraging turtles, to identify the relative importance of species contributing to the diet of hawksbill turtles at five localities in the Republic of Seychelles. Diets were remarkably similar to those of hawksbill turtles from the Atlantic and Pacific in that they fed predominantly on demosponges and anthozoans. In total, ten demosponges, four anthozoans, three seaweeds, one seagrass, one ascidian and the egg cases of a mollusc were identified. The most prevalent taxa encountered were *Stelletta* sp., *Spheciospongia* sp. (both demosponges) and *Zoanthus sansibaricus* (anthozoan). Five genera are new to the global list of taxa consumed by hawksbill turtles, viz. *Stelletta*, *Rhabdastrella*, *Haliclona*, *Pseudoceratina* and *Discosoma*. The relative merits of the various methods of dietary determination are discussed and it is concluded that in-water observations of turtle feeding yields results that are in many ways superior to oesophageal lavage or the collection of gut contents from dead animals. Recommendations are made for further research and conservation efforts, including the identification of adult hawksbill foraging grounds offshore, and the protection of habitats rich in hawksbill food.

INTRODUCTION

Populations of the hawksbill turtle (*Eretmochelys imbricata*) are more than 80% reduced globally, primarily as a result of over-

exploitation in recent centuries (Mortimer & Donnelly, 2008). Effective conservation initiatives are hindered by insufficient basic ecological information about their diet and

habitat requirements. Despite several major hawksbill diet studies in the Pacific and Atlantic Oceans (reviewed by Bjorndal, 1997), ours is the first such study in the western Indian Ocean.

Hawksbill turtles forage in a variety of soft and hard bottomed habitats throughout the tropics. Demosponges dominate their diet in the Pacific and Atlantic (Meylan, 1988), although zoanthids and corallimorphs are favoured at some sites (Mayor *et al.*, 1998; Leon & Bjorndal, 2002). As the largest spongivore on tropical reefs, hawksbill turtles play a key role in the coral reef ecosystem by relieving corals from space competition with sponges (Hill, 1998; Leon & Bjorndal, 2002; Bjorndal & Jackson, 2003) and promoting biodiversity and ecosystem function through bio-excavation of the coral reef (von Brandis, 2011).

Hawksbill turtles are widespread in the neritic environment of the Seychelles Bank, Amirantes Bank and especially in shallow waters adjacent to some 115 islands that comprise the Republic of Seychelles (Mortimer, 1984). Sea turtles received full legal protection in the Seychelles in 1994 and anecdotal accounts suggest that the foraging population is now increasing.

The Seychelles government is currently contemplating expansion of its Marine Protected Area (MPA) network. Considering that the numbers of foraging hawksbill turtles appear to be increasing, sufficient foraging habitat needs to be identified and protected. This study will help define suitable habitats by identifying and ranking the importance of species that comprise hawksbill diet.

METHODS

The dietary composition of hawksbill turtles was determined by oesophageal lavage, examination of the stomach contents of dead turtles and in-water observations at five locations throughout the Seychelles, viz. the Inner Islands group (Mahé and Praslin Islands), D'Arros Island in the Amirantes Group, and the Aldabra, Cosmoledo and Farquhar Atolls (Fig. 1). The inner islands comprise some 41 islands (mostly granitic)

situated on the Seychelles Bank (depth range 10-60 m; area ~40 000 km²). D'Arros Island is a small sand cay located on the Amirantes Bank (depth range 10-60 m; area ~3 500 km²). Aldabra, Cosmoledo and Farquhar are mid-oceanic, upraised limestone atolls situated 1 100 km southwest of the inner islands. All islands in the Seychelles are encircled by fringing reefs comprising a shallow reef flat extending from the shore to the reef crest followed by a gradually deepening reef slope.

Oesophageal lavage was conducted on immature turtles foraging on the reef flats of D'Arros Island in 2006 (n = 20) and Aldabra Atoll in 1992 (n = 19) by the first and second authors respectively. Oesophageal lavage involves the non-lethal extraction of ingesta from the anterior region of the oesophagus by means of a water pump (Forbes & Limpus, 1993). Turtles were hand-captured using the 'beach jump' and 'rodeo' methods (Limpus & Reed, 1985) and restrained in an upside-down and posteriorly elevated position. Gentle pressure was applied to the tip of the mandible using a tongue depressor. As the mouth opened, another depressor was positioned between the mandible and maxilla to maintain the opening. Next, a lubricated, flexible plastic tube was inserted through the mouth into the bottom of the oesophagus. The tube length was determined prior to insertion by laying it along the midline of the plastron and measuring from the junction of the humeral and pectoral scutes to the tip of the mouth. An inner tube diameter of 5 mm was used for turtles larger than 40 cm in curved carapace length and 3.5 mm for smaller individuals. Saltwater was delivered via a hand pump at a steady rate of approximately 10 l min⁻¹. Expelled food items were collected in a mesh bag below the head and stored in 70% ethanol. The turtles were tagged with conventional flipper tags, measured and released unharmed.

