





**The Behaviour of Immature and Female  
Hawksbill Turtles  
(*Eretmochelys imbricata*)  
at Sea**

Dissertation

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The water was warm. There was plenty to eat.

The turtles had everything turtles might need.

And they were all happy. Quite happy indeed.

...

And the turtles, of course... all the turtles are free

As turtles and, maybe, all creatures should be.

(from: Yertle the Turtle by Dr. Seuss)



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## 1 GENERAL INTRODUCTION

Of the total of 8 species of sea turtles 7 species, including the Hawksbill Turtle (*Eretmochelys imbricata*, Linnaeus 1766), belong to the family *Cheloniidae*, while only the Leatherback Turtle (*Dermochelys coriacea*) belongs to the family *Dermochelyidae*.

In contrast to *Dermochelys* the *Cheloniidae* are characterised by keratin scutes, covering the well-developed bony carapace and plastron. The digits of the extremities are bound together by connective tissue as an adaptation to the aquatic life of sea turtles. Adult *Cheloniidae* propel themselves by using the conspicuously elongated forelimbs for powerstroking while steering with the rear flippers (as reviewed by Wyneken 1996 in Lutz & Musick 1996). Head and flippers are non-retractile and covered with numerous small scales (see Witzell 1983 for review).

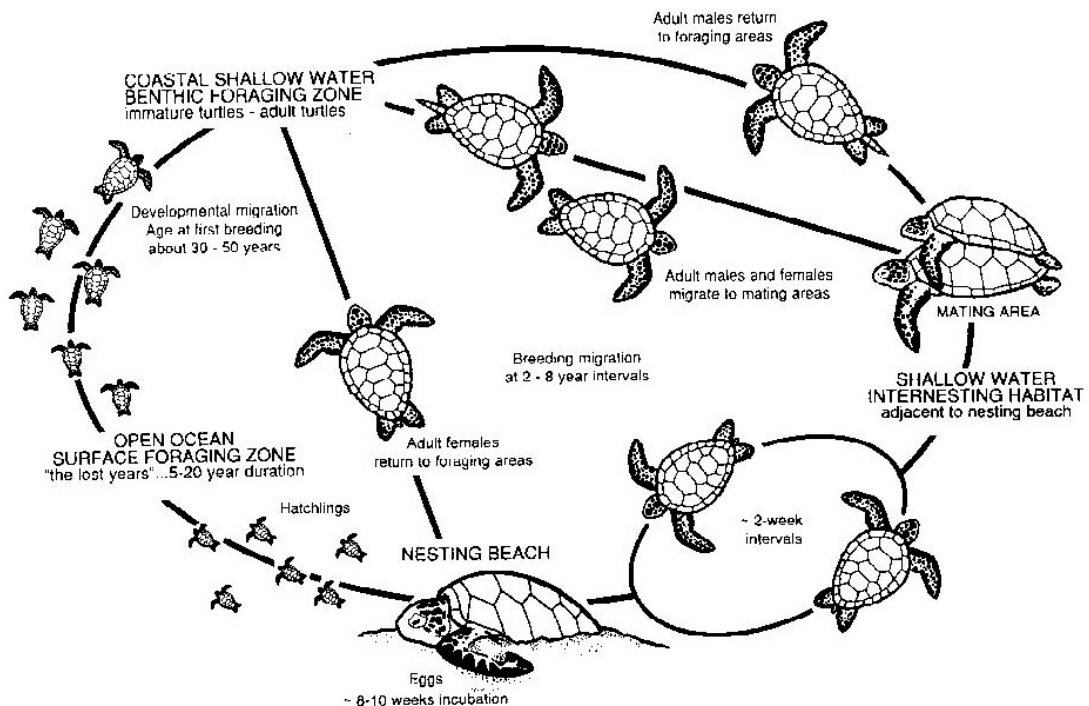
The Hawksbill Turtle is the only species of the genus *Eretmochelys*. This species has a narrowly tapered, beak-like mouth (hence the English name) that it uses to pick food out of reef crevices (Carr 1966). Adult Hawksbill Turtles, both sexes typically weighing between 43 and 76 kg (Márquez 1990), feed on a variety of benthic invertebrates, but are highly specialised to take sponges in the Caribbean part of their distribution range (Meylan 1988). In contrast to other species of sea turtles that can be found at higher latitudes, Hawksbill Turtles are strictly limited to tropical areas of the oceans (Atlantic, Pacific, Indian Ocean, Red Sea), where they inhabit coastal reefs, bays, estuaries and lagoons (see Witzell 1983). The keratin scutes are typically imbricated (hence the Latin name) and particularly thick, i.e. they are well adapted to endure abrasions and impact from sharp reef overhangs. The scutes were, and still are, highly priced as 'tortoiseshell' due to their beautiful coloration. The traditional use of bekko (Japanese for tortoiseshell) in Japan is believed to date back to more than 1000 years ago (Ecchu 1992), however, it was only in the 16<sup>th</sup> century that an industry was established as the international tortoiseshell trade began to flourish. While the Hawksbill Turtle shares the threats such as destruction of feeding and nesting habitat, by-catch and egg-harvesting with the other species of sea turtles, the heavy commercial exploitation for the tortoiseshell (demanded for jewellery, decorative art or as entire stuffed specimen) places an unique additional pressure on their populations.

Together with the Kemp's Ridley (*Lepidochelys kempii*) *E. imbricata* is considered to be the most endangered of all marine turtles (Plotkin 1995). The Hawksbill Turtle has been listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) since 1977, recognising the threat of extinction that is, or may be, affected by trade. Furthermore, this species is ranked in the Red List of Threatened Animals by the International Union for the Conservation of Nature and Natural Resources (IUCN) as 'Critically Endangered' (Baillie & Groombridge 1996) and as 'Endangered' in the United States Endangered Species Act (ESA). The recent Hawksbill populations at the U.S. Caribbean and Pacific coast are only a small fraction of the stock of Hawksbills that was found before the severe depletion in the 20<sup>th</sup> century (Plotkin 1995). The illegal domestic harvest of eggs and turtles continues.

However, trends in population size and status of these turtles are difficult to determine as they are, in contrast to e.g. the Green Turtle (*Chelonia mydas*) or the Kemp's and Olive Ridley (*Lepidochelys kempii* and *L. olivacea*), disperse nesters in both time and space (Groombridge & Luxmoore 1989). Instead of showing mass nesting events as the other species mentioned, Hawksbill Turtles emerge individually often on remote islands and usually with only one to ten females per night and beach (cf. Witzell 1983).

### Life history

Sea turtles typically show a slow growth-rate, a long life-span and a high age at maturity (as reviewed by Witzell 1983, Miller 1996). Fig. 1 shows a generalised life cycle of sea turtles together with estimates for the duration of the different phases and intervals. After leaving the beach as hatchlings sea turtles acquire an aquatic lifestyle, with the males never returning onto land (except for some cases of terrestrial basking, see e.g. Whittow & Balasz 1982) and only the females regularly come ashore briefly to lay eggs.



**Fig. 1:** Generalised life cycle of sea turtles (taken from Miller 1996).

Mature female Hawksbill Turtles typically reproduce every two to four years, with two to five clutches, consisting of 70 to 180 eggs each, being laid per nesting season (Groombridge & Luxmoore 1989, Pritchard & Mortimer 1999). The procedure of nesting can be subdivided into 8 phases; the duration of each phase is given below (Hillis-Starr unpubl. data).

- 1) emergence from water (1-2 min)
- 2) approach crawl (2-4 min)
- 3) excavation of the body pit (10-20 min)
- 4) excavation of the nest hole (15-25 min)

- 5) oviposition (20-30 min)
- 6) covering eggs (10-15 min)
- 7) camouflaging nest site (5-15 min)
- 8) return to the sea (30 sec to 5 min)

Successive nests within a season are usually laid at intervals of 13 to 15 days (Witzell 1983), denoted hereafter as the inter-nesting interval. Reproducing females show a high nest site fidelity both within and over several nesting seasons (Bjorndal et al. 1985).

To date the majority of studies on sea turtles have been conducted during the short terrestrial phases of their life cycle, thus concerning aspects of reproduction. In contrast to the nesting behaviour diving performance at sea is not accessible through direct observation. It was only after progress in microelectronics over the last two decades that the movements of the highly-mobile and often shy sea turtles could be studied. The techniques rapidly evolved from simple VHF transmitters over satellite transmitters to microprocessor data-loggers and the combination of each of these methods. All of these methods can be conveniently grouped together under the term of 'telemetry', originally only referring to systems transmitting data, but today generally used in the wider sense.

The goal of this study is to elucidate the behaviour of Hawksbill Turtles at sea and to gain new insights into patterns of habitat use. The investigations are designed to describe factors influencing the dive behaviour of a highly specialised, marine reptile, considering the differences between various phases of the life cycle.

In the following, descriptions of the study sites and the methodologies are given before the chapters deal with different aspects of the obtained data. On behalf of the different aspects each chapter is independent and has a short introduction. Where applicable, a short section about assumptions and specific methods of analysis is given before results are presented and discussed.

Finally, a short outlook and recommendations for further investigations are given.

## 2 STUDY AREAS

The two study sites are situated within the chain of the Antilles that form the northern border of the Caribbean Sea towards the Atlantic Ocean (Fig. 2). The distance between the two islands, being located east and west of Puerto Rico, is approx. 350 km.



**Fig. 2:** The two study sites, Mona Island (Puerto Rico) and Buck Island (U.S. Virgin Islands).

### 2.1 BUCK ISLAND

Data on nesting female Hawksbill Turtles were collected at Buck Island Reef National Monument (64°37'W, 17°47'N), US Virgin Islands (subsequently referred to as Buck Island). This protected, uninhabited island is 1.6 km long and 0.8 km wide, situated 2.7 km northeast off the island of St. Croix (Fig. 3). First protected in 1948, it was designated a National Monument in 1961 for the elkhorn coral (*Acropora palmata*) barrier reef surrounding the island's east end. The Monument is managed by the National Park Service

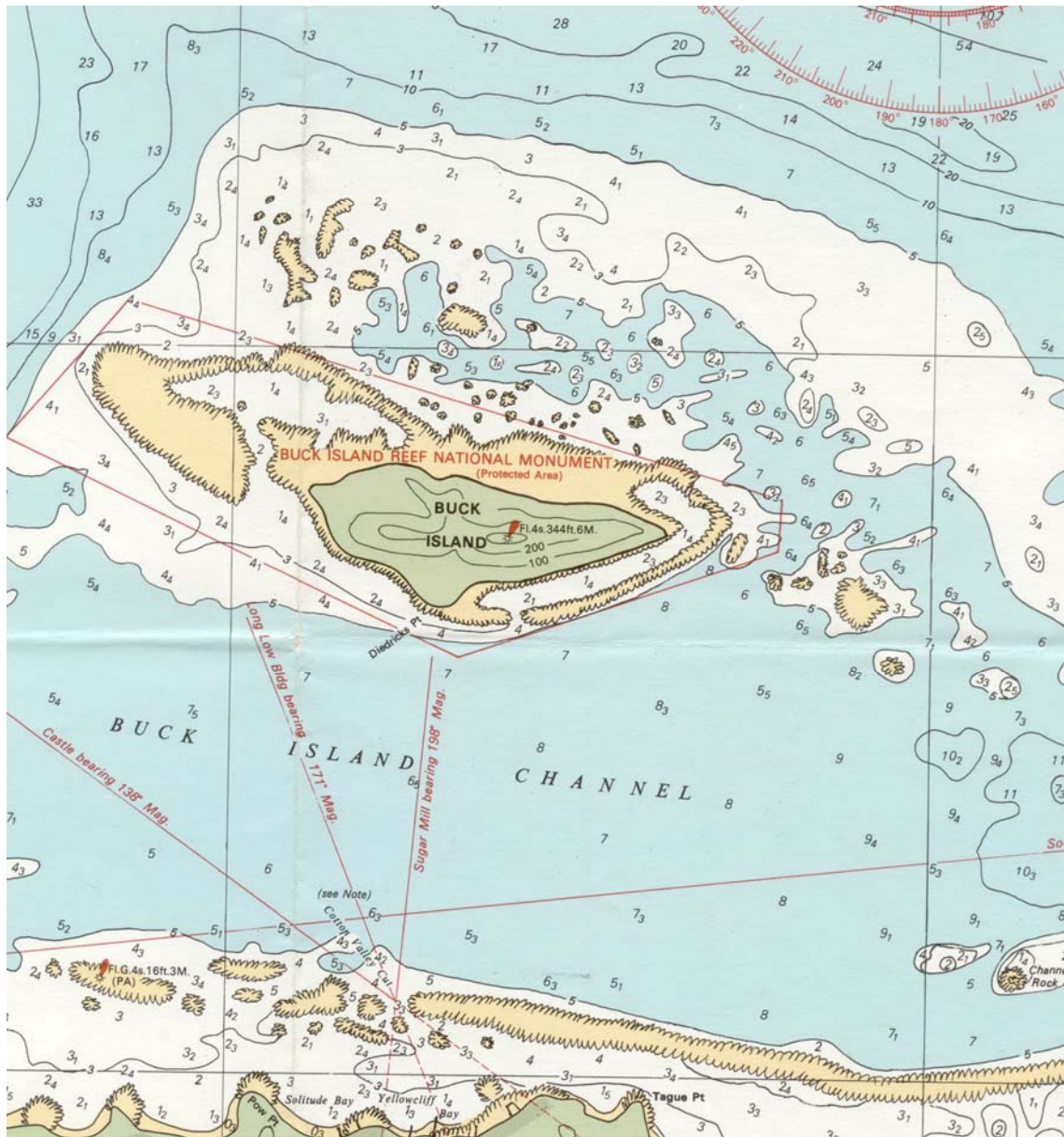
## 2 Study Areas

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(NPS) and, after being enlarged in 2001, includes 176 acres of land and 18135 marine acres of coral reefs, sea grass beds, octocoral hardbottom, sand communities, algal plains, shelf edge and oceanic habitats. A characteristic feature of the seafloor outside the barrier reefs are the "haystacks", patches of elkhorn coral that rise from the seafloor at depths of about 15 m, nearly reaching to the surface of the water. The waters of the lagoon, where large brain corals (*Diploria spec.*) grow protected by the barrier reef, are 4 m deep or less. Within the lagoon, as well as outside, many species of reef fish, invertebrates and crustaceans can be found. Only few kilometres from the West Beach of Buck Island the shelf edge falls off to reach depths of more than 4000 m.

Buck Island rises 104 m above the sea level and is largely covered by tropical dry forest. Several threatened and endangered species use the Island for reproduction, including the Brown Pelican (*Pelecanus occidentalis*), Least Tern (*Sterna antillarum*), Hawksbill Turtle (*Eretmochelys imbricata*), Leatherback Turtle (*Dermochelys coriacea*) and the Green Turtle (*Chelonia mydas*). It provides 1.3 km of nesting beach for sea turtles. The eastern part of the coast is composed of rocks and boulders and is therefore inaccessible to turtles. While Buck Island plays only a minor role as a nesting site for Green and Leatherback Turtle, it is one of the most significant nesting areas for the Hawksbill Turtles within the USA. The Recovery Plan for Hawksbill Turtles in the U.S. Caribbean Sea, Atlantic Ocean, and Gulf of Mexico (National Marine Fisheries Service 1993) identified Buck Island as an index beach for the recovery of this species in the whole Eastern Caribbean. Since the initiation of the Buck Island Sea Turtle Research Program (BUIS) in 1988 and the saturation tagging program, approx. 120 female Hawksbill Turtles have been identified nesting at Buck Island. The annual number of nests is around 130. Nesting occurs year round, with a distinctive peak nesting season from July through October. During these months the beach is closed to the public between sunset and sunrise.





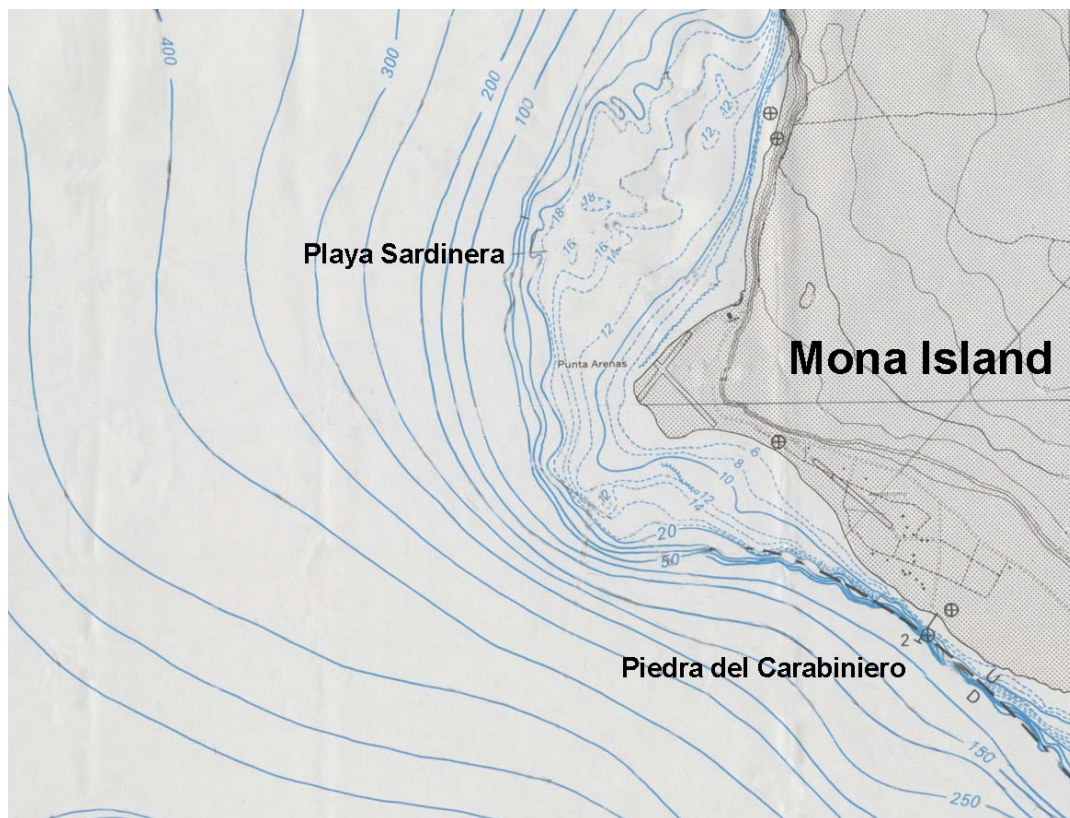
**Fig. 3:** Buck Island Reef National Monument, U.S. Virgin Islands, off the coast of St. Croix (visible at the bottom of the chart). Depths are given in fathoms and feet. Shallow reef patches and ridges are coloured yellow.

A great part of the data presented in this thesis was collected while the animals resided in the described area. However, additional data sets were obtained from animals leaving the waters adjacent to the nesting beach. The areas visited by the turtles are specified briefly below where relevant.

## 2 Study Areas

### 2.2 MONA ISLAND

Data on immature Hawksbill Turtles were obtained off Mona Island ( $67^{\circ}55'W$ ,  $18^{\circ}05'N$ ), Puerto Rico (Fig. 4). This island is a natural reserve that has been administered by the Puerto Rico Departamento de Recursos Naturales y Ambientales (DRNA) since 1975. Mona Island does not have any permanent inhabitants, although a group of rangers, rotated on a weekly basis, is stationed at Playa Sardinera on the west coast. Biologists are allowed to stay at the ranger station and tourists can anchor offshore or camp out on the island after obtaining a permission at the DRNA office in San Juan.



**Fig. 4:** South-west coast of Mona Island, Puerto Rico, and adjacent waters. Depths are given in meter.

Mona Island is situated in the centre of the Mona Passage between the west coast of Puerto Rico and the east tip of the Dominican Republic. The flat-topped, bean-shaped island is

about 12 km long and 7 km wide, with the highest elevation rising up to 100 m above sea level. The typical vegetation of Mona is tropical dry forest. The north coast of Mona Island is bounded by vertical cliffs averaging 60 m in height above, and further 20 to 30 m below the sea level. The southern part of the Island is fringed by a low coastal plain with areas of moist forest and sandy beaches, interrupted by rocky sections. The most conspicuous animal of the coastal plain is the giant Mona Iguana (*Cyclura stejnegeri*), a threatened species that is endemic to this island. The cliffs provide breeding habitat for e.g. the Red-Billed Tropicbird (*Phaethon aethereus*), the Brown Booby (*Sula leucogaster*), the Masked Booby (*S. dactylatra*) and the Red-Footed Booby (*S. sula*).