Stomach contents of salvaged dead hawksbill turtles were collected opportunistically between 1982 and 2003 by the second author. Those from Cosmoledo (n = 26) and Farquhar (n = 2) were collected in 1982-83 from animals legally killed for their shell (Mortimer, 1984). Those from the Inner Islands (n = 20) were collected between

1995 and 2003 and were derived animals that died from accidental entanglement in nets, propeller strikes, dynamite blasting or unknown causes. A single gut sample from Aldabra was collected in 1987 from a turtle that had died from unknown causes. The date, location, carapace length and relative state of maturity were noted for each dead turtle and the contents of the oesophagus and stomach were surgically removed, fixed in 5% formalin for 24 h and stored in 70% ethanol.

Stomach and lavage samples were drained before analysis, blotted dry and inspected under a dissecting microscope (Olympus SZ61, 0.67-4.5x). Distinguishable ingesta were separated and their wet weight measured to the nearest tenth of a gram; indeterminate slurry was disregarded. Species in the diet were identified to the lowest possible taxonomic rank based on gross appearance and spicule morphology (sponges) using available literature (Gosliner *et al.*, 1996; Allen & Steene, 1996; Debelius, 2001; Richmond, 2002; Hooper & van Soest,

2002). A small fragment of each sponge ($\pm 0.3 \text{ cm}^3$) was dissolved in sodium hypochlorite (NaOCl) for 15 minutes for spicule analysis. Settled material was extracted and photographed under a compound microscope (Olympus BX45) at 50x, 100x and 400x.

The percentage occurrence, percentage weight and an Index of Relative Importance (IRI) was calculated for each diet species encountered per lavage and gut sample:

$$\% \text{ occurrence of species } x = \frac{\text{number of samples in which species } x \text{ occurred}}{\text{total number of samples}} * 100$$

$$\% \text{ weight of species } x = \frac{\text{combined weight of species } x \text{ in the samples}}{\text{total weight of all samples}} * 100$$

$$\text{IRI of species } x = \frac{\% \text{ occurrence} * \% \text{ weight}}{100}$$

In-water observations of juvenile hawksbill foraging behaviour ($n = 501$) were conducted at D'Arros Island by the first author over a period of eight months between 2006 and 2009 on a small (approx.

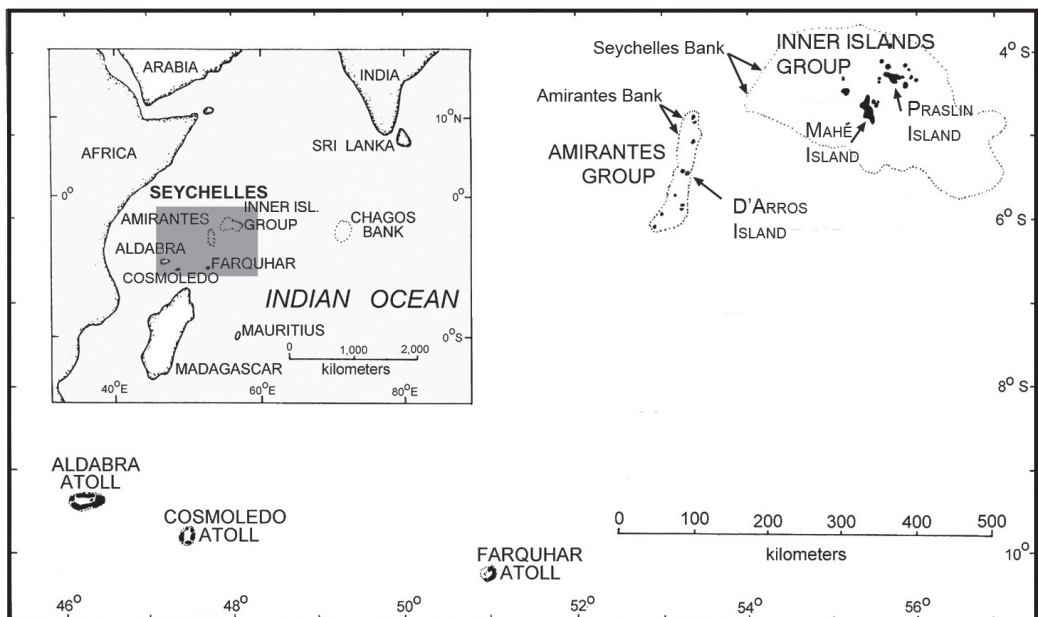


Figure 1. Map of Seychelles indicating locations where hawksbill diet samples were collected.

1 ha) insular platform reef (6-25 m depth) situated approximately 100 m from the shore (von Brandis *et al.*, 2010). The reef was systematically searched using SCUBA gear, up to four times daily ($n = 235$ dives, mean duration = 86 min) and, upon locating a turtle, it was observed for as long as possible. Several turtles with distinct natural markings (damaged marginal scutes and/or presence of epibionts) were re-sighted almost daily and became increasingly habituated to the presence of observers, eventually enabling close observation of their natural behaviour for extended periods. Each time the turtle stopped to feed, the observer positioned himself no less than 1.5 m from the turtle's head and recorded the species consumed and feeding duration on an underwater writing slate. If species of a selected dietary item was unknown, a sample was collected for later identification.

The frequency of consumption was used as an Index of Relative Importance (IRI) for each diet species selected during in-water observations:

$$\text{IRI} = \frac{\text{number of feeding events in which species x was ingested}}{\text{total number of feeding events}} * 100$$

RESULTS

Diet species included sixteen animal and four plant species. With the exception of one ascidian, all could be identified to at least genus level (Table 1). Animals comprised 10 sponges, four cnidarians, one chordate and the egg cases of a mollusc. Sponges belonged exclusively to the class Demospongiae (sponges containing siliceous spicules and/or spongin fibres). Cnidarians were all from the class Anthozoa and comprised a hard coral, soft coral, zoanthid and a corallimorph. The chordate was an unidentified ascidian (class Ascidiacea) and the molluscan egg cases belonged to the triton shell (*Charonia* sp.; class Gastropoda). Plants included three seaweeds (Rhodophyta and Phaeophyta) and a seagrass (Magnoliophyta).

The stomach contents of 17 turtles (age classes: 8 adults, 8 immature and 1 unknown) that perished in the vicinity of Mahé and Praslin Islands contained seven demosponges, three plant species and the unidentified ascidian (Table 1). These gut samples weighed between 2.1 and 114 g and comprised 1-7 dietary species. Demosponges (*Stelletta* sp., *Chondrilla australiensis*, *Tethya* sp. and *Chondrosia* sp.) were the most important taxa in the diet (IRI = 17, 12, 10 and 5 respectively). The remaining three demosponges, the three plant species and the unidentified ascidian featured poorly in the samples (IRI <1).

The combined stomach contents of the eight resident immature turtles from the inner islands contained all 11 of the above diet species but the adults lacked *Rhabdastrella rowi*, *Aaptos suberitoides* and *Hypnea cornuta*. Adults (7 males and 1 nesting female) were presumed to be transient breeding turtles since the nearshore foraging population comprises exclusively juveniles (first and second authors *pers. obs.*) and they all died during the annual nesting season (October – January; Mortimer & Bresson, 1999).

At D'Arros Island, the foraging population comprised only resident immature turtles. The dietary components included four demosponges, four anthozoans, one seaweed and one seagrass (Table 1). The 20 turtles from the shallow reef flats that were subjected to oesophageal lavage yielded the demosponge *Sphaciospongia* sp. (IRI = 43) and the anthozoan *Zoanthus sansibaricus* (IRI = 24). The seagrass *Thalassia hemprichi* and the seaweed *Euचेuma denticulatum* were also ingested but scored IRIs of less than one. Lavage samples were generally small (0.5-9 g) and contained between one and three diet species.

In-water observations of 501 feeding events on the deeper platform reef at D'Arros Island yielded consumption records of three demosponges and three anthozoans. Feeding events lasted on average nine minutes (SD

Table 1. Index of Relative Importance (IRI) of diet species consumed by hawksbill turtles in the Seychelles at the Inner Islands (I), D'Arros Island, and the Aldabra, Cosmoledo and Farquhar Atolls.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Inner Islands	D'Arros Island	Aldabra Atoll	Cosmo.	Farqu.		
Diet determination method (G = Gut contents; L = Oesophageal lavage; I = In-water observation)							G n=17	L n=20	I n=501	L n=19	G n=1	G n=26	G n=2
Animalia	Chordata	Ascidiaceae	-	-	-	-	<1				<1	9	
		Cnidaria	Anthozoa	Alcyonacea	Alcyoniidae	<i>Dendronephthya</i>	-		<1				
				Corallimorpharia	Discosomatidae	<i>Discosoma</i>	-		3				
				Scleractinia	Caryophylliidae	<i>Physogyra</i>	-		<1				
				Zoantharia	Zoanthidae	<i>Zoanthus</i>	-	24		<1			29
		Mollusca	Gastropoda	Neotaenioglossa	Ranellidae	<i>Charonia</i>	-				<1		
		Porifera	Demospongiae	Astrosporida	Ancorinidae	<i>Ecionemia</i>	-			3		10	
						<i>Rhabdastrella</i>	-	<1					
						<i>Stelletta</i>	-	17		45	<1	48	2
				Chondrosida	Chondrillidae	<i>Chondrilla</i>	-	12		6			
						<i>Chondrosia</i>	-	5					
				Hadromerida	Suberitidae	<i>Aptos</i>	-	<1					9
					Clionaidae	<i>Spheciospongia</i>	-		43		13	23	23
					Tethyidae	<i>Tethya</i>	-	10				<1	
				Haplosclerida	Chalinidae	<i>Haliclona</i>	-	<1		<1		6	
				Verongida	Pseudoceratinidae	<i>Pseudoceratina</i>	-			13			
	Plantae	Magnoliophyta	Monocotyledon	Hydrocharitales	Hydrocharitaceae	<i>Thalassia</i>	-	<1	<1	1		1	3
Phaeophyta		Phaeophyceae	Fucales	Sargassaceae	<i>Turbinaria</i>	-	2		<1		<1		
Rhodophyta		Florideophyceae	Gigartinales	Solieraceae	<i>Euclima</i>	-		<1	<1		<1		
				Cystocloniaceae	<i>Hypnea</i>	-	<1			17	29	<1	