The sub-littoral of the south coast is a shallow inclined platform that extends to a depth of up to 20 m. This platform, with both sandy bottom and rather flat patches of coral reef, ranges in width from 1.2 km off Playa Sardinera to 0.1 km off Piedra del Carabinero (Fig. 4). Dominant species of the reef patches are soft and hard corals, providing habitat for numerous species of reef fish and invertebrates. During the winter Humpback Whales (*Megaptera novaengliae*) with their young can regularly be observed. The waters off Mona Island provide feeding grounds for immature Hawksbill and Green Turtles (*Chelonia mydas*), as well as for adult sea turtles of both sexes (Thurston 1976).

The number of nests laid by Hawksbill Turtles on the beaches of Mona Island exceeds the counts at Buck Island (200 to over 800 nests p.a., van Dam and Sarti unpubl. data, van Dam and Diez pers. comm.). However, nesting activities of the Hawksbill Turtles at Mona Island are much more difficult to monitor than at Buck Island as beach sections are separated by cliffs and access is impossible at times.

### 3 METHODS

Field work at Buck Island was carried out during the local peak nesting season of Hawksbill Turtles (July to September) in 1998 and 1999. Data collection using long-term operating data-loggers continued through 2001. Further deployments were conducted in September 2002 at Mona Island.

#### 3.1 SHORT-TERM DATA RECORDERS DK600/602

##### *3.1.1 Field Season at Buck Island 1998*

The deployed DK600 (Driesen & Kern, Bad Bramsted, Germany) were approx. 12 cm long, 6.5 cm in width, 3 cm in height and weighed less than 200 g in air (Fig. 5).

The sensors linked up to the six channels of the device collected data with 16 bit resolution on

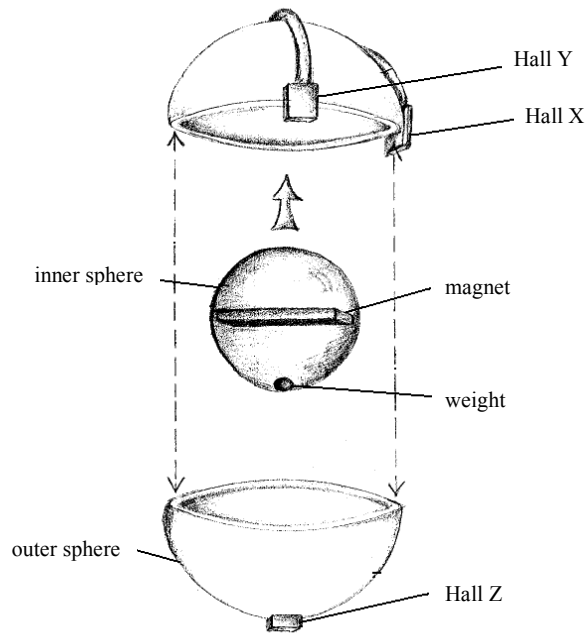
1. temperature
2. light intensity
3. velocity
4. depth
5. compass channel I
6. compass channel II.



**Fig. 5:** Data-logger DK600 (Driesen & Kern, Bad Bramsted, Germany).

Speed data from 1998 were dropped due to damaged speed valves and low sensitivity of valves to slow swim speeds. Light data from short-term deployments were not used for Geo-Location System-calculations (see section 3.4) due to the small range of action of the observed animals.

The compass data from channels 5 and 6 are given in mV as signals from two Hall-sensors, mounted on the outer shell of a miniature spherical ship's compass (Fig. 6) incorporated in the data-logger. The temperature was measured at an accuracy of  $0.1^{\circ}\text{C}$  ( $-20$  to  $+80^{\circ}\text{C}$ ). Depth readings could be taken up to a maximum depth of 400 m at a resolution of better than 1 cm and an accuracy of approx. 20 cm.



**Fig. 6:** Miniature spherical compass (after Hochscheid & Wilson 1999). The inner sphere (approx. 0.9 cm in diameter) floats in an outer shell (approx. 1.2 cm in diameter) filled with silicon oil. Three Hall-sensors detect the position of magnet attached within the inner sphere.

Data readings of all channels were taken at intervals of 15 sec in the non-volatile 1 Mbyte memory. Recording stopped when the memory was complete (after ca. 16 days).

Data were downloaded from the loggers to a PC using Dklog200<sup>®</sup> software (Driesen & Kern, Bad Bramsted, Germany).

#### 3.1.2 Field Season at Buck Island 1999

The DK601 that was used for data-recording in 1999 differed from the devices deployed in 1998 in a few features. While weight and size did not change, the capacity of the memory was increased to 2 Mbyte. The light sensor was omitted in favour of a third compass sensor. The logger was set to record data at intervals of 8 sec. Recording stopped when the memory was complete (after ca. 16 days).

### 3.1.3 Field Season at Mona Island 2002

The latest version of the multi-channeled data-loggers, DK602 (Fig. 7), measuring 9 x 6.5 x 3 cm and weighing 139 g in air, recorded data in the 12 channels as specified below:

1. internal temperature (for compensation of pressure data)
2. depth
3. velocity
4. external temperature
5. light intensity (with blue filter)
6. light intensity (no filter)
7. compass channel I
8. compass channel II
9. compass channel III
10. position (upright or tilted  $>90^\circ$ )
11. pitch (tilt head-down or head-up)
12. roll (tilt sideways left or right)

Only channels No. 1 through 4 and No.12 are relevant here. The temperature probes were as previously specified (see section 3.1.1). The depth gauge allowed measurements of dive depths of up to 100 m at a resolution of better than 1 cm and an accuracy of ca. 4 cm. The velocity was measured by a miniature paddle that, being subject to the water flow over the device, induced a speed-dependent signal onto a pressure gauge corrected for hydrostatic pressure. Swim speeds of 25 cm/s or more could be detected (see section 3.5). The electronic pitch sensor gave inclination-dependant mV signals for head-down or head-up positions of max.  $70^\circ$  to an accuracy of better than  $1^\circ$ . Recording frequencies were either 4 or 2 Hz. The memory of 4 Mbyte was sufficient for 24 or 48 hrs of data, respectively. Data were downloaded from the loggers to a PC using InfraLog<sup>®</sup> software (Driesen & Kern, Bad Bramsted, Germany).





**Fig. 7:** The data-logger DK602 with miniature paddle for velocity readings.

During the field experiments at Mona Island in 2002 acoustic tags (CHP-87-S, Sonotronics, Tucson, USA) were deployed together with the DK602 to locate the equipped animals for recapture. The conical CHP-87-S measured 67 mm in length and 18 mm in diameter. The weight in air was 8 g and the battery allowed signals to be emitted for about 7 months. When the devices were operating, sets of signals were emitted with pauses of 1 sec. between a set of one, two or three emissions. A complete circle of three sets of signals distinctively coded one device, i.e. one individual animal. The signals were received and amplified with a directional hydrophone and a receiver (model N15A235B, Dukane, St. Charles, USA) connected to a set of headphones.

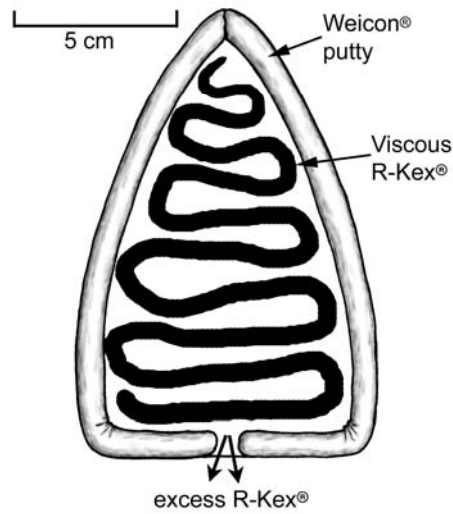
#### *3.1.4 Attachment of DK600/602*

Data-loggers were attached to the anterior of the carapace (2nd central scute) of the turtles. The general attachment method described below was used in all three field seasons to attach slightly different metal base plates to the carapaces of the turtles.



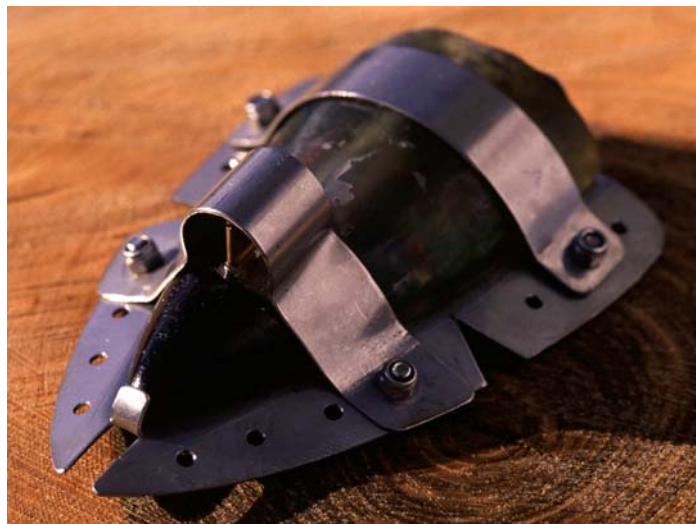
The carapace of nesting hawksbill turtles is usually relatively dry by the time the first eggs are laid (average time after emergence from water is approx. 40 min, Z. Hillis-Starr unpubl. data). However, the carapace was scrubbed with a brush and freshwater to remove the film of algae and salt crystals, as well as loose sand and to prepare the surface of the scutes for the adhesive. All barnacles on, or near, the attachment area on the first and second central scutes were removed using pliers. The attachment area was dried with a towel and roughened with sand-paper.

Following Mitchell (2000) I used a combination of a fast setting epoxy putty (Repair stick ST115 steel, WEICON<sup>®</sup> worldwide GmbH & Co. KG, Münster, Germany, info@weicon.de), which cures within approx. 5 min at 20°C, together with a slower-setting viscous epoxy from a cartridge (R-Kex<sup>®</sup>, synonym Foil-Fast<sup>®</sup>, Rawl, Glasgow, UK, info@rawlplug.co.uk), that cures within approx. 30 min. Like all epoxy resins, these materials consist of two components that react when mixed and cure within a temperature-dependent predictable time. Since under tropical conditions the fast-reacting epoxy cures too fast to be handled properly, the putty was stored in an insulated bag with ice-packs. Just prior to use, two pieces of the epoxy putty (ca. 25 g each) were taken from the bag and simultaneously kneaded to allow the two components of each piece to mix evenly and be warmed. I then rolled two pieces of the putty into a cylindrical shape and attached them beneath the edges of a metal plate, one being placed on each side (Fig. 8). While the ends of the pieces met at the tip, a gap (ca. 0.5 cm) was left in the middle of the trailing edge. The area between the rolls of putty was filled with R-Kex (approx. 85 g), that is readily mixed while being manually pumped from the cartridge through the nozzle onto the bottom of the base plate. The covered bottom of the base plate was pressed onto the prepared attachment area of the carapace. Any excess R-Kex discharged through the gap at the posterior end (Fig. 8) was wiped away with a cloth. The putty coils were firmly pushed onto the carapace and the protruding edges of the plate covered with additional (ca. 25 g) Weicon<sup>®</sup> putty. To ensure a firm bond between the fast-setting epoxy and the carapace it was important to avoid any slow-setting R-Kex seeping between the two layers, as this resulted in slipping of the plate. Approximately 5 min after kneading, the putty started to cure, the reaction being moderately exothermic.



**Fig. 8:** Epoxy adhesives applied to the bottom of the base plate (see also Mitchell 2000).

After first trials with 0.5 mm strong stainless steel I developed a plate made from 1 mm stainless steel. This material was chosen because of its resistance to UV light and saltwater and to avoid magnetic interference of the base plate with the compass in the device. The shape of the plate enabled the device to be secured by four self-securing nuts and bolts onto the plate (Fig. 9).



**Fig. 9:** Base plate (1 mm stainless steel) and data-logger used in the 1999 field season.

The logger was held in place by two stainless steel bands. The anterior band served for device retention and protected the speed valve of the logger against impact. Numerous holes drilled into the edges of the plate allowed the epoxy to seep through when the plate was pressed onto the carapace. The base plate was completely flat at the device attachment site, but the protruding edges were bent down to match the domed shape of the anterior part of the carapace. This detail reduced the maximum thickness of the epoxy layer between carapace and plate by approx. 5 mm. Upon return of the equipped turtle the device was easily and quickly exchanged by loosening the four retaining nuts. The device was taken out of the plate and a new logger was secured by tightening the nuts. The exchange could be completed within 2 minutes.

After completion of the study the plate was easily removed by using a hacksaw to cut a slit into the epoxy at one of the corners of the plate. A screwdriver was placed into the slit and hit with a hammer until the plate and the epoxy layer were detached from the carapace (Fig. 10). In most cases the plate and epoxy were removed in one piece. Otherwise the remaining epoxy was removed with the screwdriver and hammer.



**Fig. 10:** Removal of base plate.

### 3 Methods

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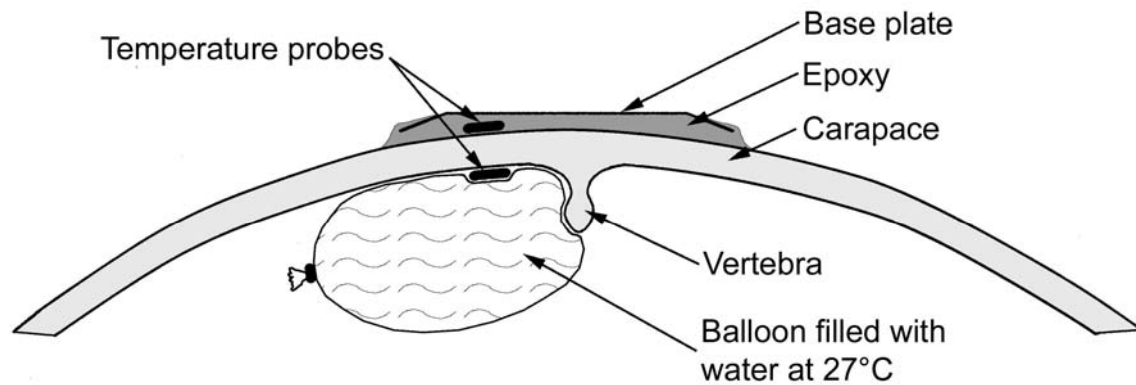
In the field study in 2002 the additional acoustic tags were attached across the trailing end of the DK602 setup described above. The CHP-87-S were fixed by two stainless steel lines to the metal base plate (Fig. 11).



**Fig. 11:** Juvenile Hawksbill Turtle (Mona Island) with DK602 data-logger and sonic tag attached.

#### *3.1.5 Test of attachment material under laboratory conditions*

The thermal characteristics of the epoxy during the bonding reaction were examined under laboratory conditions. A sea turtle carapace was equipped with two probes to measure the temperature within the epoxy mass and underneath the bony carapace during the attachment procedure (Fig. 12). A balloon filled with approx. 1 l of water was pressed against the lower probe during the experiment to simulate the insulating effect of the body flesh of the turtle.



**Fig. 12:** Experimental set-up for temperature measurements during exothermic epoxy curing process (cross section showing placement of temperature probes).

The temperature of the air in the laboratory and the water in the balloon was 27°C to approximate typical night temperatures under field conditions. Measurements were taken until the temperature within the epoxy mass fell below 40°C and the R-Kex epoxy was cured. The weight of all materials attached to a turtle in the field (device, plate and epoxy) was measured in air and in salt water (35 ppm, 28°C) using a spring balance.

### 3.2 LONG-TERM DATA RECORDERS MK7

Between 1 and 15 September 1999 a total of six female Hawksbill Turtles was equipped with time depth recorders (TDRs, Mk7 by Wildlife Computers, Redmond, USA; Fig. 13) while nesting at Buck Island. Four of the devices were attached to females, that, based on the long-term monitoring data collected by the Buck Island Reef Sea Turtle Research Program, were expected to re-nest after two years, i.e. in 2001. Two more equipped turtles were scheduled to return to Buck Island in 2002 or 2003, however, to date they have not been re-sighted.



**Fig. 13:** The Mk7 (Wildlife Computers, Redmont, USA) used for the long-term study.

The TDRs recorded light intensity, temperature and dive depth, allowing temperature measurements over a range from 20 to 40°C with a resolution of 0.1°C. Depth and temperature were recorded at intervals of 30 sec, while temperature was measured every 900 sec. The Mk7 incorporates a 2 MB non-volatile Flash EEPROM for data storage. To cover a period of approx. 22 months (the estimated duration of one re-migration interval, see section 10 for definition) it was necessary to use a duty-cycle. The Mk7 were then programmed to store data for two days, then stop for four days and cycle these shifts until the memory was complete. The TDR measured 2.2 x 10.7 x 1.2 cm and weighed ca. 35 g in air.

Data were downloaded from the loggers to a PC using MK7HOST<sup>®</sup> software (Wildlife Computers, Redmont, USA).

#### *3.2.1 Attachment of MK7*

The devices were attached while the female was at the nesting beach. After egg laying commenced, the marginal scutes No.10 and 11 (see section 10 for definition) on both sides of the carapace were checked to find the optimal attachment area. The serrated scutes were



examined from below with a strong flashlight to verify the borderline between live tissue (incorporating bone) and non-innervated, translucent keratin. Two holes (diameter 4 mm) were drilled dorso-ventrally into the keratin using a hand-held cordless drill. The surface of the scutes at the attachment area was sanded with coarse sand-paper and a small amount of epoxy resin (R-Kex<sup>®</sup>, synonym Foil-Fast<sup>®</sup>, Rawl, Glasgow, UK, which cures in approx. 30 min) was applied between the holes to fill the gaps between the data-logger and the uneven surface of the scutes. The Mk7 was positioned and held in place by two stainless steel bolts (4 mm diameter x 30 mm) that were inserted into the holes from below. Two self-securing nuts were tightened from above. Finally the Mk7 was surrounded by fast-setting epoxy putty (Repair stick ST115 steel, WEICON<sup>®</sup> worldwide GmbH & Co. KG, Münster, Germany, which cures in approx. 5 min) to even the edges and to provide an instant support before the R-Kex<sup>®</sup> bonded (Fig. 14).



**Fig. 14:** Mk7 attached to posterior marginal scutes (see text) of adult female Hawksbill Turtle. The head of the animal is to the right and the right hind flipper is visible in the picture. Note the (medium-sized) barnacle beside the attachment area.

#### 3.3 HANDLING OF TURTLES AND COLLECTION OF ADDITIONAL DATA

Attachment procedures were optimised to reduce handling time and the need for restraint. Nesting females were encountered in the dark at the nesting beach. Flashlights were only used after egg-laying commenced. In this phase of nesting no restraint was necessary to carry out the attachments as described. However, the protocol of the NPS monitoring project demanded that each nesting turtle be weighed once per season. If this procedure, only possible after completion of the nest, was to be undertaken on the same nesting event as logger attachment, the latter could not be performed during a voluntary sedentary phase. Instead, the turtle had to be interrupted on its way into the water by putting a wooden corral over the animal. This procedure restrained the female for an additional 15-20 minutes on the beach, whereas normal attachment during egg-laying could be completed within the voluntary shore leave.

The body mass of each nesting turtle at Buck Island was measured by the NPS staff using a rope and pole setup attached together with a hanging scale. The females had to be turned over onto their backs after completion of the nest.

100 markers (wooden posts in the ground or metal plates fixed to rocks) have been installed by the NPS to divide the 1.3 km of nesting beach into sections of approx. 13 m. Noted activities of the sea turtles were related to the nearest marker.

In the 1999 nesting season positions of emergence from the water and return into the water of each nesting activity were taken using a backpack-mounted, differential Global Positioning System (GPS) receiver (Trimble Pathfinder, accuracy ca. 1 m).

During the field work at Mona Island immature Hawksbill Turtles were found by snorkeling and hand-captured by free diving or, in rare cases, with the help of SCUBA and brought to a small boat. The straightline carapace length (SCL, see section 10 for definition) was measured to the nearest mm using aluminium callipers. Body mass was measured with spring scales (0-20 kg x 0.2 kg or 0-50kg x 0.5kg, accordingly).



Capture locations were determined with a handheld GPS receiver. After completion of the measurements and device attachment / detachment, done within 20 min, the turtles were released within a distance of few tens of meters from the location of capture.

### 3.4 GEO-LOCATION SYSTEM

Light level thresholds for sunrise and sunset were defined from the calibration data (see section 3.5). Field data were scanned for corresponding light levels to find the time of sunset and sunrise, from which in a next step the day-length was calculated. The information on day-length on a given date of the year was used to determine the latitude of the animal's position, while the longitude was derived from the midpoint between sunset and sunrise, i.e. local noon (Wilson et al. 1992, Hill 1994, Welch & Eveson 1999). The calculation of positions was conducted using special computer software (MT-light, Jensen Software, Laboe, Germany).

The major drawback of this method is that the latitude cannot be determined around the equinox in spring and autumn (21 March and 24 September). Accordingly, several days before and after each equinox the variation in length of day proved still too little to enable the calculation of latitudinal position with a reasonable accuracy (cf. Hill 1994). In the present study data obtained within two weeks of the date of equinox (both before and after) were not used.