= 7.8) and turtles consumed 0-3 diet species per feeding event. Demosponges were considerably more important in the diet, consisting of *Stelletta* sp., *Pseudoceratina purpurea* and *C. australiensis* (IRI = 45, 13 and 6 respectively). The anthozoans *Discosoma* sp., *Dendronephthya* sp. and *Physogyra lichtensteini* (IRI = 3, <1 and <1 respectively) were rarely ingested.

At Aldabra Atoll, samples were derived only from resident immature turtles foraging on the shallow (<2 m) reef flats. Oesophageal lavage of 19 different turtles revealed four demosponges, three seaweeds, one anthozoan and one seagrass (Table 1). Sample weights varied between 0.1-9.3 g and comprised 1-3 diet species. The seaweed *H. cornuta* and the demosponges *Spheciospongia* sp. and *Ecionemia acervus* were most important in the diet (IRI = 17, 13 and 3 respectively) followed by *Stelletta* sp., *Haliclona cymaeformis*, *Z. sansibaricus*, *T. hemprichii*, *E. denticulatum* and *Turbinaria* sp., all of which scored IRIs of <1. The single gut sample from Aldabra belonged to an immature turtle that was found dead in the shallow lagoon and comprised *Stelletta* sp., *H. cornuta* and *Spheciospongia* sp (IRI = 48, 29 and 23 respectively).

At Cosmoledo Atoll, the gut contents of 26 different turtles (age classes: 9 adults, 17 immature) contained four demosponges, the unknown ascidian, three seaweeds and egg cases of the giant triton shell (*Charonia* sp.) (Table 1). Sample weights varied between 9.1-170 g and comprised 1-5 diet species. The important dietary components comprised exclusively demosponges, i.e. *Spheciospongia* sp., *E. acervus*, *H. cymaeformis* and *Stelletta* sp. (IRI = 23, 10, 6, and 2 respectively). *Tethya* sp., *T. hemprichii*, *E. denticulatum*, *H. cornuta*, the unknown ascidian, and the eggs of the giant triton shell (*Charonia* sp.) all scored IRIs of <1. It was not possible to establish whether the adults were resident or transient, but their guts contained all the above taxa except *Tethya* sp. and *E. denticulatum*. The guts of the immature turtles contained all the above dietary components, excluding the triton shell egg cases.

The guts of two turtles from Farquhar Atoll, of unknown age, comprised mostly *Z. sansibaricus* (IRI = 29) followed by demosponge *A. suberitoides*, the unknown ascidian and *T. hemprichii* (IRI = 9, 9 and 3 respectively).

DISCUSSION

Demosponges predominated in the diets of the Seychelles hawksbill turtles, as has been reported in earlier studies in the Indian Ocean (Ross, 1981; Frazier, 1985; Meylan, 1988), Pacific (Balazs, 1978; Alcalá, 1980) and Atlantic Oceans (Carr & Stancyk, 1975; Den Hartog, 1980; Acevedo, 1984; Meylan, 1988; Vicente & Carballeira, 1992; Vincente 1993; Anderes & Uchida, 1994; van Dam & Diez, 1997; Leon & Bjorndal, 2002; Martinez *et al.*, 2002; Valeris *et al.*, 2002; Flores *et al.*, 2003; Blumenthal *et al.*, 2009). Principal sponges in the diet were *Sphaciospongia* sp. and *Stelletta* sp., both scoring high IRIs at multiple locations (Table 1). Interestingly, six of the ten sponge genera (*Sphaciospongia*, *Ecionemia*, *Chondrilla*, *Chondrosia*, *Aaptos*, and *Tethya*) are also common in the diets of Caribbean hawksbill turtles (Meylan, 1988), while the remaining four genera (*Stelletta*, *Rhabdastrella*, *Haliclona* and *Pseudoceratina*) have not previously been reported in the hawksbill diet.