Data recorded at, or close to, the equator show the greatest susceptibility to the phenomenon described above, giving only poor information about latitude for most of the year with errors of about 200 km or more (Hill 1994, Hill unpubl. data). For accuracy estimates for this study see section 3.5.

For each two-day interval of data (according to the duty-cycle of the devices described in section 3.2) one position could be calculated. As each two-day interval of recording was followed by four days of shut-down, one position was obtained every 6 days.

#### 3.5 CALIBRATION PROCEDURES

The data on temperature and depth were ready to use as recorded. However, the sensors involved in measurement of compass heading, light-level and velocity needed to be calibrated before field deployments because output signals were dependent on the resin used (light), on the mechanism installed (velocity) or deployment site (compass and light).

##### Speed Sensor

The speed sensors of the DK600/602 were calibrated by pulling a model of a turtle, equipped with the concerning device, through a 15 m water-channel at pre-defined speeds of 5, 25, 50, 100 and 114 cm/s. The output of the sensors was noted as a function of speed.

##### Compass

The miniature compasses incorporated in the DK600/602 data-recorders were calibrated on site in the study areas to take account of the local features of the earth's magnetic field. A carousel made from completely non-magnetic materials was used to turn the logger into each compass heading in steps of 20°, while the horizontal position could be changed from inclined tilted down over level to inclined tilted up in steps of 10°. Using this protocol the Hall-sensors' output (in mV) was converted into compass bearing and an inclination angle of descent or ascent by interpolation.

##### Pitch Sensor

To calibrate the sensor recording the dive angle of the turtle in the latest 2002 version of the DK600/60 data-recorders, the devices were mounted onto a ramp that could be fixed in defined positions in steps of 10°. The horizontal level was defined by the flat underside of the device. The amplitude of the signal was intended to record angles between 70° tip-down to 70° tip-up (referred to as -70° to 70°, respectively).

### Light Sensor

Before deployment on the turtles the light sensors incorporated in the MK7 were calibrated on a stationary buoy located 40 m offshore in a bay at St. Croix (64°40'W, 17°46'N). During the five days of calibration the light intensity was measured at a depth of approx. 15 cm below the water surface. The location of the stationary devices could be defined at a mean accuracy of 30 km in longitude (range of errors 11 to 43 km). Data on latitude had to be interpreted carefully because of the low accuracy of positions (mean error 157 km, range of errors 41 to 243 km), caused by the influence of equinox described in 3.4 Geo-Location System.

## 3.6 DATA ANALYSES AND STATISTICS

Processing and analyses were done by writing routines within Matlab<sup>®</sup>5.3. Different phases of the data-sets were identified using characteristics of dive behaviour (see section 4.2) and separated for the analyses as stated when relevant. The temperature data were used to calculate a mean temperature for each dive event (surface period excluded to avoid the effects of evaporative cooling or of heating by radiation). Data recorded between 06:00 and 17:59 (local time) are referred to as daytime data, whereas night data were collected from 18:00 to 05:59. The vertical velocity was calculated as rate of change of depth, given in m per sec. A submergence of deeper than 2 m was considered a dive. The duration of a dive event found using this definition was calculated as the time the turtle spent at depths of  $\geq 50$  cm.

A short, well-defined data set with known positions of start and end was used for 3-dimensional computation (dead reckoning) of motions of a Hawksbill Turtle off Buck Island. Data on swim speed together with the angle of ascent or descent and the compass heading are needed for spatial calculations via vectors. When recordings of swim speed failed due to malfunction of the sensor, velocity was calculated from dive angle and rate of change of depth.

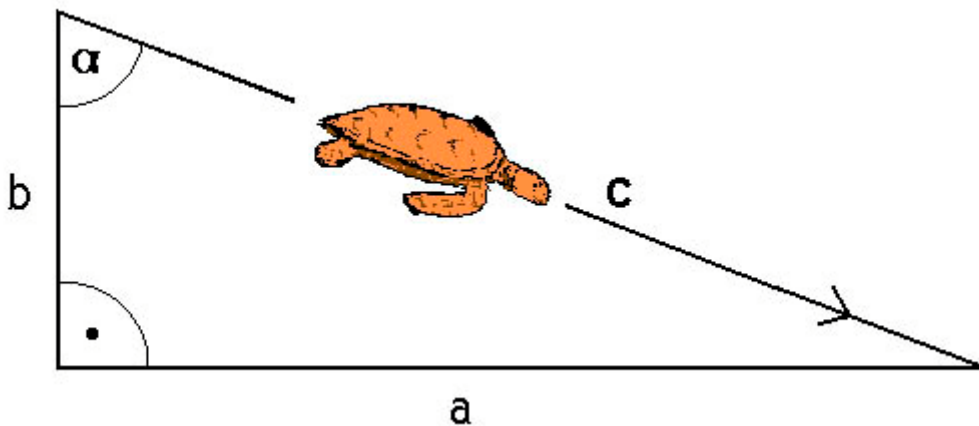
### 3 Methods

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The data on dive angle (pitch) was used to calculate the distance swum following

$$(1) \quad c = a/\sin\alpha$$

in a right-angled triangle configuration (Fig. 15).



**Fig. 15:** Right-angled triangle as a base for calculations of swim speed.  $b$  = change of depth,  $\alpha$  = angle of descent or ascent.

Using the interval at which data were recorded,  $I_{\text{rec}}$ , the swim speed  $V$  is calculated as

$$(2) \quad b[\text{m}] * I_{\text{rec}} = V [\text{m/s}].$$

The accuracy of these calculations decreases with smaller angles. Therefore, at angles  $<10^\circ$  a standard velocity of 70 cm/s was used (see section 4.2.3.2).

The expression 'dive depth', as used below, refers to the maximum depth reached during the complete dive event considered. 'Depth' refers to the instantaneous depth of the turtle.

The software used for statistical analyses was SPSS<sup>®</sup>10.0. All tests were two-tailed and the level of significance was set at 0.05. Non-parametric tests were used where data were not normally distributed. Regression lines are based on least-squares methodologies.

## 4 CHAPTERS

### 4.1 TECHNIQUE FOR REPETITIVE DATA-LOGGER ATTACHMENTS TO SEA TURTLES

#### 4.1.1 *Introduction*

Classic studies involving visual observation of larger vertebrates are difficult when animals frequent environments where direct observation is difficult, as is the case in aquatic, in particular in diving animals. The deployment of transmitters (VHF or satellite) enhanced progress, but still provided only discontinuous data, as signals can only be transmitted in air. Attached data-loggers which monitor animals continuously provide a solution to this, and periods of monitoring may be greatly extended, even to years, if attachment systems are sufficiently robust and appropriate while minimally affecting the animal concerned.

The specific aim of this section of the study was to develop an attachment method that fully meets the requirements of repeated deployments of replaceable data-loggers on sea turtles.

#### 4.1.2 *Results*

While the first trials showed that 0.5 mm stainless steel was not strong enough, the final version of the plate made of 1 mm steel enabled the successful deployment and retrieval of devices using the base plate for quick release. The steel strips and the nuts held the devices in place over the desired monitoring periods of up to 16 days (mean 12 days,  $n = 13$ ) before being exchanged or removed, but the protruding tab of the anterior band was deformed in several cases (7 of 15 deployments), leading to damage to the speed sensor in 5 cases. In two of these cases it was observed that the damage occurred during the nesting process on land while the turtle was crawling under logs in the vegetated area. The attached plates were used for up to three successive deployments so that they remained in place for up to 31 days without apparent reduced stability.

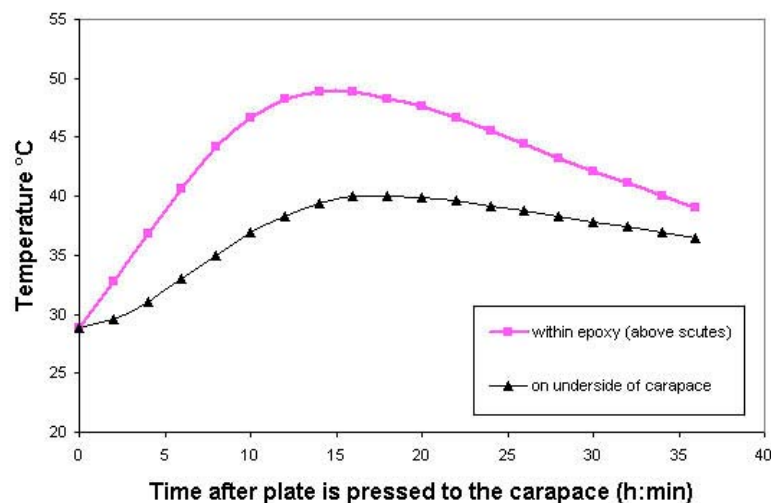
Although the initial attachment was completed in approx. 15 min, each successive

exchange took ca. 2 minutes. The exchange could be executed during egg-laying or even during crawling. I was thus able even to consider device exchange on turtles performing a false-crawl, i.e. coming ashore without actually completing a nest.

The final removal of the base plate took approx. 5 min. When the removal was conducted during the egg-laying process or by crawling behind the turtle, no apparent reaction to the procedure was observed. No materials stayed on the carapace after the removal procedure and there was no sign of damage to the carapace scutes.

The masses of loads attached to the turtles including device, battery, base plate and adhesive materials were 300 g in air (140 g in salt-water) in 1998 and 430 g in air (230 g in salt-water) in 1999. The mean body mass of the nine animals equipped during this study was 70 kg (range 49 to 95 kg), so that the maximum mass of the complete attachment was 0.6% of the mean body mass.

During the simulated attachment under laboratory conditions the measured temperatures varied between 29 and 49 °C (Fig. 16). The highest temperature, measured 14 min after beginning of measurements, occurred within the epoxy mass itself and thus affected only the turtle's non-innervated scutes. The maximum temperature measured below the bony carapace was 40 °C (16 min after the onset of the experiment). The epoxy was cured and the measurements ceased 36 min after the plate was placed onto the carapace.



**Fig. 16:** Temperatures during plate attachment under laboratory conditions.

### 4.1.3 Discussion

During deployment of telemetry devices the habits and demands of the equipped animal as well as the data-logger functions have to be given careful consideration. Hawksbill turtles typically inhabit littoral waters of tropical shelves with coral reefs (Márquez 1990). Their habit of wedging themselves into crevices (Vaughan et al. 1992) not only leaves obvious marks and scratches on the scutes of their carapace, but also often damages attached biotelemetry devices (pers. obs., Vaughan et al. 1992).

The present quick release attachment method was optimised in several aspects to meet the requirements of a state-of-the-art behavioral study. These aspects concern the duration and intensity of the handling of the animal, the toxicity and local effects of adhesive to the attachment area, as well as the secure fixation of the device.

The handling times involved in the method presented here are much shorter than in techniques using epoxy and fiberglass (e.g. Papi et al. 1997, Polovina et al. 2000, Renaud & Carpenter, 1994). The materials used are easy to handle at night under field conditions and inaccuracies in mixing ratios, leading to variation in curing time or instability of the attachment, are unlikely due to automatic mixing or predetermined ratios. Therefore attachments can proceed without delaying the animal's stay on the beach as described e.g. by Cheng (2000). According to the manufacturer's data sheet the epoxy putty does not contain any solvents. The epoxy putty can be kneaded by hand and no skin irritation was observed during contact with bare skin. However, use of gloves during application is recommended by the manufacturer and vapor should not be inhaled. Once cured, epoxy resin is inert and therefore non-irritating (Weicon<sup>®</sup> safety data sheet No. 91/155 EEC).

The rise in temperature caused by the curing process of the epoxy may be sensed by the turtle but was not considered to be harmful. Since the carapace scutes (ca. 4-5 mm thick in an adult hawksbill) are not innervated, the maximum temperatures that reach the nerves within the bony carapace are below 49 °C. The setup of my laboratory experiment represents a worst-case scenario, as the volume of water in the balloon was small compared to the volume of the tissue of the turtle that would absorb the heat of the epoxy. In this experiment the scutes did not detach from the bone, as it has been observed at high temperatures (Carr 1952). The duration of maximum heating is short under laboratory

conditions and is probably reduced further when the turtle enters the water within 10 to 15 min after the plate has been pressed onto the carapace.

The thermal reaction of any epoxy material is dependant on its volume and on the surface area:volume ratio. The thickness of the epoxy layer between the plate and the carapace should therefore be kept to a minimum. To achieve this the plate should suit the average curve of the attachment site. In this study a layer of ca. 1 cm was not found to be harmful. I found that a material thickness of 1 mm stainless steel is necessary for the base plate. However, tabs protruding from the plate should be made of 1.5 mm steel.

The base plate and the pattern of epoxy application combined in this study were designed to optimise hydrodynamics and protruding elements were avoided except for the metal arch protecting the speed sensor. The overall size of the attached load resembled the dimensions of the barnacles that are frequently found in groups on the shells of hawksbill turtles nesting at Buck Island (pers. obs.). To estimate the drag associated with the attachment assembly used here further studies of the hydrodynamic features should be done within a flume channel (Watson & Granger 1998).

The results show that the use of base plates and epoxy is a suitable technique for multiple successive logger deployments to study inter-nesting female sea turtles.



### 4.2 BEHAVIOUR DURING DIFFERENT STAGES OF THE LIFE CYCLE

#### 4.2.1 Introduction

Recently an increasing proportion of sea turtle research has been conducted on individuals at sea, only gradually compensating for the current imbalance between numerous nesting beach studies and the scant knowledge about the aquatic ecology of these marine reptiles. Modern technologies such as VHF- and satellite transmitters have delivered data about animal location (e.g. Starbird et al. 1999), migration (e.g. Papi et al. 1997) and also some basic dive parameters in the form of histograms (e.g. Godley et al. 2002). However, it is only by using data-recording devices, so-called data-loggers, that a comprehensive impression can be built up of the performance of sea turtles at sea. Systematic, chronological data are needed to draw conclusions about the causes and consequences of observed phenomena such as e.g. dive duration, surface intervals and dive depth.

Unlike Green Turtles (*Chelonia mydas*) (e.g. Hochscheid et al. 1999, Hays et al. 2000a, Hays et al. 2002a) and Loggerhead Turtles (*Caretta caretta*) (e.g. Naito et al. 1990, Minamikawa et al. 1997, Houghton et al. 2000, Minamikawa et al. 2000, Hays et al. 2002a), adult Hawksbill Turtles have been the subject of only a few of such high-tech investigations (Horrocks et al. 2001, Balazs et al. 2000). However, since the endangered Hawksbill Turtle is still a highly prized object of (illegal) hunting and because its prime habitat, the coral reef, is particularly vulnerable, there is an urgent need to understand the behaviour and the habitat use of this species during the different phases of the life cycle so as to assess impacts and propose useful and necessary protective measures.

It was only over the past decade that the formerly unknown habitat utilisation of immature Hawksbill Turtles was studied. This research was conducted at Buck Island (64°37'W, 17°47'N) using VHF- and ultrasound telemetry (Pemberton et al. 2000) as well as at Mona and Monito Island (67°55'W, 18°05'N) using ultrasound telemetry and more detailed data-logger recordings (van Dam & Diez 1996, 1997a, 1997b).

The general life cycle of sea turtles (see chapter 1), which is also valid for the Hawksbill Turtle, shows several distinct stages. The stages of the developmental phase, that come

along with at least one change of habitat when the turtles are recruited to the coral reefs, are passed through only once per individual. In contrast, the typical phases passed during adulthood by female sea turtles include the reproductive cycle with migrations and are undertaken an unknown number of times over the animals lifecycle. Adult females are relatively accessible on the nesting beaches and thus lend themselves to device deployment e.g. to record data during the inter-nesting interval. The same easy deployment situation can be used for studies aimed at collecting data over the time span of the re-migration interval, i.e. the non-nesting season that lasts 2 to 4 years in Hawksbill Turtles (see chapter 1 ). However, to keep a device operational for more than several months on a sea-going turtle has been proven to be a major challenge (Schroeder & Balazs 2000, Hickerson 1999). The destructive forces of impact e.g. between the turtle's carapace and reef corals cause less damage or loss of devices in smaller, immature turtles which facilitates attachment methodologies. However, due to the exclusively marine life of immature turtles, lacking any terrestrial component, such as is apparent in reproducing females, these animals have to be caught in the water.

During all stages of their life cycle, sea turtles belong to a group defined as 'surfacers' by Kramer (1988). In his description the author differentiates diving animals into 'divers' and 'surfacers'. Divers typically spend less than 50% of their time submerged and perform a behaviour that is characterised by discrete bouts of dives, interrupted by long periods at the surface (or even on land). In contrast, surfacers spend, by definition, most of their time under water, surfacing only briefly for gas exchange. In other words, divers live at the surface and submerge for a well-defined purpose, usually foraging, whereas surfacers live underwater and only return to the sea surface for a well-defined purpose, usually gas exchange.

Although sea turtles spend an enormous percentage of their time spent submerged, the level of activity of sea turtles under water has generally only been indirectly approached in research, if at all. Researchers have concluded whether dives are active or resting either from the shape of the dive profile (e.g. Hays et al. 2000a) or from the duration of the dives (e.g. Hays et al. 2001b). Over the last few years a compass has been developed, that has enabled the direct recording of movements of sea turtles and has given a solid base for the assessment of activity (Hochscheid et al. 1999, Storch et al. 2002, Jeschke et al. 2002).

This compass was included in the DK600-602 devices (see description in section 3.1) that were used to monitor inter-nesting females and immature Hawksbill Turtles in this study.

It is hypothesised that the behaviour of the turtles changes along with the phases of the life cycle, especially when a change of habitat is involved (as in migrating mature females). Furthermore, even though juvenile Hawksbill Turtles share the same coastal reef habitats with adult conspecifics a difference in behaviour between the two groups can be expected due to the considerable size difference; small juveniles of ca. 5 kg eventually grow to adults weighing up to 95 kg (this is the size range encountered within the present study).

The first part of this chapter describes the activities of female Hawksbill Turtles around Buck Island during the inter-nesting interval. Patterns of dive behaviour directly after and before nestings are differentiated from each other and from the rest of the inter-nesting interval.

Following this, the data obtained from a long-term study are presented, revealing the behaviour of adult females between nesting seasons and showing migratory and foraging behaviour in distinctive phases.

Finally, submergence and surfacing patterns of immature turtles off Mona Island are described and there is a comparative discussion of the findings from the three groups.

### 4.2.2 *Specific Methodology*

The presence or absence of variations in the output signals of the compass (see section 3.1) was used to distinguish between resting behaviour and active phases (see also Hochscheid et al. 1999, Storch et al. 2002, Jeschke et al. 2002). Activity was defined as a change in body orientation of  $3^\circ$  or more in any direction within a recording interval of 8 sec. Accordingly, the turtle was assumed not to have moved when the angle changed less than  $3^\circ$  or not at all between two subsequent recordings. The data obtained from the immature turtles at intervals of  $\frac{1}{2}$  or  $\frac{1}{4}$  sec were reduced to match the same recording frequency at intervals of 8 sec by taking only every 16<sup>th</sup> or 32<sup>nd</sup> data-point, respectively.

A complete dive was classified as ‘active’ when 80% or more of the total number of data points of the dive showed activity. A resting dive was defined as a dive with less than 40% of active recording intervals. All other dives were intermediate dives that were not ascribed to the two above described categories, although they were nevertheless considered in the total sum of dives.

The Mann-Whitney test was used to test for differences between non-normally distributed sets of data. Median, first and third quartile are given for these data and interquartile range

$$(3) \quad \text{IQR} = \text{third quartile} - \text{first quartile}$$

was calculated to describe the scatter of data.

For a random selection of dives from the immature turtles all dives from each individual were brought into a random order using Microsoft Excel<sup>®</sup> and the first 10 dives per data set selected as a sub-sample.

### 4.2.3 Results

#### 4.2.3.1 The Inter-Nesting Intervals

In the two field-seasons at Buck Island data from 9 different nesting females were obtained, representing 186 d of recording. Malfunction of the device caused an unscheduled early end to the recording in 3 cases (Tab. 1). In three cases, PPW 847 with device number 33, QQD 384 with device number 35 and QQD 025 with device number 34, the equipped turtles were observed undertaking false crawls that were long enough to allow me to approach the animal without being noticed. In these cases, the new attachment method (see section 4.1) enabled exchange of the device at this time. The recordings of the relevant inter-nesting intervals were continued by the new logger (Tab. 1). The duration of the inter-nesting intervals ranged from 13 to 17 d (mean 15 d).

## 4.2 Behaviour During Different Stages of the Life Cycle

**Tab. 1:** Files obtained from nesting females during the 1998 and 1999 field-season and duration of inter-nesting intervals (= days between successful nestings).