Anthozoans in the diet consisted of the genera *Zoanthus*, *Dendronephthya*, *Physogyra* and *Discosoma*, of which only the latter is new to the global list of species consumed by hawksbill turtles. *Zoanthus sansibaricus* is an important dietary component of hawksbill turtles foraging on the reef flats of Seychelles. The only other location where zoanthids comprise a significant portion of the diet is at Buck Island Reef National Monument in the Caribbean (Mayor *et al.*, 1998; Pemberton *et al.*, 2000). There, a congener, namely *Zoanthus sociatus*, accounted for 85% of the lavage weight recorded by Mayor *et al.* (1998). In-water observations of turtles in Brazil (Stampar *et al.*, 2007) and Honduras (Dunbar *et al.*, 2008) revealed that hawksbill turtles also consume the zoanthid *Palythoa caribaeorum*, which is known to be extremely toxic (Mereish *et al.*, 1991). *Ricordea florida*, a corallimorph similar to that eaten at D'Arros Island (*Discosoma* sp.), occurred in 63.6% of lavage samples in the Dominican Republic (Leon & Bjorndal, 2002) and less frequently at Buck Island (Mayor *et al.*, 1998).

At D'Arros, turtles occasionally consumed *Physogyra lichtensteinii* (bubble coral) and *Dendronephthya* sp. (thistle coral). Obura *et al.* (2010) observed hawksbill turtles eating *P. lichtensteinii* at Aldabra Atoll and reported anecdotal accounts of similar behaviour in Thailand, Madagascar and the Sudanese Red Sea. Because these anthozoans secrete copious mucus when disturbed (first author's *pers. obs.*), their infrequent ingestion may provide greater physiological than nutritional benefits, i.e. the mucus may protect the alimentary canal from abrasion by sponge spicules as suggested by Leon & Bjorndal (2002) in the case of mucus secreted by *Ricordea florida*.

Ascidians were consumed at the Inner Islands, Cosmoledo Atoll and Farquhar Atoll. Elsewhere, they have appeared in the hawksbill diet at Costa Rica (Carr & Stancyk 1975), Cuba (Lazara & Anderes 1998) and in Venezuela where ascidians accounted for 63% of a stomach sample (Valeris *et al.* 2002). Isolated instances also suggest that Seychelles hawksbill turtles occasionally ingest a variety of obscure items such as the eggs of giant triton shells (*Charonia* sp.), plastic, fishing bait, and even fish and bread (second author's *pers. obs.*).

Seaweeds and seagrass occurred frequently in samples but, because they tend to grow in close association with certain demosponges and generally accounted for <5% of sample weight, it appears that they may be ingested incidentally. Yet, at Aldabra, turtles seemed to target *H. cornuta* (IRI = 17). Also, the seaweed *E. denticulatum* at D'Arros comprised 83% of one lavage sample and a turtle was observed feeding on floating fragments of *Turbinaria* sp. for over half an hour. Several authors have reported plant matter in hawksbill stomach samples (Carr, 1952; Carr & Stancyk, 1975; Alcalá, 1980; Meylan, 1988; Green, 1996; van Dam & Diez, 1997; Lazara & Anderes, 1998; Mayor *et al.*, 1998; Leon & Bjorndal, 2002; Martinez *et al.*, 2002; Valeris *et al.*, 2002; Flores *et al.*, 2003), although only Green (1996) and Lazara and Anderes (1998) reported noteworthy quantities (80% and 25% of gut contents

respectively). Irrespective of its potential nutritional benefits, perhaps occasional gorging of plant material facilitates digestion. Unlike other spongivores, hawksbill turtles do not possess morphological adaptations to facilitate the passage of copious sponge spicules (Meylan, 1988).

Gut content removal from salvaged dead animals and oesophageal lavage are valid diet determination methods that have been used extensively (e.g. Balazs, 1980; Forbes & Limpus, 1993; van Dam & Diez, 1997; Forbes, 1999; Leon & Bjørndal, 2002; Berube *et al.*, 2012). Nevertheless, both methods pose limitations that may introduce bias in the assessment of dietary composition and selectivity. In the case of gut contents, some items may have been ingested incidentally, differential digestion may hamper diet identification and, where cause of death is unknown, samples may not reflect the diet of healthy individuals. Limitations of oesophageal lavage include the fact that samples are small (mean = 3.2 g in this study) as only small pieces of recently ingested items are removed, some items may have been ingested incidentally, and certain ingesta may flush more easily from the oesophagus on account of their size, shape and texture.

There are several difficulties associated with the observation of turtles underwater, including adequate access to the study subject, variable underwater visibility and sea conditions, and depth-related SCUBA limitations (Hooker & Baird, 2001; von Brandis *et al.*, 2010). Furthermore, because animals are unmarked, pseudoreplication involving repeat observations of the same subject, may present bias in quantitative studies such as this. However, despite these constraints (Booth & Peters, 1972; Houghton *et al.*, 2000; Houghton *et al.*, 2003; Schofield *et al.*, 2006; Dunbar *et al.*, 2008; Blumenthal *et al.*, 2009; von Brandis *et al.*, 2010), in-water observation is, in many ways, a superior technique to determine diet composition and selectivity. Not only are the limitations associated with gut content and lavage

analysis eliminated, but related behavioural data can also be collected and individual subjects can be re-observed in subsequent surveys (von Brandis *et al.*, 2010). Immature hawksbill turtles are especially suitable for in-water studies because they commonly forage in shallow, near-shore environments (Musick & Limpus, 1997), have small home ranges (van Dam & Diez, 1998) and, when feeding, often remain unaffected by observers (von Brandis *et al.*, 2010).

Despite the wide geo-spatial distribution of our sampling sites in Seychelles, diet determination was only conducted in relatively shallow nearshore foraging grounds inhabited primarily by immature turtles. Although the scarcity of adults at nearshore foraging sites could be an artifact of past exploitation (Leon & Diez 1999), this does not appear to be the case in Seychelles where it is better explained by developmental migration, that is, migration from shallower juvenile feeding grounds to progressively deeper adult foraging grounds (Carr & Caldwell, 1956; Limpus, 1992, Mortimer & Donnelly, 2008), and by migration of adults between nearshore reproductive habitats and distant foraging grounds (Mortimer, 1984). In support of this, five post-nesting, satellite-tracked females moved from the Inner Islands in 1998 (Mortimer & Balazs 1999) and seven from D'Arros Island in 2014 (von Brandis & Mortimer unpublished data) to deeper (>40 m) off-shore foraging grounds (>100 km from land) on the Seychelles Bank (Figure 1) where different dietary material may well occur. Turtles may also make use of deeper foraging habitats along the verges of the Seychelles and Amirantes Banks and the mid-oceanic islands (Mortimer, 1984). Our study, although limited to relatively shallow nearshore habitats is, nevertheless, the first of its kind in the Western Indian Ocean and provides a list of hawksbill turtle dietary species representative of that environment.

The Government of Seychelles passed legislation in 1994 and implemented social programmes to eliminate all trade in hawksbill

shell (Mortimer, 2000). Conservation and monitoring programmes currently underway at more than 20 hawksbill breeding sites nationwide have demonstrated population increases at protected nesting sites (Mortimer, 2006) and increased numbers of foraging turtles in Seychelles waters. It follows that the future of habitats rich in hawksbill forage need to be protected, and such sites ought to be identified and prioritised during the planning of new MPAs currently underway in Seychelles.

Taking evidence into account that the majority of post-nesting hawksbill turtles from beaches in the inner islands and D'Arros forage within Seychelles territory (Mortimer & Balazs, 1999; von Brandis & Mortimer, unpublished data), further research is needed to locate and describe heretofore undocumented foraging habitats on the Seychelles and Amirantes Banks, and on other deeper reefs in the region. Basic ecosystem mapping of most of these deeper sites has yet to be conducted. Further research entailing satellite telemetry to track turtles to their foraging grounds is also needed.

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References

- Acevedo M (1984) Alimentación de tres especies de quelonios marinos en la plataforma suroccidental De Cuba. *Revista De Investigaciones Marinas* 5: 29-35
- Alcala AC (1980) Observations on the ecology of the pacific hawksbill turtle in the central visayas, Philippines. *Fisheries Research Journal of The Philippines* 5: 42-52
- Allen GR, Steene R (1996) Indo-Pacific coral reef guide. Tropical Reef Research, Singapore, 401 pp
- Anderes BL, Uchida I (1994) Study of hawksbill turtle (*Eretmochelys imbricata*) stomach content in Cuban waters. In: Study of the hawksbill turtle in Cuba (I). Cuba: Ministry Of Fishing Industry, pp 27-40
- Balazs GH (1978) A hawksbill in Kaneohe Bay, Ohau. *Elapaio* 38: 128
- Balazs GH (1980) Field methods for sampling the dietary components of green turtles *Chelonia mydas*. *Herpetological Review* 11: 5-6
- Berube M, Dunbar SG, Rützler K, Hayes WK (2012) Home range and foraging ecology of juvenile hawksbill sea turtles (*Eretmochelys imbricata*) on inshore reefs of Honduras. *Chelonian Conservation and Biology* 11: 33-43
- Bjorndal KA (1997) Foraging ecology and nutrition in sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, pp 199-231
- Bjorndal KA, Jackson JBC (2003) Roles of sea turtles in marine ecosystems: Reconstructing the past. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles*. CRC Press, Boca Raton, pp 259-273
- Blumenthal JM, Austin TJ, Bell CDL, Bothwell JB, Broderick AC, Ebanks-Petrie G, Gibb JA, Luke KE, Olynik JR, Orr MF, Solomon JL, Godley BJ (2009) Ecology of hawksbill turtles *Eretmochelys imbricata* on a western Caribbean foraging ground. *Chelonian Conservation and Biology* 8: 1-10