<i>Year</i>	<i>Tag number</i>	<i>Device number</i>	<i>Duration of recording</i>	<i>Days between successful nestings</i>	<i>Notes</i>
1998	QQD 374	20	14 d	14	
	QQD 148	01	15 d	15	
	QQD 176	21	7 d	not observed due to hurricane, retrieved after 28 d	recording interrupted, depth data corrupted
	QQD 148	20	16 d	16	see section 4.3
1999	PPW 847	33	14 d	}	depth data corrupted
	PPW 847	35	4 h		15
	PPW 842	34	16 d	16	
	QQD 384	35	14 d	}	16
	QQD 384	39	2 d		
	QQD 025	36	13 d	13	
	QQD 384	37	14 d	14	
	QQD 280	38	15 d	15	depth data corrupted
	QQD 401	40	16 d	16	
	PPW 847	01	13 d	13	
	QQD 025	34	15 d	}	17
	QQD 025	40	2 d		
	QQD 280	36	5 h	14	recording interrupted

### 4.2.3.2 Dive Behaviour During Inter-Nesting Intervals

Ten complete inter-nesting intervals could be recorded, representing data from 7 different individuals (Tab. 1). The frequency distribution of the dive duration, combined for all observed inter-nesting intervals, was bimodal (Fig. 17). The median dive duration of females during the inter-nesting interval was 35.9 min (25% quart. = 14.1, 75% quart. = 46.7,  $n = 6285$ ). The longest dive observed was 93.5 min. The median surface interval lasted 1.2 min (25% quart. = 0.8, 75% quart. = 1.5,  $n = 6285$ ). As described later in this chapter, unusually long surface intervals, grouped together in the class  $>5.5$  min (Fig. 18), are mostly caused by surface oriented behaviour before coming ashore to nest. The time spent under water during the 10 observed inter-nesting intervals ranged from 91 to 97% (mean = 95, SD = 1.8).

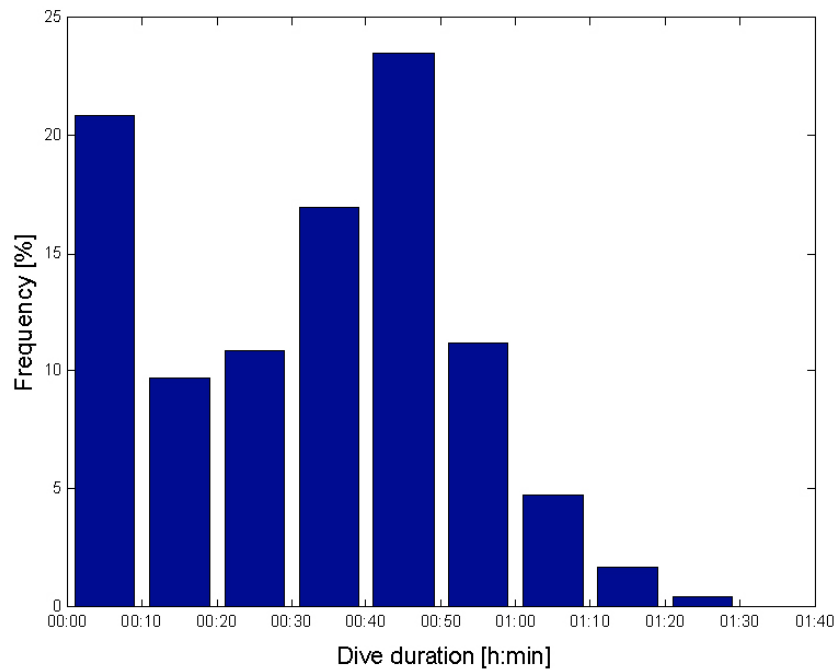
The overview over the 10 inter-nesting intervals that were recorded completely revealed three periods of behaviour (Fig. 19):

phase 1) moving away from the beach after re-entering the water (post-nesting),

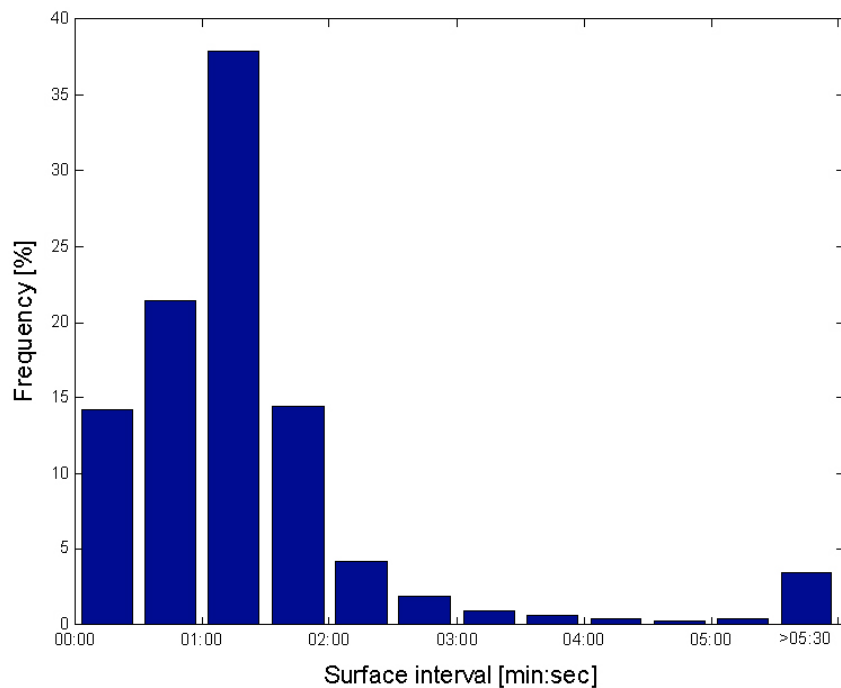
phase 2) regular dive behaviour with little variation and

phase 3) irregular dive behaviour prior to nesting (nesting restlessness).

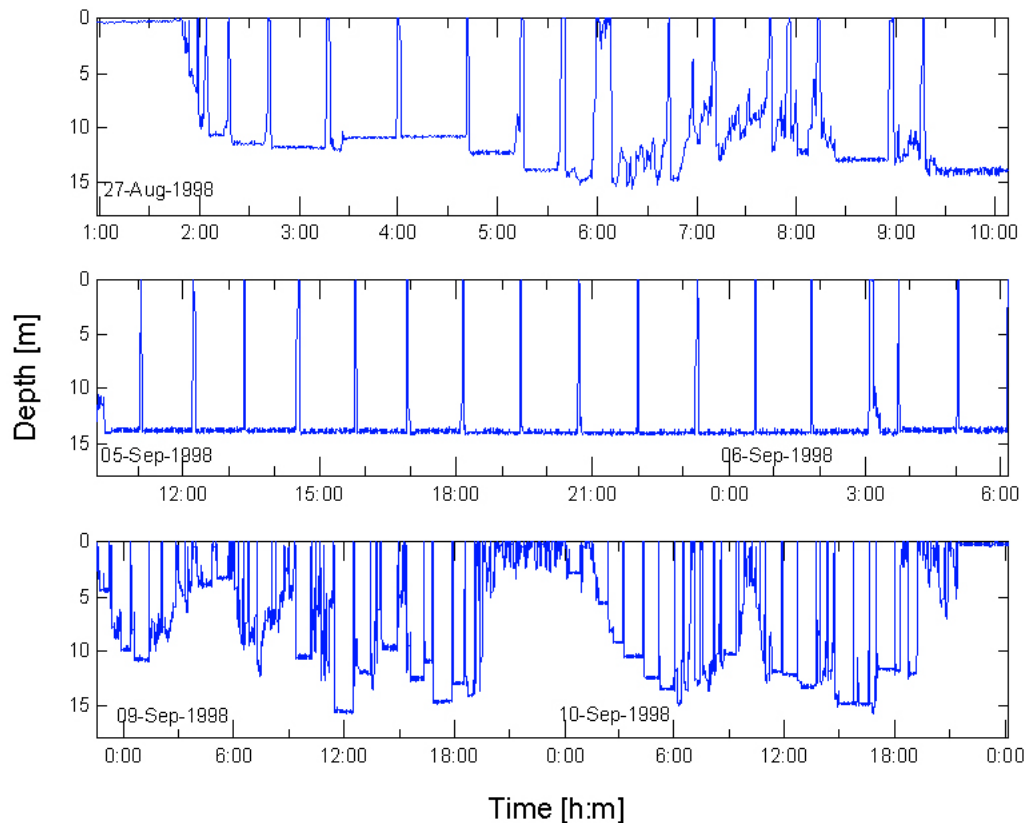
Analysis of data files revealed that phase 1, moving away from the nesting beach, typically covers the hours from re-entering the water until noon of the first day. The duration of this phase ranged from 9 to 13 hours (mean 10.7, STD = 1.34,  $n = 10$ ). The preparation for the successive nesting (see Fig. 19, bottom) started around the 12<sup>th</sup> day after the previous nesting. Therefore, the beginning of the 12<sup>th</sup> day (06:00 a.m.) of the inter-nesting interval was used to delineate the end of phase 2 and the beginning of phase 3. Phase 3 covered the last 17 to 114 hrs of the inter-nesting interval (mean 64.9, STD = 33.10,  $n = 10$ ), depending on the individual time between the two successive nestings. Phase 2, by definition, always lasted 282 hrs (noon of first day to 06:00 a.m. 12<sup>th</sup> day) and comprises the major part of the inter-nesting interval.



**Fig. 17:** Frequency distribution of dive duration observed during 10 inter-nesting intervals (number of dives considered is 6285). The class between 1:30 and 1:40 hrs is represented by a single dive, equivalent to 0.02%.



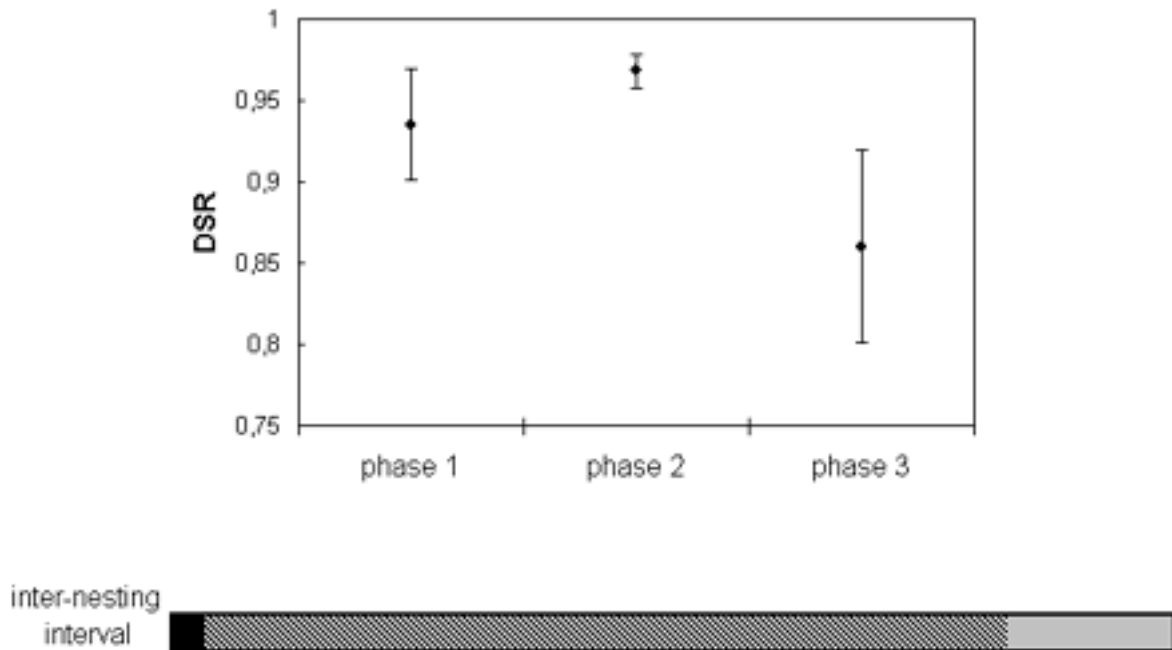
**Fig. 18:** Frequency distribution of surface interval duration observed during 10 inter-nesting intervals (number of surface intervals considered is 6285).



**Fig. 19:** Phases of the dive behaviour during the inter-nesting interval of QQD 148 from 27 August to 10 September 1998. Top: leaving the beach after nesting. Middle: regular dive behaviour throughout the major part of the interval (only a section is shown). Bottom: 'nesting restlessness' prior to the next nesting.

The three phases of the 10 inter-nesting intervals show significant differences in the dive/surface ratio (DSR), given in Fig. 20 (phase 1 vs. 2,  $t = 2.6$ ; phase 2 vs. 3,  $t = 5.1$ ; phase 1 vs. phase 3,  $t = 2.7$ ,  $p < 0.05$ ). This quotient of the time spent submerged divided by the duration of a complete dive cycle (dive time plus surface interval) reveals that the DSR is highest in phase 2 (97%), with little variation ( $SD = 1$ ,  $n = 10$ ). The ratios were lower in phase 1 and 3 (94 and 86%, respectively) and the range of variation was larger ( $SD = 3.4$  and  $5.9$ , respectively,  $n = 10$ ) than in phase 2.



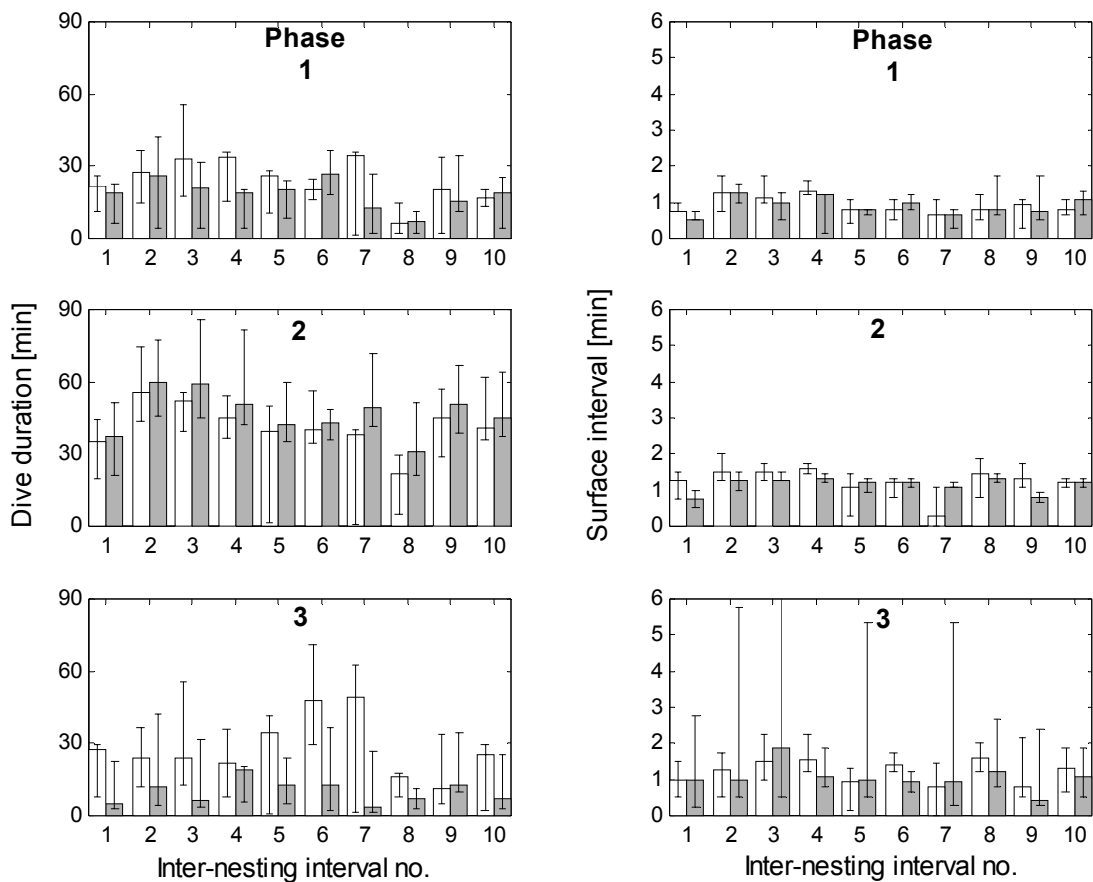


**Fig. 20:** Different dive/surface ratio (DSR) in the three phases of the inter-nesting interval (mean  $\pm$  SD). The bar in the bottom gives average relative duration of the three phases in a complete inter-nesting interval. All phases were significantly different from each other (see text).

#### Diel Patterns in Dive Duration and Surface Interval

The high DSR in phase 2 stems from long dive durations paired with short surface intervals (Fig. 21, middle graphs). This pattern occurred in all observed inter-nesting intervals with rather little variation. Both surface interval and dive duration showed little variation according to day/night during phase 2 (indicated by the similar extents of grey and white bars in the two middle graphs in Fig. 21).

The switch from phase 2 to phase 3 (Fig. 21, middle and bottom) is characterised by an increase in interquartile range (IQR, see Appendix, Tab. A 1 and Tab. A 2). The IQR of dive duration increased in 13 of 20 cases by a mean factor of 2.2 (range 1.1 to 5.3), while IQR of the surface intervals increased in 17 of 20 cases by a mean factor of 8.3 (range 1.4 to 36.5).



**Fig. 21:** Diel differences in median dive duration (left) and median surface interval (right) for day (white columns) and night period (grey columns) during phases 1-3 of the inter-nesting intervals. Error-bars give the first and third quartile. The cut-off error-bar (third quartile) of surface duration in phase 3 in interval 3 was 11 min. Numbers of inter-nesting intervals are as given in Tab. 2. For sample sizes and statistics see Appendix (Tab. A 1, Tab. A 2 and Tab. A 3).

In all 10 recorded inter-nesting intervals the nocturnal dive duration was significantly shorter in phase 3 than in phase 2 ( $p < 0.001$ ). Significant reductions of daytime submergence durations were found in 9 of the 10 cases (see Appendix, Tab. A 3). For the majority of the cases no significant change in surface intervals was found between phase 2 and phase 3 (see Appendix, Tab. A 3). The extent of the reduction was largest in the nocturnal dive durations (Fig. 21). The restlessness of the turtles prior to nesting is therefore characterised by a nocturnal decrease of dive duration and a highly variable

surface behaviour (Fig. 21, bottom), causing the low DSR of the this phase (Fig. 20). The unusually short median surface interval in the inter-nesting interval number 7 in phase 2 (Fig. 21, middle right) stems from the habit of the animal of interrupting most of the surface intervals by one to three very short dives to depths of only 3 to 5 m. This is also reflected by the accordingly low first quartile of the dive duration data (Fig. 21, middle left). Data of interval number 5 were obtained from the same individual earlier in the season and show the same phenomenon in a less distinctive manner. The unusually high variation in the nocturnal surface intervals prior to nesting (intervals number 2, 3, 5 and 7 in Fig. 21, bottom right) stems from approaches of the nesting beach with animals touching the beach or even actually emerging (proven by sharp drops in temperature due to evaporative cooling). These attempts can lead to surface periods of more than 1 hr duration.

The comparatively short dive durations in phase 1 and especially at night in phase 3 result in the previously-described bimodal shape of the frequency distribution in Fig. 17.