- Booth J, Peters JA (1972) Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Animal Behaviour* 20: 808-812
- Carr AF (1952) Handbook of turtles. New York, Cornell University Press, 321 pp
- Carr AF, Caldwell DK (1956) The ecology and migration of sea turtles. Results of field work in Florida, 1955. *American Museum Novitates* 1793: 1-23
- Carr AF, Stancyk S (1975) Observations on the ecology and survival outlook of the hawksbill turtle. *Biology Conservation* 8: 161-172
- Debelius H (2001) Indian Ocean reef guide. Frankfurt, Ikan Unterwasser-Archiv, 205 pp
- Den Hartog JC (1980) Notes on the food of sea turtles: *Eretmochelys imbricata* and *Dermochelys coriacea*. *Netherlands Journal of Zoology* 30: 595
- Dunbar SG, Salinas L, Stevenson L (2008) In-water observations of recently released juvenile hawksbills (*Eretmochelys imbricata*). *Marine Turtle Newsletter* 121: 5-9
- Flores EC, Liceaga-Correa MA, Garduno-Andrade M (2003) Mapping and characterizing foraging habitat of immature hawksbill turtles in front of the Ria Lagartos Biosphere Reserve, Yucatan, Mexico. In: Pilcher NJ (ed) Proceedings of the 23rd annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-536: 178-181
- Forbes GA (1999) Diet sampling and diet component analysis. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. 4th Pub. IUCN/SSC Marine Turtle Specialist Group, pp 144-148
- Forbes GA, Limpus CJ (1993) A non-lethal method for retrieving stomach contents from sea turtles. *Wildlife Research* 20: 339-343
- Frazier J (1985) Marine turtles in the Comores Archipelago. *Verhandeling Der Koninklijke Nederlandse Akademie Van Wetenschappen. Afdeling Natuurkunde* 2: 84
- Gosliner TM, Behrens DW, Williams GC (1996) Coral reef animals of the Indo-Pacific. *Sea Challengers*, Monterey, California, 609 pp
- Green D (1996) Sea turtles of north Yemen. In: Keinath JA, Barnard DE, Musick JA, Bell BA (eds) Proceedings of the 15th annual symposium on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-387: 116-118
- Hill MS (1998) Spongivory on Caribbean reefs releases corals from competition with sponges. *Oecologia* 117: 143-150
- Hooker SK, Baird RW (2001) Diving and ranging behaviour of odontocetes: A methodological review and critique. *Mammal Review* 31: 81-105
- Hooper JNA, Van Soest RWM (2002) *Systema Porifera: A guide to the classification of sponges*. Kluwer Academic / Plenum Publishers, New York, 1810 pp
- Houghton JDR, Callows MJ, Hays GC (2000) Sea turtle diving and foraging behaviour around the Greek island of Kefalonia. *Journal of the Marine Biological Association UK* 80: 761-762
- Houghton JDR, Callows MJ, Hays GC (2003) Habitat utilisation by juvenile turtles (*Eretmochelys imbricata*) around a shallow water coral reef. *Journal of Natural History* 37: 1269-1280
- Lazara B, Anderes A (1998) Hawksbill turtle feeding habits in Cuban waters. In: Abreu-Grobois FA, Briseño-Dueñas R, Márquez-Millán R, Sarti-Martínez L (eds) Proceedings of 18th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum MFS-SEFSC-436: 65-66