### Dive Depth

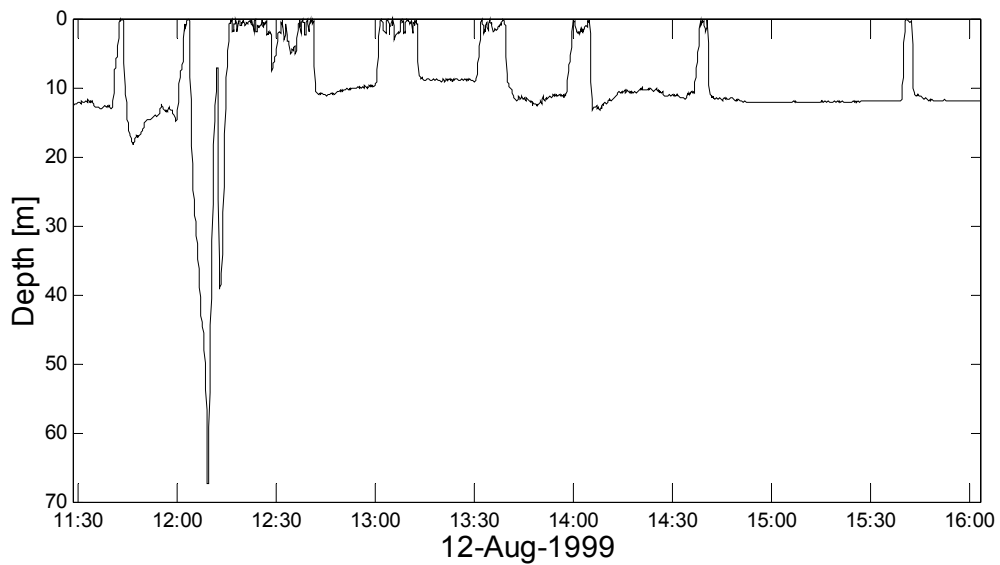
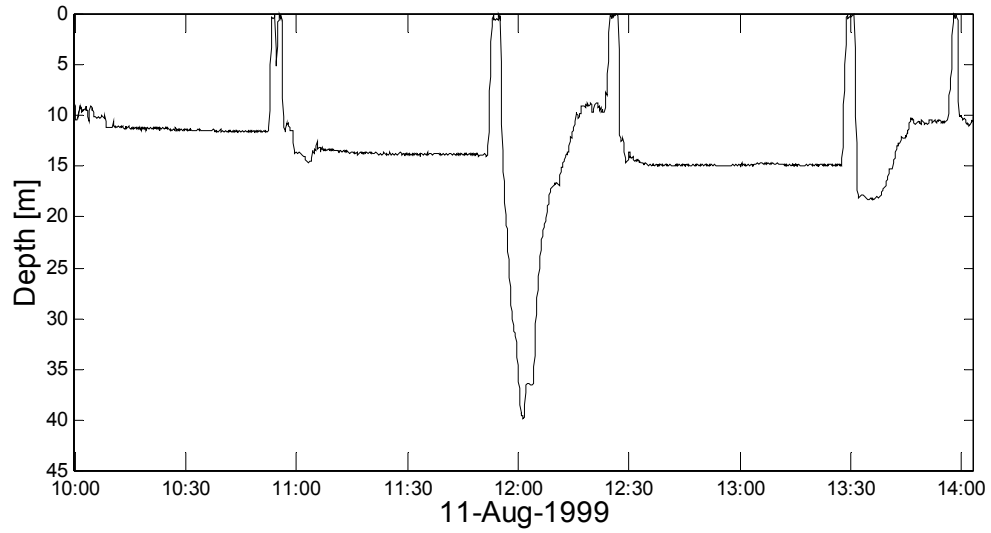
While the maximum depths that the turtles reached within the inter-nesting intervals ranged between 12.2 and 29.3 m in 8 of the 10 cases, two animals dived to depths of 67.3 and 69.0 m (see Tab. 2). The mean dive depths of the same two individuals (PPW 842 and QQD 401) indicated, however, that the maximum values represent exceptional behaviour, as the average dive depths of interval no. 4 and 8 were within the lower end of the scale.

While female PPW 842 performed only two exceptionally deep dives (days 14 and 15 of the inter-nesting interval, Fig. 22), turtle QQD 401 undertook a series of 11 deep dives on day 16 (Fig. 23). Two dives, marked with arrows in Fig. 23, showed distinctively flat bottom phases which are discussed later in this chapter. All exceptional deep dives occurred during the day between 7:00 a.m. and 12:30 p.m. in both females. After diving to a depth of 39.9 m at 11. August 1999 (Fig. 22, top) PPW 842 did not significantly increase the successive surface time (2.3 min) compared to average surfacing events (mean 2.0 min, SD = 4.5, n = 588). However, returning from a depth of 67.3 m on the next day (Fig. 22, bottom) the surface intervals within the following 2 hours appear prolonged (3.7 to

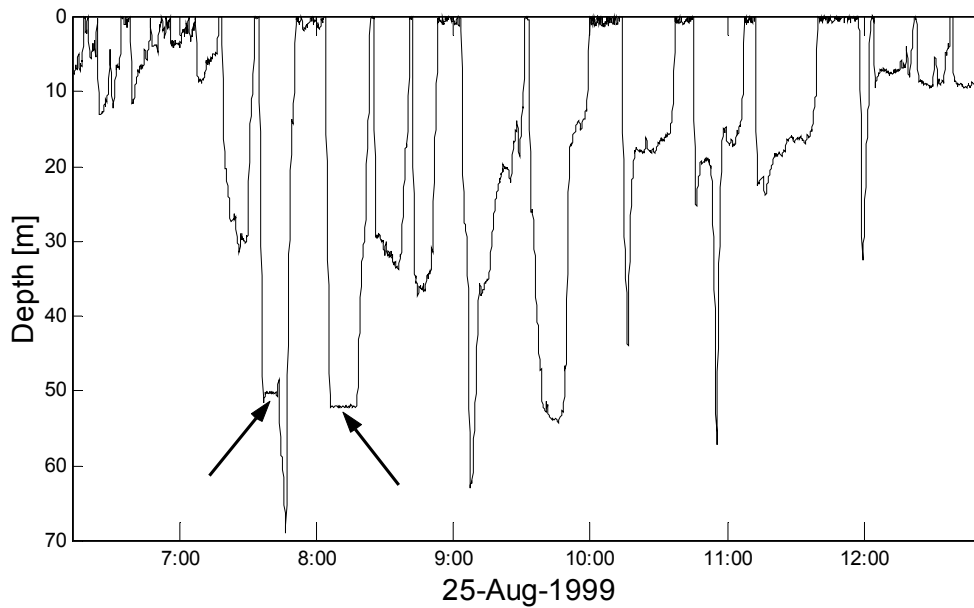
10.8 min) compared to the usual mean pause of 2 min duration. Within the set of 11 deep dives 6 distinctively prolonged surface intervals occurred, lasting between 4.3 and 18.0 min (Fig. 23).

**Tab. 2:** Dive depths reached by female Hawksbill Turtles during the inter-nesting interval.

<i>Interval No.</i>	<i>Tag No.</i>	<i>Maximum depth [m]</i>	<i>Mean depth [m]</i>	<i>SD</i>	<i>n</i>
1	QQD 374	12.2	7.8	± 2.4	713
2	QQD 148	16.9	11.9	± 3.1	491
3	QQD 148	18.0	11.8	± 3.8	477
4	PPW 842	67.3	8.6	± 3.7	587
5	QQD 384	14.8	10.7	± 3.6	698
6	QQD 025	21.9	10.2	± 1.7	476
7	QQD 384	14.2	9.7	± 4.1	651
8	QQD 401	69.0	8.3	± 5.2	1048
9	PPW 847	29.3	12.0	± 4.5	459
10	QQD 025	24.6	10.1	± 3.5	687



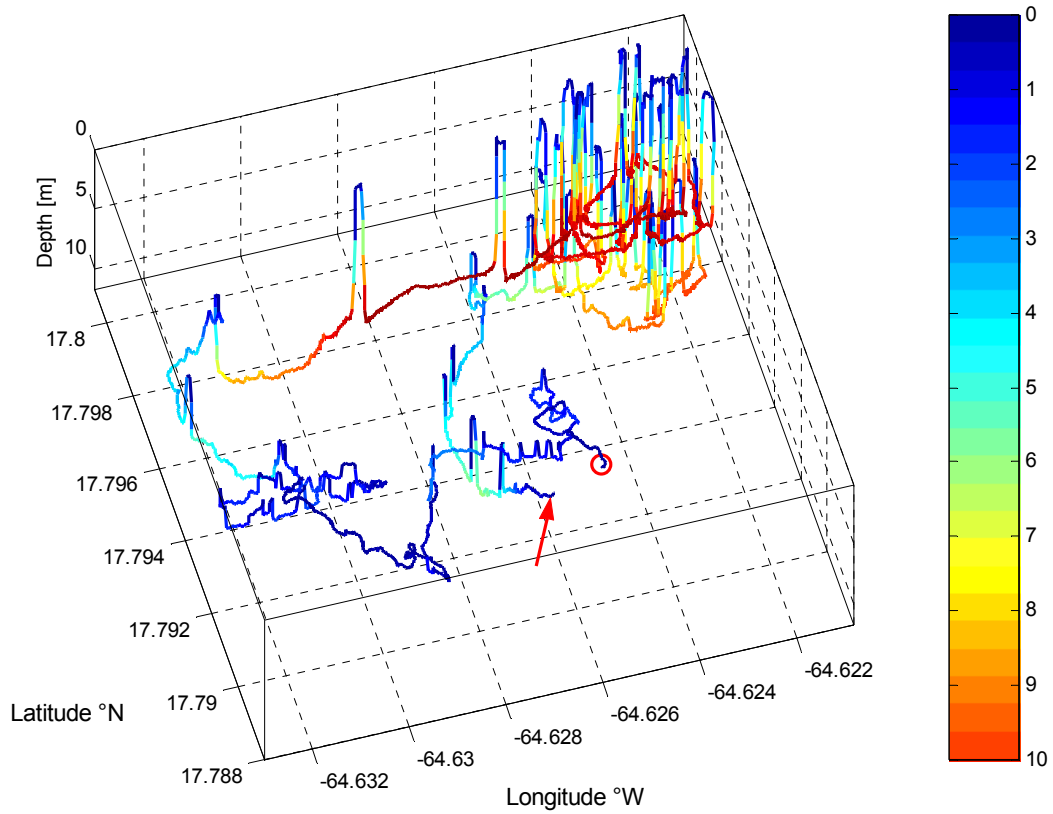
**Fig. 22:** Exceptional deep-diving behaviour of Hawksbill Turtle PPW 842 during the inter-nesting interval. Dives occurred during phase 3, on day 14 (top) and 15 (bottom) of the inter-nesting interval.



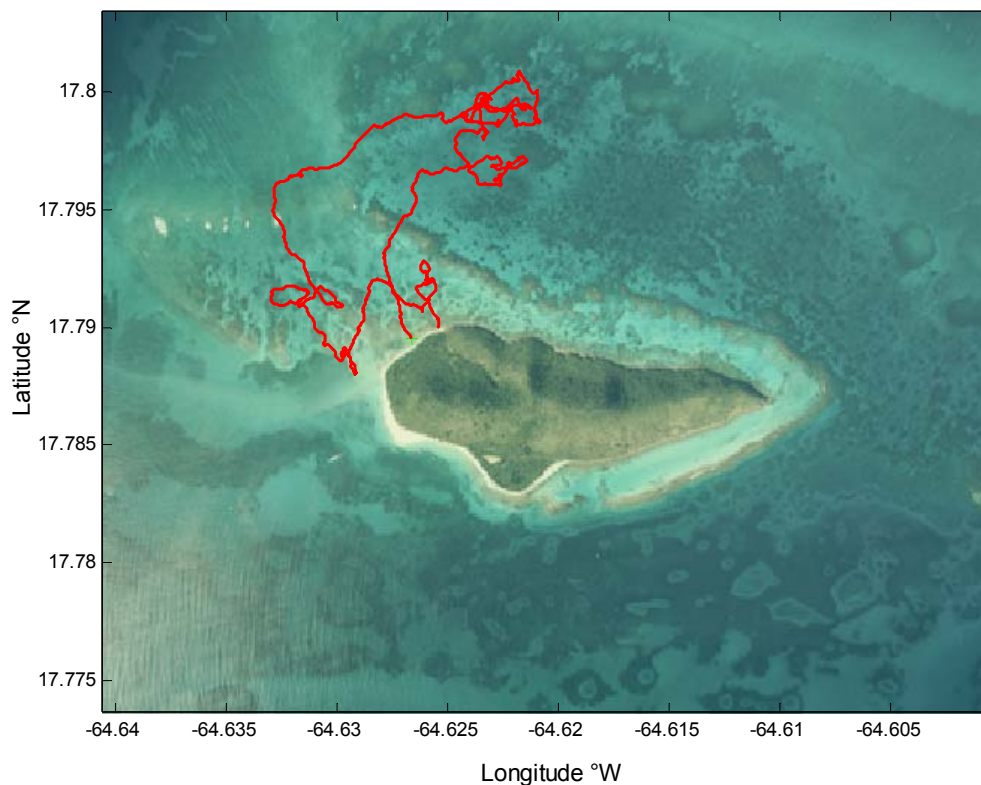
**Fig. 23:** Exceptional deep-diving behaviour of Hawksbill Turtle QD 401 during the inter-nesting interval. Dives occurred during phase 3, on day 16 of the inter-nesting interval. The arrows mark two dives with a distinctively flat bottom which will be discussed later in this chapter.

### 3-dimensional Route

Device number 39 was deployed on turtle QD 384 during a false crawl (see Tab. 1) on 8 August 1999 and was seen on another unsuccessful emergence the following night. The turtle successfully nested on 10 August and the device was retrieved. The first part of this data set (approx. 22 hrs) was therefore taken as the shortest file with known locations of entering and leaving the water, determined as N 17° 47' 20.2", W 64° 37' 35.8" and N 17° 47' 23.0", W 64° 37' 32.5", respectively. Vectorial analysis of the data as described in section 3.6 revealed the movements of the turtles in 3-dimensional space (Fig. 24). The turtle left the shore travelling in a virtually straight line, obviously tracing the sea floor of the lagoon (depth about 6 m) as judged by its dive profile, and crossed the crest of the barrier reef (Fig. 25). The deeper dives outside the lagoon lead to depths of around 10 m. The female approaches the beach performing circles and bends at or close to the surface, swimming parallel to the shoreline before emerging.



**Fig. 24:** 3-dimensional plot of movements of female QQD 384 over 22 hrs between a false crawl and the subsequent nesting event. The location where the animal entered the water is marked with an arrow, the emergence with a circle.



**Fig. 25:** Aerial view of the route taken by QQD 384 over 22 hrs between a false crawl and the subsequent nesting. The crest of the barrier reef enclosing the lagoon along the south-eastern and northern coast is visible. For depth information see chart in Fig. 3.

### Swim Speed

Measurement of swim speed was problematic because the turtles sometimes appeared to swim slower than the stall speed of the sensors ( $< 20$  cm/s) and because many speed sensors were damaged during the inter-nesting interval by impact with reef structures. However, sequences of successful speed measurements showed that typical velocities the turtles achieved while they were swimming in the water column were around 70 cm/s.

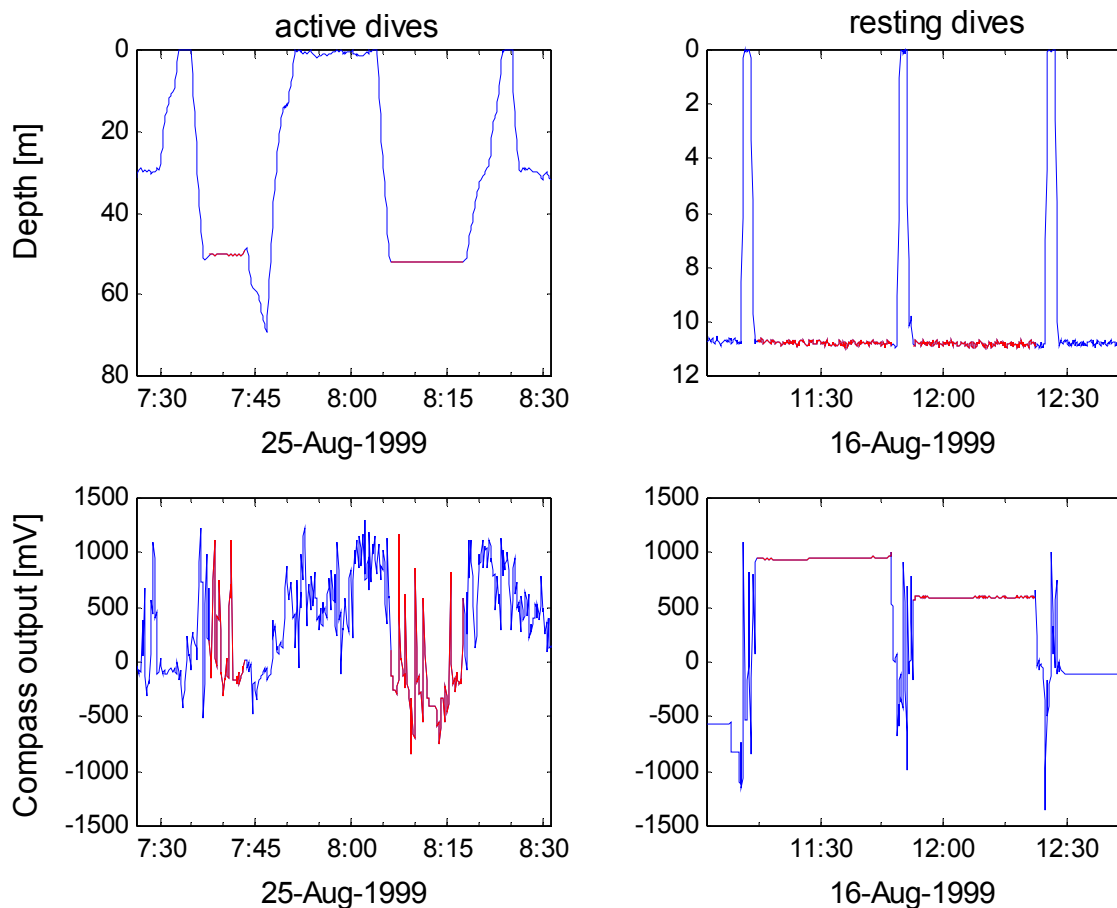
### Active Dives and Resting Dives

The routine dive behaviour of females during the major part of the inter-nesting intervals consisted of very uniform dives (see Fig. 19, middle). The compass output during such dives (Fig. 26, bottom right) depicted a characteristically flat line during the bottom phase



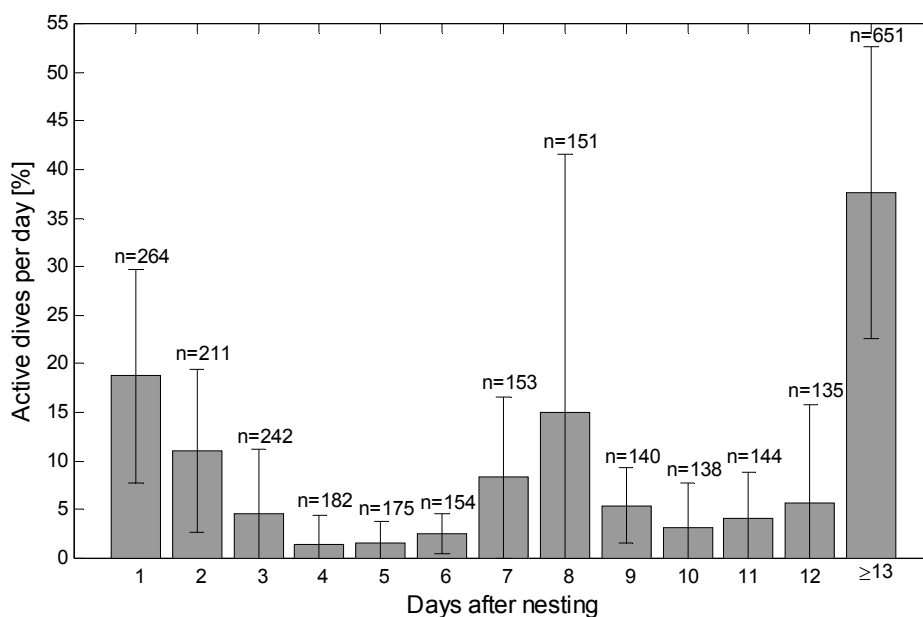
of the dive profile (Fig. 26, top right, marked in red). Variations in the signal only occurred during the ascent and descent phases of the dives.

The dive profiles of QQD 401's series of exceptional diving behaviour showed distinctive phases without depth change over time in two cases (marked with arrows in Fig. 23). These two dives are enlarged in Fig. 26 (top left) and, again, combined with the parallel output of the compass sensor (bottom left), revealing the high variation in compass signals during the bottom phase (marked in red).



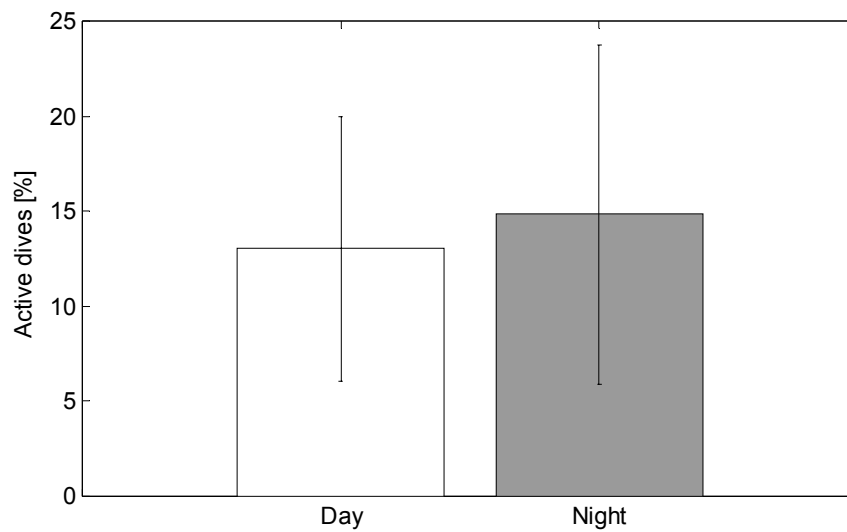
**Fig. 26:** Depth profiles (top) and compass output (bottom) during exceptional deep dives (left) and during routine dives in phase 2 (right) of the inter-nesting interval of female QQD 401. The flat bottom phases are marked red, showing the strong variations in the compass signal during the deep dives and the stable output at the maximum depths of the routine resting dives.

Systematic differentiation of active and resting dives, as described in section 4.2.2, throughout the inter-nesting intervals of four female Hawksbill Turtles revealed the chronological pattern shown in Fig. 27. All four individuals showed increased daily percentages of active dives shortly after nesting (days 1 and 2), during a one day period in the middle of the inter-nesting interval (either day 7 or day 8) and, most distinctively, from day 13 until the end of the considered inter-nesting interval. The mean percentage of daily activity was below 6% on 8 days of the inter-nesting interval (Fig. 27).



**Fig. 27:** Percentage of active dives (see text for definition), plotted chronologically for the different days of the inter-nesting intervals. Data from four females are combined, with durations of inter-nesting intervals ranging from 13 to 16 days. Days number 13 and more are included in the last column. The columns mark the mean values. The error-bars indicate SD and n gives the total number of dives considered per column.

Differentiation of these data into day- and night time (06:00 to 17:59 and 18:00 to 05:59 local time, respectively) showed no significant difference (t-test,  $t = 0.3$ ,  $p > 0.1$ ) in the percentage of active dives between day and night (Fig. 28).

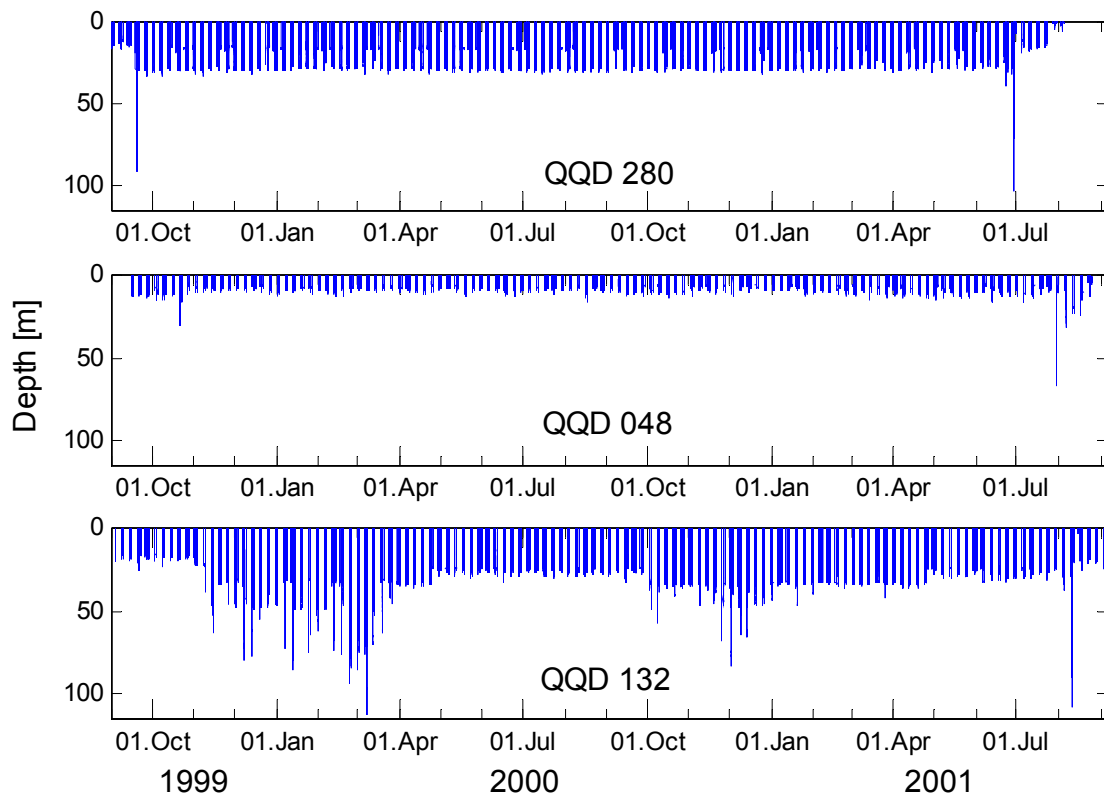


**Fig. 28:** Percentage of active dives (see text for definition) during the daylight hours (white column, 06:00 to 17:59 local time) and during the nights (grey column, 06:00 to 17:59 local time) of the inter-nesting intervals. The columns mark the mean values of four individual turtles, the error-bars give the standard deviation. The total number of dives considered is 2740.

### 4.2.3.3 Dive Behaviour During Re-Migration Intervals

All four turtles that had been equipped in 1999 with Mk7 for long-term recording and, according to NPS monitoring data (Hillis-Starr, pers. comm.), were expected to re-nest after a 2 year re-migration interval were observed at Buck Island between July and September 2001. Devices were retrieved from three animals (QQD 280, QQD 048 and QQD 132) while no remains of the device or the attachment system could be found on the carapace of the fourth (QQD 401).

The duration of successful recording of dive depth was between 22 and 24 months (QQD 280: 690 days, QQD 048: 710 days and QQD 132: 732 days). Fig. 1 shows the similarity in the 2-year pattern of dive depth of QQD 280 and QQD 048, while the third turtle, QQD 132, showed more depth variation. The average time spent submerged was 95, 97 and 96%, respectively.



**Fig. 29:** Overview over the chronological dive depth data of the three female Hawksbill Turtles QQD 280, QQD 048 and QQD 132 between two successive nesting seasons (equipped 1999, retrieved 2001). Following plots of depth profiles later in this chapter are parts of these data-sets using more detailed time scales.

The first two sets of data were clearly subdivided into 5 different periods of behaviour, that are named in the following and described in detail below.

- a) As all females nested again after the attachment of the device (see Tab. 3), the first phase was considered to correspond to one or two inter-nesting intervals.
- b) The second period, being the first one not assigned to reproductive behaviour, included marked deep diving behaviour and led the turtles away from the nesting ground towards their foraging areas (see section 4.4) and is therefore designated as 'foraging migration'.
- c) The pattern for the following period was maintained for the major part of the re-migration interval, marking the phase of 'stationary foraging'.

- d) The phase after the next obvious change in the dive profiles can be assigned to the return to the nesting grounds (see section 4.4) and is termed 'breeding migration'.
- e) A few days of 'pre-nesting' behaviour followed before the first nesting event of the season was observed and the data recorders retrieved.

**Tab. 3:** Dates of equipment of three Hawksbill Turtles for the long-term study and dates of successive nests within the nesting season 1999 as derived from sighting or from logger data.

	<i>Date equipped</i>	<i>Date(s) re-nested</i>	<i>source of information</i>
<i>QQD 280</i>	01.09.1999	17.09.1999	sighted
<i>QQD 048</i>	15.09.1999	01.10.1999	logger data
		18.10.1999	logger data
<i>QQD 132</i>	03.09.1999	21.09.1999	logger data
		07.11.1999	logger data

The devices were programmed to record data for 2 days and shut off for the next 4 days, repeating this duty-cycle until the memory was completely filled (see section 3.2). As a result the exact time of the transition from one pattern of behaviour to another could not always be exactly defined.

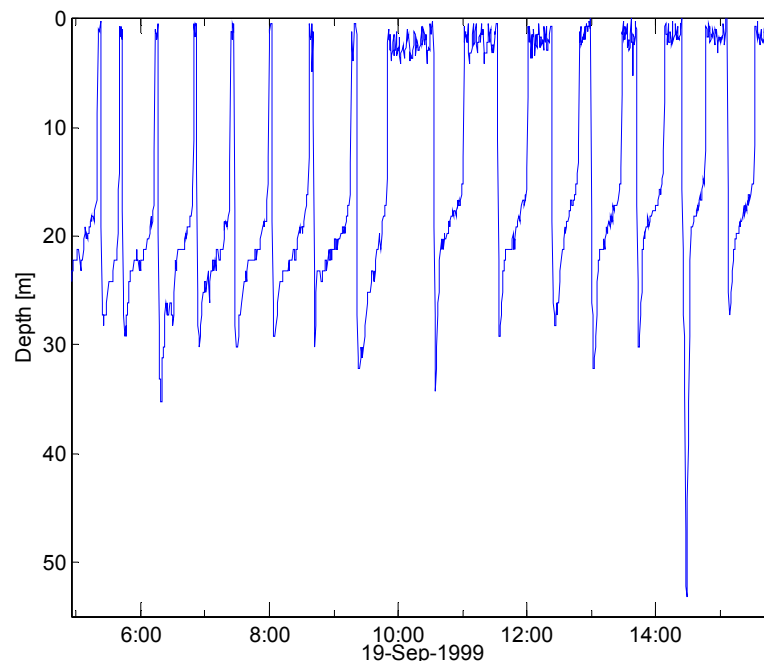
### Description of the dive behaviour during the phases

*Inter-nesting Interval* The behaviour during the inter-nesting intervals has already been described in detail (see section 4.2.3.2). The present long-term study was not suitable to record the rather short inter-nesting intervals in detail due to the interruptions caused by the duty-cycle. Therefore, no detailed analysis of this section of the data was undertaken.

*Foraging Migration* The foraging migrations were found to begin immediately after the last nesting activity and lasted between 2 to 12 days (see section 4.4.3.2). Fig. 30 shows an example of dive profiles during the foraging migration, those being found to be similar in all individuals. Dives were characterised by gradual ascent phases following a maximum

depth of the dive of approximately 30 m, obviously representing a characteristic maximum depth of travelling dives. No dives deeper than the travelling depth of 30 m were recorded during the foraging migration of QQD 048. In contrast, the deepest recorded dives during the foraging migrations of QQD 280 and QQD 132 were 91 and 108 m, respectively (see Fig. 29 for overview).

During daylight hours (10:00 to 22:00 GMT or 06:00 to 17:59 local time) the surface intervals were found to be significantly longer than at night in QQD 280 (Fig. 30 and Tab. 4), while this was not apparent for QQD 048 (Tab. 4). The third female, QQD 132, stayed within the upper 2.5 m of the water column for periods of 6, 7 and 10 hrs during the daylight hours of the three days of recorded migration behaviour. Due to the exceptionally long surface periods during the foraging migration these data were not normally distributed and thus median values and quartiles are given in Tab. 4. More data on diel patterns are presented later in this chapter.



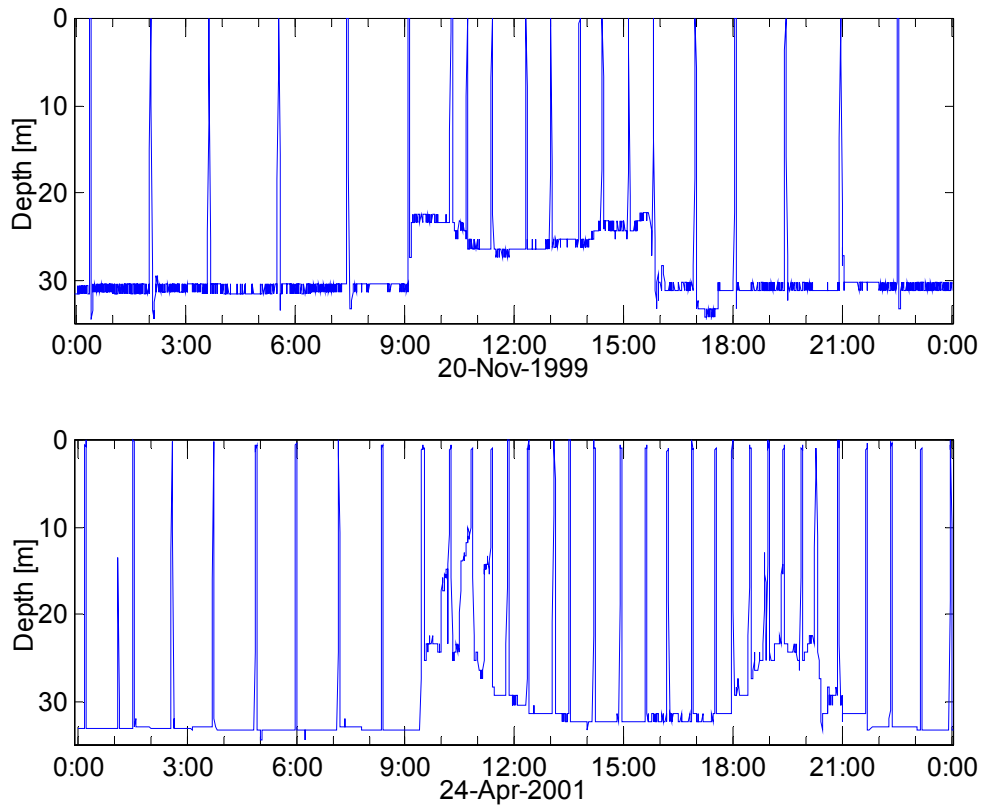
**Fig. 30:** Sequence of dives during the foraging migration of QQD 280. Time given on x-axis is GMT (local time + 04:00 h). Prolonged surface intervals (see text and Tab. 4 also) occur after sunrise (10:00 GMT or 06:00 a.m. local time).

**Tab. 4:** Median duration of surface intervals recorded during day-time (06:00 to 17:59 local time) and night-time hours (18:00 to 05:59 local time) of the foraging migration of females QQD 280, QQD 048 and QQD 132. First and third quartiles are given in brackets and sample sizes below. Mann-Whitney test ( $p < 0.05$ ) was conducted to test for significant differences between day and night.

	<i>Surface interval day</i> [min]	<i>Surface interval night</i> [min]	<i>Difference</i> day vs. night
QQD 280	4.5 (2.5; 11.0) n = 36	1.5 (1.0; 2.5) n = 39	* Z = 4.9
QQD 048	0.5 (0.5; 1.0) n = 45	1.0 (0.5; 1.0) n = 24	n.s. Z = 0.5
QQD 132	2.5 (1.0; 26.0) n = 38	1.3 (1.0; 2.0) n = 20	n.s. Z = 1.8

*Stationary Foraging* The phase of stationary foraging represented the major part of the re-migration interval (average 21 months). An example of the pattern of the dive behaviour at the foraging ground is shown in Fig. 31. This particular turtle, QQD 132, apparently crossed the same bottom structure at a depth of 24 m when moving from the area frequented during daylight to the resting site at a depth of 33 m used at night (see repeated variations in the depth profile in Fig. 31 top and bottom).

All three females were found to perform significantly longer dives at night than during day (Tab. 5), with average submergence durations of 60 and 38 min, respectively. The differences in mean dive depth between nocturnal and diurnal dives ranged from only 0.3 m to a substantial 8.3 m, but all three individuals consistently showed a significantly greater variation in dive depths during day than at night (Tab. 6).



**Fig. 31:** Depth profiles of an adult female Hawksbill Turtle (QQD 132) during two different days of the stationary foraging phase. Time given on the x-axis is GMT (local time + 04:00 h). The bathymetry of the seafloor, implied through the bottom phases of the dive profiles, appears to be the same despite the long time between the two sections of data. (The difference in dive duration between November 1999 and April 2001 is analysed in section 4.5).



## 4.2 Behaviour During Different Stages of the Life Cycle

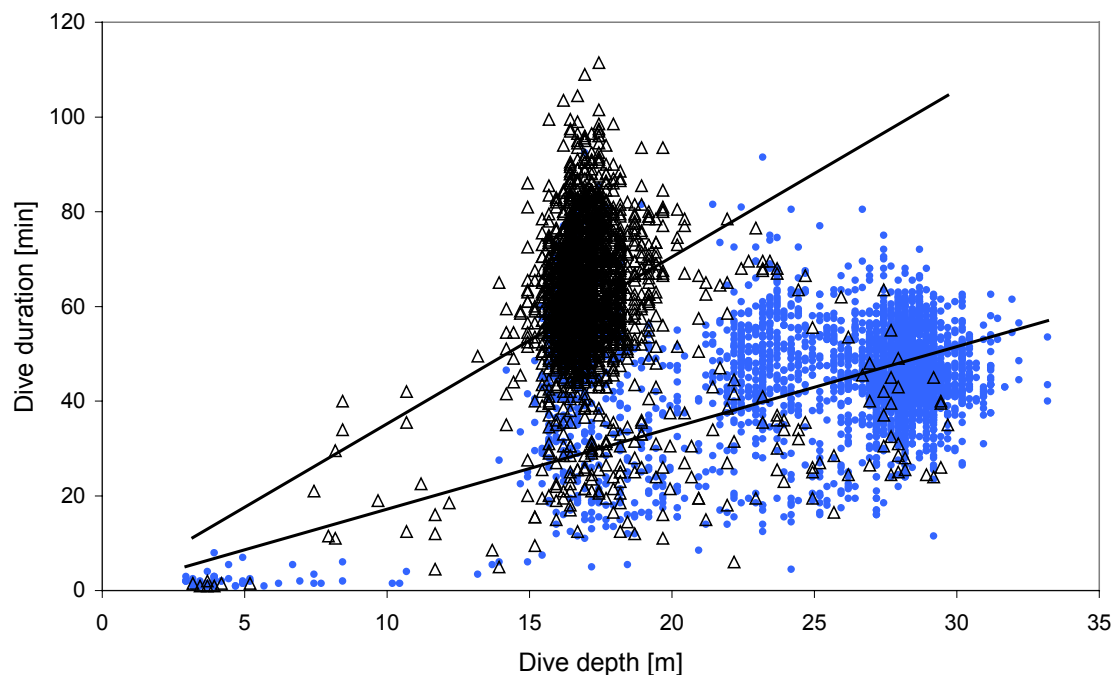
**Tab. 5:** Mean dive duration recorded during day-time (06:00 to 17:59 local time) and night-time hours (18:00 to 05:59 local time) of the foraging phase of females QQD 280, QQD 048 and QQD 132. Standard deviations are given in brackets and sample sizes below. t-test was conducted to test for significant differences between day and night.

	<i>Dive duration day</i> [min]	<i>Dive duration night</i> [min]	<i>Difference</i> day vs. night
QQD 280	44.7 (± 12.0) n = 3272	61.0 (± 15.3) n = 2357	* t = 44.5
QQD 048	30.8 (± 10.8) n = 4907	53.5 (± 19.2) n = 2567	* t = 65.3
QQD 132	37.2 (± 13.3) n = 3770	65.2 (± 18.2) n = 2153	* t = 68.0

**Tab. 6:** Mean depth of dives recorded during day-time (06:00 to 17:59 local time) and night-time hours (18:00 to 05:59 local time) of the foraging phase of females QQD 280, QQD 048 and QQD 132. Standard deviations are given in brackets and sample sizes below. Levene-test for similarity of variance ( $p < 0.01$ ) was conducted to compare the variance of depth during day and night.

	<i>Dive depth day [m]</i>	<i>Dive depth night [m]</i>	<i>Similarity of variance</i> day vs. night
QQD 280	25.5 (± 4.9) n = 3272	17.2 (± 2.2) n = 2357	* different F = 1470.5
QQD 048	9.0 (± 1.5) n = 4907	7.8 (± 0.8) n = 2567	* different F = 658.0
QQD 132	29.2 (± 9.0) n = 3770	29.0 (± 5.1) n = 2153	* different F = 33.6

The data obtained from QQD 280, which showed a strong dichotomy in the mean dive depth between night and day throughout the foraging phase (day mean = 25.5 m, night mean = 17.2 m, see Tab. 6), was used to plot the relationship between dive duration and dive depth (Fig. 32). The dive durations during day and during night increased significantly with the depth reached (F-test,  $F = 160.7$ ,  $F = 473$ ,  $p < 0.0001$ ). Comparable dive depths were found to be paired with longer dive durations at night than during day.