- León YM, Bjorndal KA (2002) Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Marine Ecology Progressive Series* 245: 249-258
- León YM, Diez CE (1999) Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. *Chelonian Conservation and Biology* 3: 230-236
- Limpus CJ (1992) The hawksbill turtle (*Eretmochelys imbricata*) in Queensland: Population structure within a southern Great Barrier Reef feeding ground. *Wildlife Research* 19: 489-506
- Limpus CJ, Reed PC (1985) The green turtle (*Chelonia mydas*) in Queensland: A preliminary description of the population structure on a coral reef feeding ground. In: Grigg G, Shine R, Ehmann H (eds) *Biology of Australasian frogs and reptiles*. Sydney: Royal Zoological Society of New South Wales, pp 47-52
- Martinez C, Fallabrino A, Carrillo D, Escudero A, Guada H (2002) Analysis of stomach contents of a hawksbill turtle entangled in a net in the Peninsula De Paria, Sucre State, Venezuela. Poster Presentation: Feeding and growth. In: Seminoff JA (eds) *Proceedings of the 22nd annual symposium on sea turtle biology and conservation*. NOAA Technical Memorandum NMFS-SEFSC-503: 203-204
- Mayor PA, Phillips B, Hillis-Star Z (1998) Results of the stomach content analysis on the juvenile hawksbill turtles of Buck Island Reef National Monument, U.S. Virgin Islands. In: Sheryan P, Epperly SP, Braun J (eds) *Proceedings of the 17th annual symposium on marine turtle biology and conservation*. NOAA Technical Memorandum NMFS-SEFSC-415: 244-246
- Meylan AB (1988) Spongivory in hawksbill turtles: A diet of glass. *Science* 239: 393-395
- Mortimer JA (1984) *Marine turtles in the Republic of Seychelles: Status and management*. Publication of the IUCN Conservation Library: Gland, Switzerland, 80 pp
- Mortimer JA (2000) Conservation of hawksbill turtles (*Eretmochelys imbricata*) in the Republic of Seychelles. In: Pilcher N, Ismail G. (eds) *Sea Turtles of the Indo-Pacific: Research management and conservation*. Proceedings of the second ASEAN symposium and workshop on sea turtle biology and conservation. ASEAN Academic Press Ltd, London, 361 pp
- Mortimer JA (2006) Simple, yet effective: Protection at the nesting beach. *SWoT State of the World's Sea Turtles Report*, 1: 8
- Mortimer JA, Balazs GH (1999) Post-nesting migrations of hawksbill turtles in the Granitic Seychelles and implications for conservation. In: Kalb H, Wibbels T (eds). *Proceedings of the 19th annual symposium on sea turtle biology and conservation*. NOAA Technical Memorandum NMFS-SEFSC-443: 22-26
- Mortimer JA, Bresson R (1999) Temporal distribution and periodicity in hawksbill turtles (*Eretmochelys imbricata*) nesting at Cousin Island, Republic of Seychelles, 1971-1997. *Chelonian Conservation and Biology* 3: 318-325
- Mortimer JA, Donnelly M (2008) Marine turtle specialist group IUCN red list status assessment: Hawksbill turtle (*Eretmochelys imbricata*). Available at: <http://www.iucnredlist.org/documents/attach/8005.pdf>
- Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. Boca Raton, CRC Press, pp 137-164

- Obura DO, Harvey A, Young T, Eltayeb MM, von Brandis RG (2010) Hawksbill turtles as significant predators on hard coral. *Coral Reefs* 29: 759-759
- Pembererton R, Coyne M, Musick JA, Phillips B, Hillis-Starr Z (2000) Habitat utilization of hawksbill sea turtles at Buck Island Reef National Monument: The Zoanthid question. In: Mosier M, Foley A, Brost B (eds) Proceedings of the 20th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-477: 69-70
- Richmond MD (2002) A field guide to the seashores of eastern Africa and the western Indian Ocean islands. 2nd Ed. Sida, Dar Es Salaam, 461 pp
- Ross JP (1981) Hawksbill Turtle (*Eretmochelys imbricata*) in the Sultanate of Oman. *Biological Conservation* 19:99
- Schofield G, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2006) Behaviour analysis of the loggerhead sea turtle (*Caretta caretta*) from direct in-water observation. *Endangered Species Research* 2: 71-79
- Stampar SN, Da Silva PF, Luiz OJ (2007) Predation on the zoanthid *Palythoa caribaeorum* (Anthozoa, Cnidaria) by a hawksbill turtle in south-eastern Brazil. *Marine Turtle Newsletter* 117: 3-5
- Valeris C, Barrios-Garrido H, Montiel-Villalobos MG (2002) Analysis of the stomach and intestinal contents of a hawksbill turtle (*Eretmochelys imbricata*) captured in Porshoure, Zulia State, Venezuela. In: Seminiff JA (ed) Proceedings of the 22nd annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-503: 234
- Van Dam RP, Diez CE (1997) Predation by hawksbill turtles on sponges at Mona Island, Puerto Rico. In: Schroeder BA (ed) Proceedings of the 8th international coral reef symposium 2: 1421-1426
- Van Dam RP, Diez CE (1998) Home range of immature hawksbill turtles (*Eretmochelys imbricata*) at two Caribbean Islands. *Journal of Experimental Marine Biology And Ecology* 220: 15-24
- Vicente VP, Carballeira NM (1992) Studies on the feeding ecology of the hawksbill turtle (*Eretmochelys imbricata*) In Puerto Rico. In: Salmon M, Wyneken J (eds) Proceedings of the 11th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS 302: 117-119
- Vicente VP (1993) Spongivory in Caribbean hawksbill turtles, *Eretmochelys imbricata*: Data from stranded specimens. In: Schroeder BA, Witherington BE (eds) Proceedings of the 13th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-302: 185-188
- von Brandis RG (2011) Foraging ecology of hawksbill turtles at D'Arros Island, Republic Of Seychelles. Doctorate Technologiae Thesis, Tshwane University of Technology, 241 pp
- von Brandis RG, Mortimer JA, Reilly BK (2010) In-water observations of the diving behaviour of immature hawksbill turtles (*Eretmochelys imbricata*) on a coral reef at D'Arros Island, Republic of Seychelles. *Chelonian Conservation and Biology* 9: 26-32