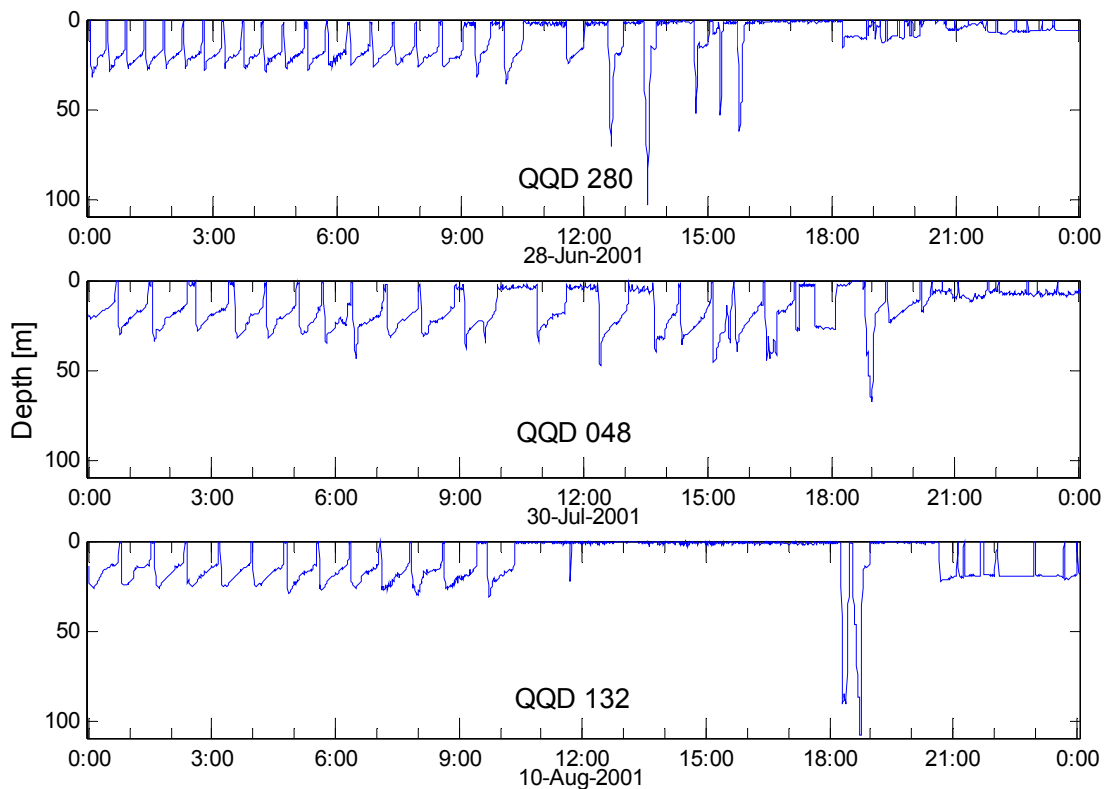


**Fig. 32:** Relation between the duration and the depth of the dives of QQD 280 recorded during the foraging phase. Data-points are separated into day (blue dots,  $n = 3254$ ) and night (black triangles,  $n = 2325$ ). Linear regressions are  $y = 3.5x$  ( $r^2 = 0.2$ ) for night-time and  $y = 1.7x$  ( $r^2 = 0.1$ ) for day-time data, both significant at  $p < 0.0001$ .

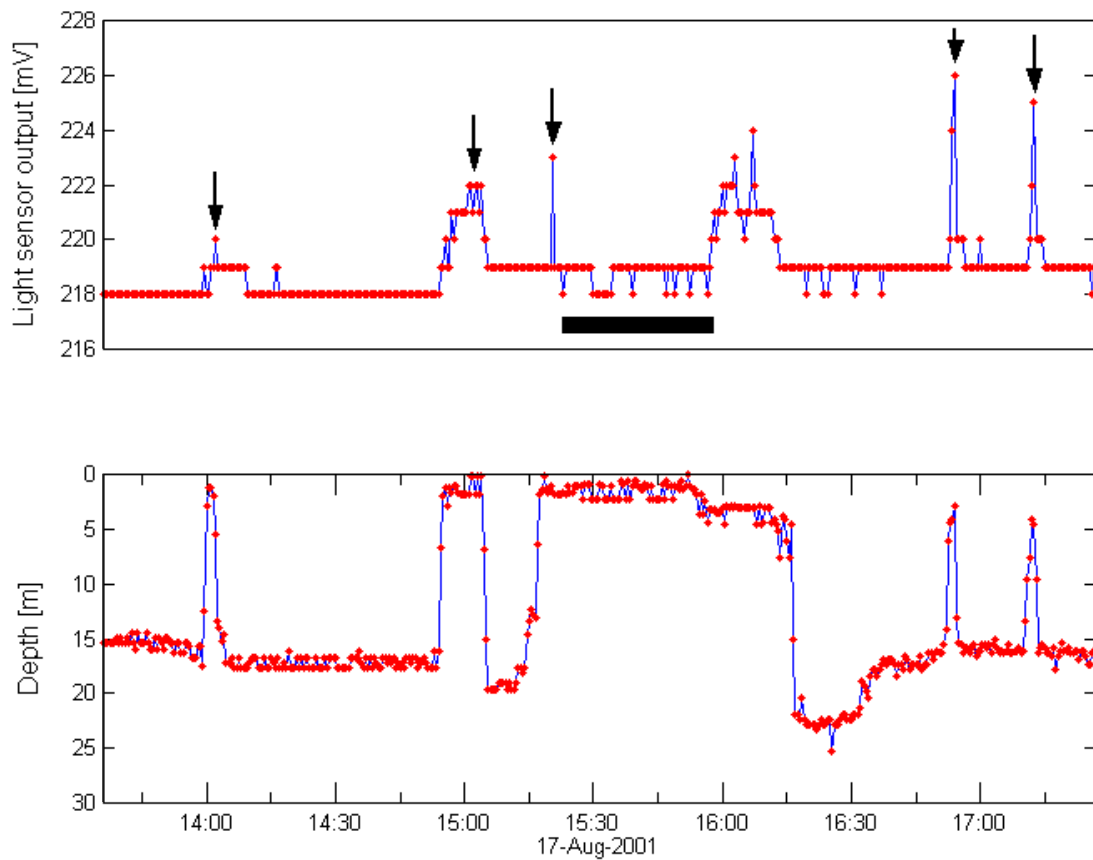
*Breeding Migration* The migrations of the three females back to their nesting site at Buck Island lasted between 1 and 16 days (see section 4.4.3.2). Fig. 33 shows 24 h-sections of depth data recorded during these breeding migrations of QQD 280, QQD 048 and QQD 132. It is particularly striking that in the foraging migrations the travelling dives in all three individuals are similar as are the prolonged surface intervals of up to 6 ½ hrs (Fig. 33 bottom).

## 4.2 Behaviour During Different Stages of the Life Cycle

The light sensors of all three devices had ceased normal operation by the onset of the breeding migrations, showing extremely reduced amplitudes and shifted ranges. However, the relative signals of the sensors still enabled the detection of sudden decreases of light intensity during day. Such an event of shading was recorded once in QQD 048 (30. July 2001, ca. 06:00 to 07:00 a.m. local time) and twice in QQD 132 (10. August 2001, ca. 11:00 to 13:00 a.m. and 17. August 2001, ca. 11:20 to 12:00 a.m. local time), during long surface periods (see Fig. 34 for an example).



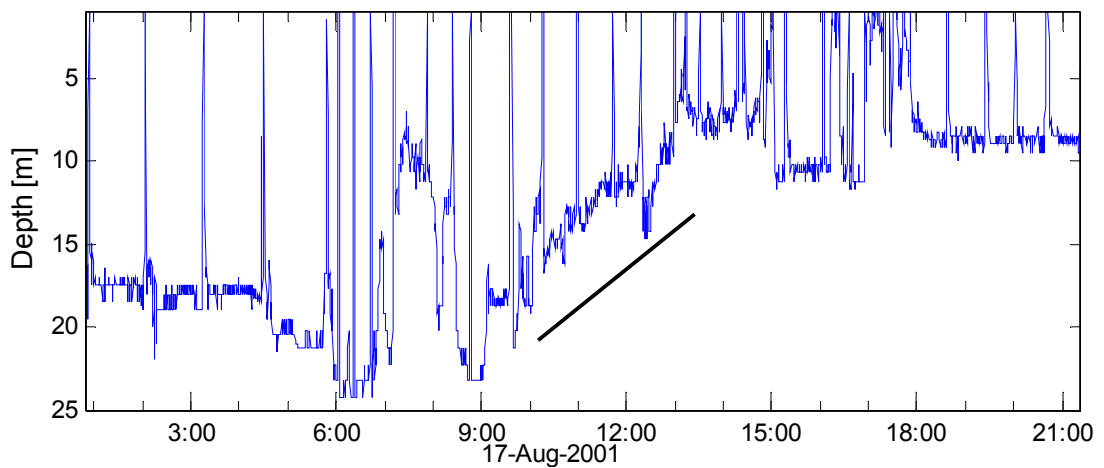
**Fig. 33:** Depth profiles of the breeding migrations of the three females. Time given on x-axis is GMT (local time + 04:00 h).



**Fig. 34:** Evidence for mating behaviour, given through low light intensity during a surface interval of female QQD 132. The sequence (ca. 35 min) of data marked by the black bar in the top graph shows light intensities similar to that at a depth of 10 to 15 m although the turtle was close to the water surface, as proven by the dive profile in the bottom graph. The arrows mark the usual high light levels when the turtle surfaces. Such high light intensities are reached after the obvious shading, just when the turtle dove approx. 4 m deep, implying the end of coupling.

*Pre-nesting* The duration of this last phase, defined as the time between the end of recognisable migration behaviour and the first emergence from the water to nest, was 24 days in QQD 280 and QQD 132, but only between 13 to 17 days in QQD 048. The transition to pre-nesting was marked by the decrease of maximum dive depths of 18.5, 21.5 and 24.2 m in QQD 280, QQD 132 and QQD 048, respectively, to depths that are typical of the inter-nesting intervals (see section 4.2.3.2, Tab. 2). The record from female QQD 132 presumably reflected the approach to the lagoon off Buck Island because, based on the distinctive shape of the dive profiles, the turtle was assumed to have followed the gradual ascent of the sea floor (Fig. 35). The end of this last phase of the re-migration interval

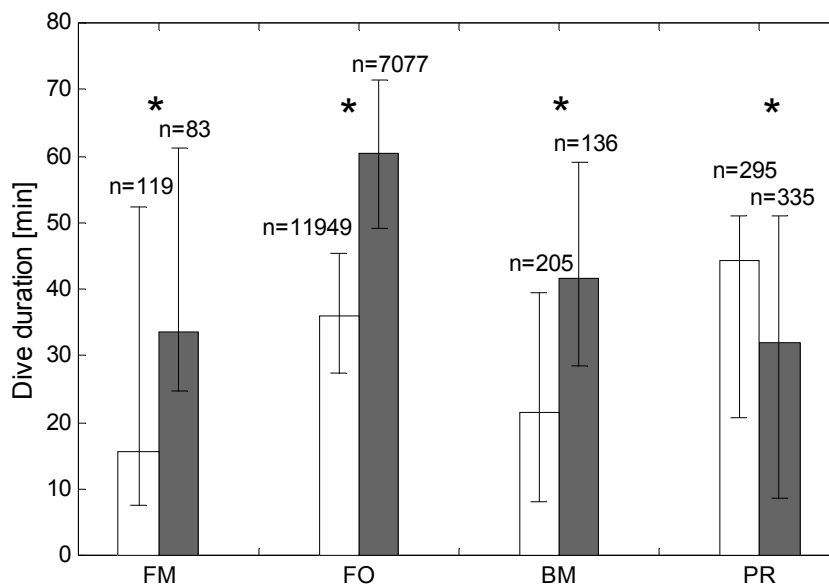
showed dive profiles equal to the nesting restlessness of the inter-nesting intervals, with frequent surface activity during the night.



**Fig. 35:** Section of the depth profiles obtained from female QQD 132, indicating that the turtle followed the gradual ascent (black line) of the sea floor when reaching shallow waters off Buck Island.

### Diel Patterns

The diel difference in dive duration between day and night is shown in Fig. 36 in relation to the phases of the re-migration interval. During the foraging migration, the stationary foraging phase and the breeding migration nocturnal dives had median durations ranging from 34 to 61 min and were longer than day-time submergences, that lasted between 16 and 56 min (Mann-Whitney,  $p < 0.001$ , FM:  $Z = 5.7$ ; FO:  $Z = 76.4$ ; BM:  $Z = 7.0$ ). In contrast, during the pre-nesting phase this relation was reversed ( $p < 0.001$ ,  $Z = 3.7$ ; Fig. 36), as the median values of dive duration during the night and the day were 32 min and 44 min, respectively.



**Fig. 36:** Nocturnal (grey columns) and diurnal dive duration (white columns) during the phases of the re-migration interval using data from three female Hawksbill Turtles (QQD 280, 048 and 132). FM: foraging migration, FO: stationary foraging, BM: breeding migration and PR: pre-nesting. Columns mark the medians, error bars indicate first and third quartiles. Numbers of dives considered are given above columns. Mann-Whitney test (see text) was conducted to test for significant differences, marked with an asterisk.

**Tab. 7:** Surface intervals of three female Hawksbill Turtles during the phases of the re-migration interval. Abbreviations used are the same as in Fig. 36.

<i>Phase</i>		<i>Median surface interval [min]</i>	<i>1<sup>st</sup> quartile</i>	<i>3<sup>rd</sup> quartile</i>	<i>n</i>
FM	day	1.5	1.0	3.0	119
	night	1.0	1.0	1.5	83
FO	day	1.5	1.0	2.5	11949
	night	1.5	1.0	2.0	7077
BM	day	1.5	0.5	2.0	205
	night	1.5	1.0	2.0	136
PR	day	1.5	1.0	3.0	295
	night	1.5	1.0	3.5	335

The sampling interval, i.e. the resolution in time, of 30 sec used within this long-term study appeared to be insufficient to find patterns and differences for short events as the surface intervals, which mostly lasted less than 2 min (Tab. 7). No statistical analyses of the day / night patterns of surface times were therefore undertaken.

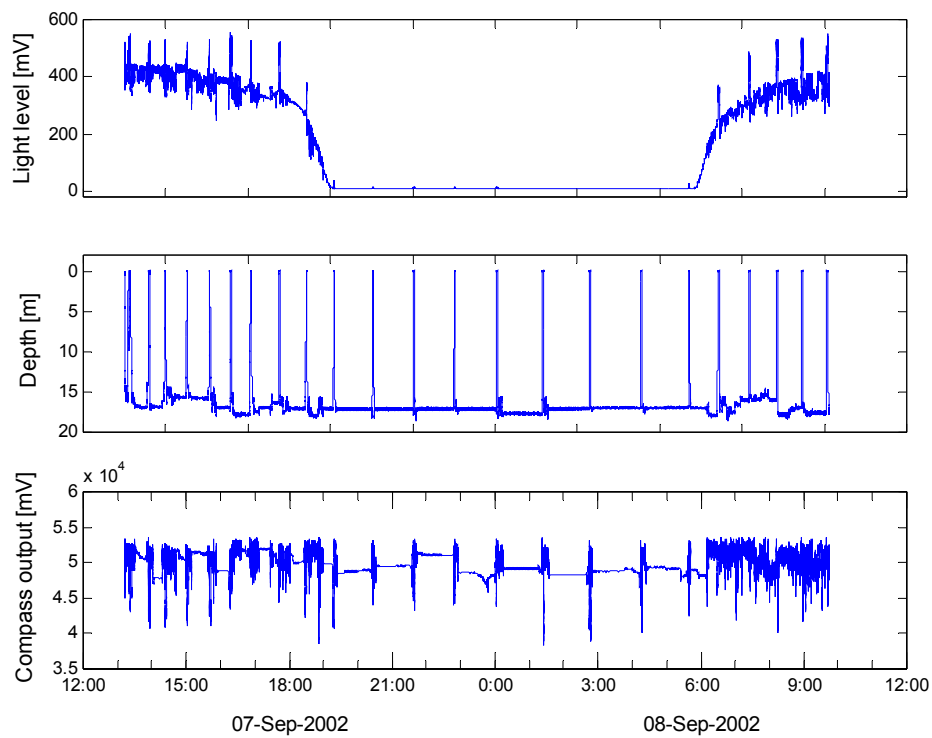
### 4.2.3.4 Dive Behaviour of Immature Hawksbill Turtles

The diving behaviour of five immature Hawksbill turtles was successfully recorded with high temporal resolution (2 Hz and 4 Hz sampling frequency) over 9 to 46 hrs (Tab. 8). A sample of obtained dive profiles with parallel data of light intensity and compass output is shown in Fig. 37, being representative for the findings in all five individuals. All immatures were observed to spend 97% of the time under water.

Low levels of the light sensor output indicate the period of darkness over night (Fig. 37, top). The depth profiles obtained at night were more regular in depth and duration than during the day (Fig. 37, middle). During the bottom phases of nocturnal dives the variation in the compass signal was minimal, while during ascent and descent, as well as during day-time bottom phases, the output of the compass showed substantial fluctuations (Fig. 37, bottom). The median dive durations from all immatures considered here were consistently and significantly longer at night than during day (Fig. 38 and Tab. 9), averaging 46 and 29 min, respectively. The pattern of inter-individual variation in dive durations was matched by respective variations in surface intervals (Fig. 39). However, the diel differences in surface intervals tended to be reversed compared to the dive durations (i.e. surfacing events were longer during day than at night), although not statistically significant in some cases (Tab. 9).

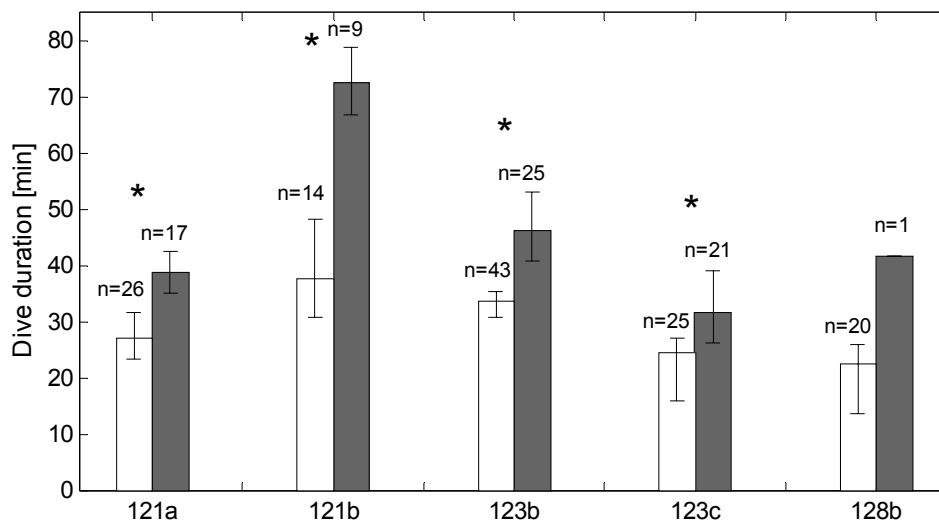
**Tab. 8:** Overview over files obtained from five immature Hawksbill Turtles off Mona Island using DK6002 data-loggers. File numbers are used for further reference in this and following chapters.

<i>File No.</i>	<i>Hours recorded</i>	<i>Sampling interval [Hz]</i>	<i>Body mass [kg]</i>
121a	24	2	10.8
121b	21	4	34.0
123b	46	2	8.6
123c	22	4	4.9
128b	9	2	12.5

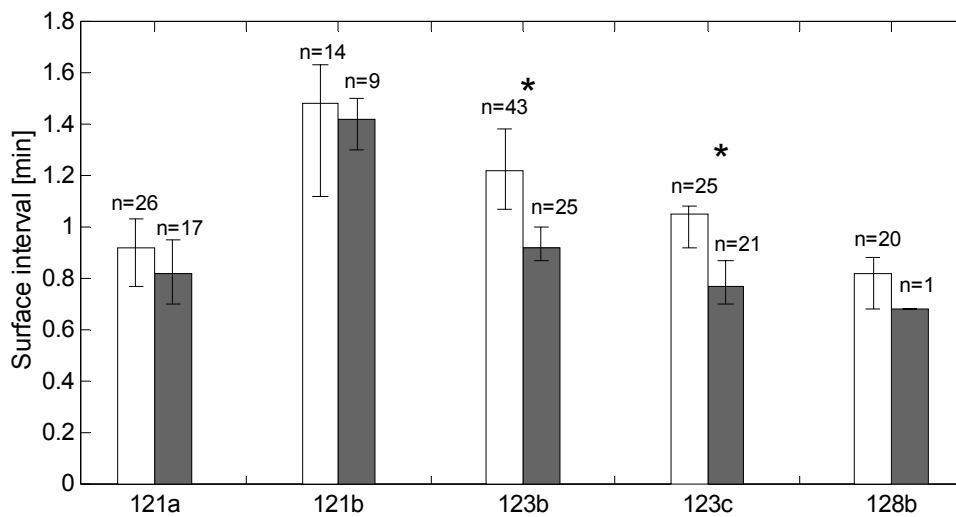


**Fig. 37:** Parallel data from light (top), depth (middle) and compass sensor (bottom) obtained from an immature Hawksbill Turtle off Mona Island (file no. 121b). Local time is given on the x-axis.





**Fig. 38:** Differences in dive duration between day (white columns) and night (grey columns) from five immature Hawksbill Turtles. The columns mark the median values, error-bars give first and third quartile. The sample sizes are given above each column. Mann-Whitney test (see Tab. 9) was conducted to test for significant differences, marked with an asterisk.

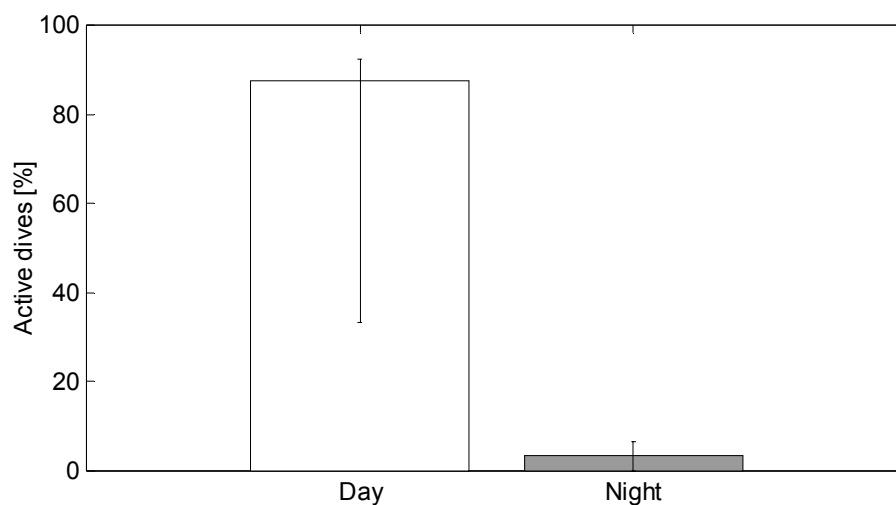


**Fig. 39:** Differences in surface interval between day (white columns) and night (grey columns) from five immature Hawksbill Turtles. The columns mark the median values, error-bars give first and third quartile. The sample sizes are given above each column. Mann-Whitney test (see Tab. 9) was conducted to test for significant differences, marked with an asterisk.

**Tab. 9:** Results of the Mann-Whitney test for differences in dive duration and surface interval of immature turtles between night and day (see Fig. 38 and Fig. 39).

		<i>121a</i>	<i>121b</i>	<i>123b</i>	<i>123c</i>	<i>128b</i>
Dive duration	U	424	123	995	430	no statement
		* p < 0.001	* p < 0.001	* p < 0.001	* p < 0.001	due to n = 1
Surface interval	U	259	65	997	443	no statement
		n.s.	n.s.	* p < 0.001	* p < 0.001	due to n = 1

In four of the turtles (except for 128b with only one nocturnal dive) the percentage of active dives was calculated, based on the definition given in section 4.2.2. The percentages of active dives during day (median 87.5%) and night (median 3.3%), plotted in Fig. 40, showed a very obvious significant diel difference (t-test,  $t = 4.9$ ,  $p < 0.01$ ).



**Fig. 40:** Percentage of active dives (see text for definition) of four immature Hawksbill Turtles during the daylight hours (white column, 06:00 to 17:59 local time) and during the night (grey column, 18:00 to 05:59 local time). The columns mark the median values from four individual turtles, the error-bars give the first and third quartile. The total number of dives considered is 178.

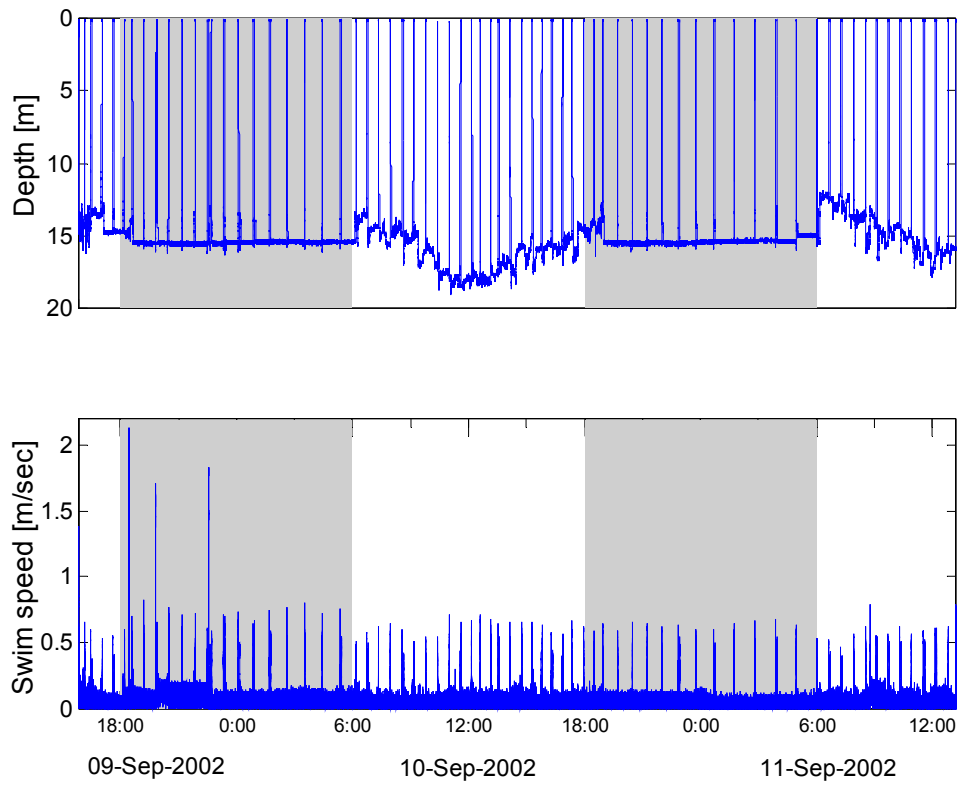
### Swim speed

Successful measurements of swim speed were achieved in three cases (files 123b, 123c and 128b). The data of all data sets revealed that the turtles accelerated during ascents as well as during descents (see Fig. 41 for an example). Speeds during bottom phases were lower than during transit, however, constant fluctuations in the output signal occurred even during nocturnal dives (Fig. 41).

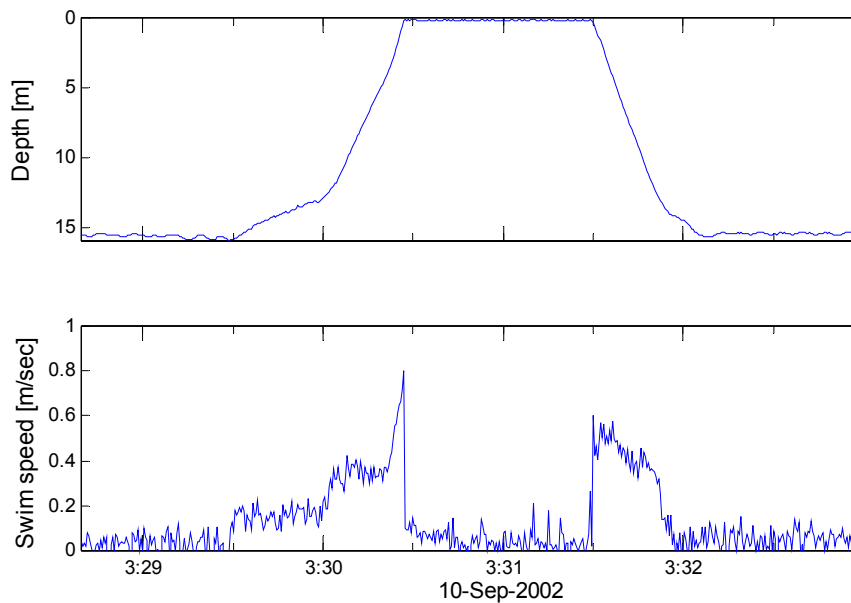
Mean speeds during the transit events were 0.1 m/sec (SD = 0.03, n = 2463), 0.2 m/sec (SD = 0.1, n = 12281) and 0.4 m/sec (SD = 0.1, n = 4735) for files 128b, 123c and 123b, respectively. Maximum observed velocities were 0.4 m/sec, 2.1 m/sec and 2.1 m/sec, respectively. These maximum speeds were reached only occasionally (see Fig. 41).

The typical, repeated sequence of increasing and decreasing swim speed during a single surfacing event is shown in Fig. 42. Here, after leaving the sea floor (at approx. 16 m) the turtle increased its swim speed gradually in several distinctive steps. A first slow phase of ascent at speeds around 0.16 m/sec led the turtle up to a depth of 13 m, where a higher level of velocity was reached (approx. 0.34 m/sec). At a depth of 3.8 m the last phase of ascent commenced when the speed constantly increased to its maximum of 0.8 m/sec immediately below the sea surface. After the surface pause with velocities close to zero the descent started at a speed of 0.52 m/sec. Between 4.8 m and 13 m the turtle continuously decreased the swimming speed down to 0.3 m/sec and then abruptly slowed down to below 0.2 m/sec just before reaching the sea floor again.

This pattern was found in the surfacing events of all three individuals. A random selection of 10 dives from each file showed that the mean depth at which the continuous acceleration of ascent started was between 2.2 and 5.4 m (Tab. 10). Inter-individual differences or similarities could not be correlated either to mean dive depth or to body mass (Tab. 10).



**Fig. 41:** Example (file 123b) of parallel data of dive depth (top) and swim speed (bottom). The time given on the x-axis is local time.



**Fig. 42:** Section of file 123b showing dive depth (top) and swim speed (bottom) during a surfacing event (see text). The time given on the x-axis is local time.

**Tab. 10:** Depth of acceleration during the ascent phase of 10 random surfacings from three immature Hawksbill Turtles.

	<i>Mean depth of acceleration [m]</i>	<i>SD</i>	<i>Range [m]</i>	<i>Mean dive depth [m]</i>	<i>Body mass [kg]</i>
123b	5.4	1.1	3.9 to 7.4	16.2	8.6
123c	2.2	0.7	1.4 to 3.5	16.5	4.9
128b	2.2	0.7	1.7 to 3.8	11.1	12.5

#### 4.2.4 Discussion

The following discussion will first deal with the 'normal' dive behaviour found in the studied groups of Hawksbill Turtles and this baseline will be used to differentiate exceptional behaviour. Temporal patterns in the dive performance are discussed before concluding with a first approach towards the interpretation of swim speeds with regard to energetic principles.

The data obtained from the depth gauge attached to female Hawksbill Turtles during the re-migration interval cover the longest recordings of diving behaviour in any sea turtle species to date. The previous longest studies were deployments of satellite transmitters, sending location information and, in some cases, summarised samples of dive data assigned to histograms. These studies were conducted on two Leatherback Turtles for one year (Eckert 1998), on three Hawksbill Turtles tracked (locations only) for 13.5 months (Mortimer & Balazs 2000) and on three Green Turtles in the Mediterranean for up to 293 days (Godley et al. 2002). Unlike all earlier studies, the 690 to 732 days of data presented here covered not only the period of the foraging migration and the stay at the feeding grounds, but also the return to the nesting site.

### 4.2.4.1 General Dive Behaviour

Following Kramer's (1988) definition a Hawksbill Turtle that spends an average of 95% of its time under water (this holds for all stages monitored in this study) may clearly be defined as a surfacer. Since feeding and resting both occur under water, the short surface pauses appeared to be almost exclusively dedicated to gas exchange between dives. This situation changes during the nights in the phase of nesting restlessness (see section 4.2.4.2), when the animals spend extended time at the surface for other reasons, i.e. nesting attempts and preparations.

In contrast to e.g. the Leatherback Turtles (see Márquez 1990 for review) Hawksbill Turtles are considered benthic feeders (Meylan 1988, Léon & Bjorndal 2002). As such, the dive performance of foraging Hawksbill Turtles depends largely on the bathymetry of the habitat, i.e. the bottom phases of the dives reflect the depth of the seafloor. The observed routine dives of adult Hawksbill Turtles in this study to depths of 20 to 30 m appeared to be deeper than in other benthically-feeding chelonids such as Loggerhead Turtles, Kemp's Ridley and Green Turtle (see Lutcavage & Lutz 1996 for review). This is likely to be related to the distribution of food, because seagrass, the prevailing food of Green Turtles and the likely preferable foraging grounds for crustacean-eating Loggerhead Turtles and

Kemp's Ridleys, are found in shallower water (up to 25 m, Humann 1992), the preferred prey of Hawksbill Turtles are sponges (Meylan 1988) that can grow at much greater depths (45 m for identified prey species, Humann 1992, >70 m for potential prey species, Meylan pers. comm.).

Resting sea turtles may float neutrally buoyant within the water column, as assumed for Loggerhead Turtles (Minamikawa et al. 1997, 2000), but inactive Hawksbill Turtles appear to be bottom-bound (Hillis and van Dam pers. comm., own observation). Therefore, as is the case in foraging dives, resting dives also indicate the depth of the seabed. The pattern found during the phase of stationary foraging of female QQD 280 indicates that the animal did not feed and rest in the same spot, but rather moved between two areas with depths of approx. 17 and 26 m, respectively (cf. section 4.2.3.3). The horizontal extent of the movements between sites cannot be evaluated, however, because reef structures can show large horizontal variability within a short distance or they can be rather flat (see e.g. the different bathymetries off Carabiniero and Sardinera at Mona Island, Fig. 4).

The longest dive durations and the longest surface intervals found in immature Hawksbill Turtle came from the largest animal considered during the field study at Mona Island. The size dependency of differences in dive behaviour of immature and adult Hawksbill Turtles will be analysed and discussed in section 4.6.

### 4.2.4.2 Exceptional Diving and Surfacing Behaviour

Within the study of inter-nesting behaviour of Hawksbill Turtles off Buck Island two females undertook exceptional deep dives (see section 4.2.3.2, Tab. 2). Consideration of the features of these dives shows that the turtles were definitely active and probably feeding at great depths. This behaviour appears exceptional for adult female Hawksbill Turtles during the inter-nesting interval off Buck Island since it has not been described in literature before. As these deep dives occurred late in the inter-nesting interval they did not

coincide with the observed increase of activity on days 7 and 8 after the previous nesting event which is discussed later (see section 4.2.4.4).

Two females of the re-migrational study were found to show surface oriented behaviour during both migrations to and from the foraging grounds. Since this behaviour only occurs during daylight hours it can be interpreted as basking, as previously described by Sapsford & van der Riet (1979). Furthermore, surface travelling during the day might allow the animals to orientate visually. The distinctive decrease in light intensity during some extremely long surface periods of the breeding migration (Fig. 34) implies mating behaviour, with the mounting male shading the light sensor of the device attached to the posterior marginal scutes. Such pairing events may last for hours (see Witzell 1983 and Miller 1996 for review). Mating has often been described as occurring in the vicinity of the nesting beaches (reviewed in Witzell 1983), however, evidence exist for off-shore coupling (Pitman 1992, Plotkin et al. 1996, Kopitsky 2000). The assumed mating events observed in this study occurred shortly before or after deep diving behaviour (up to 68 and 108 m) and therefore definitely took place away from shallow coastal waters. It can be speculated that the associated unusually deep dives perhaps represent behaviour by the females to avoid further mounting after a successful copulation. Also, the deep dives recorded during the foraging migration may be a reaction by non-receptive females to encounters with males. Actual mating seems unlikely to occur while the females travel towards the foraging grounds (cf. Ehrhart 1982), but since Hawksbill Turtles nest in the Caribbean all year-round, despite having a peak in July, August and September (Hillis 1995), males might still search for receptive females by the time when the observed individuals undertook their foraging migration. To date no data exist on the reproductive cycle of male Hawksbill Turtles.

No dive deeper than the maximum dive depth observed in the present study (108 m) has been published for Hawksbill Turtles, although Loggerheads Turtles (Sakamoto et al. 1990) and Pacific Ridleys (*Lepidochelys olivacea*) (see Lutcavage & Lutz 1996 and references therein) have been observed to reach depths exceeding 200 m. It is unlikely that animals rest at such depths and the reason for this diving behaviour remains speculative. Besides avoiding encounters with males an alternative explanation might be avoidance of



predators such as the Tiger Shark (*Galeocerdo cuvier*), the only shark species specialised in taking large cheloniid turtles (Witzell 1987).

The striking similarity of dive profiles during the migrations, equal in shape as well as in depth, indicates that these obviously pelagic submergences reflect an optimised travelling behaviour, presumably depending on fundamental physical parameters. The phase of gradual ascent is comparable to a gliding flight after gaining height (or depth, in this case), relying on the force of gravity (here: up-thrust) and using the shape of body and extremities to alter the angle of the fall (here: lift) (cf. Norberg 1990). The gain in both cases is spatial locomotion. The high efficiency of prolonged gliding periods during ascent has been previously described for aquatic mammals (e.g. Sato et al. 2003) and penguins were shown to use positive buoyancy for passive ascents (Sato et al. 2002). The relatively constant depth of 30 m for the onset of the glide in Hawksbill Turtles appears to be a key parameter necessitating further investigation.

### 4.2.4.3 Diel Patterns in Diving and Surfacing

Diel patterns in dive behaviour were found to occur during most of the life cycle, i.e. in the immature stage and the stationary foraging phase of the adult females. Both groups showed reduced dive durations during the day. Nocturnal dives were not only longer, but the bottom phases of the depth profiles showed only minor variance within, and often between, dives indicating stationary behaviour and probably even site fidelity. These dives are characterised through their U-shaped depth profile. Contrasting, active day-time dives can be interpreted as foraging dives where the dive depth depends on food distribution and may vary within and between dives, leading to W-shaped profiles.

The diel dimorphism in dive duration and profiles disappeared during the nesting season (Fig. 19, middle) and, finally, during the short last phase of the inter-nesting interval appeared to be reversed (Fig. 21). The nesting-restlessness of phase 3 was characterised by reduced dive duration but strikingly prolonged surface times at night (see also Fig. 19, bottom), which cannot be reasonably explained by an increased need for gas exchange but

rather by behaviour tending to lead the animal to land induced by the progress of gravity. Preparations for the time at shore may include visual orientation towards a known beach section as well as unsuccessful emergence attempts (due to physical obstacles or people visible at the beach).

The three turtles observed during the re-migration showed a broad variety of pattern in diel rhythms, from minimal depth change between day and night (QQD 048, Tab. 6), via regular and considerable depth changes (QQD 280, Tab. 6), to occasional, extreme variations in diurnal dive depth (QQD 132, Tab. 6 and overview Fig. 29, bottom). As the females were taking up residence at three different foraging grounds with unknown bathymetry these inter-individual differences are probably due to local structures of the sea floor, either providing foraging and resting sites at the same level or not. The characteristic pattern found in the depth profiles of QQD 132 while commuting between resting and foraging (Fig. 31) indicates the fidelity of the female to a limited home range.

#### 4.2.4.4 Patterns in Activity

From the clear diel difference in the dive durations of immature Hawksbill Turtles (Fig. 38) it would appear that the rate of oxygen depletion i.e. the energy expenditure during the routine dives was higher during the day than at night, this causing the shortened day-time submergences. In other words it is postulated that the animals performed a behavioural pattern of diurnal (feeding-)activity and nocturnal resting, with decreased rates of oxygen consumption during resting in the reef facilitating prolonged submergence at night. This is supported by a parallel dimorphism dive profiles, with flat-bottomed (U-) dives at night and structured (W-) dives with depth variations during the day. The same differentiation was used by van Dam & Diez (1996, 1997a), who concluded that immature Hawksbill Turtles off Mona Island actively feed for 11.4 hrs d<sup>-1</sup> during the daylight hours (Diez & van Dam 2002).

In contrast to previous investigations, the present study is the first direct to measure the underwater activity of free-ranging Hawksbill Turtles using a motion-sensitive compass. In the case of the immature Hawksbill Turtles off Mona Island conclusions about activity or resting, drawn from relative dive durations, could be confirmed by the compass signal and the identification of active dives based on the latter (Fig. 40). It therefore appears that the criterion of the shape of the dive profile is sufficiently suitable to distinguish between foraging and resting behaviour in immature Hawksbill Turtles off Mona Island. However, the good correlation between activity and depth fluctuations depends on the vertically structured habitat of the reef (van Dam & Diez 1997a) and, even more, of the cliff wall (van Dam & Diez 1996) that are frequented by the turtles in search of food. This bathymetry makes it either necessary, or at least most likely for an essentially benthic sea turtle to change depth when moving horizontally. However, since the horizontal movement itself cannot be assessed in the analysis of depth fluctuations, it is probable that this method is not suitable for sea turtles that either

- 1) feed on the spot, without moving from one prey item to another, or
- 2) feed in habitats lacking marked topography.

The first might have been the case in the observed inter-nesting female undertaking exceptionally deep dives off Buck Island (Fig. 26, left). Despite the strikingly flat bottom phases of the dive profiles these represented active periods, as proved by the compass signal.

The second possible cause for misinterpretation can be expected for Green Turtles grazing in a sea grass bed. Hochscheid (1998) used data-loggers with included compass on inter-nesting females and found that 40% of U-shaped dives were active, 46% were intermediate and only 14% were actually resting dives. The results may be even more extreme in non-nesting individuals. Therefore, the differentiation between active and resting dives merely based on depth data, as conducted in previous studies (e.g. Hays et al. 2000a, 2001b) is likely to be erroneous and the question of under-water activity of Green Turtles should, in future, be addressed through direct measures of activity e.g. by the use of compass units.

No such direct assessment of the activity was obtained in the re-migrating females observed in this study, as devices without a compass were used. However, Fig. 32 shows

that the two distinct groups of data-points (day and night data) do not share a single regression line but rather describe two different significant relations between dive duration and maximum depth of the dive. A general increase in dive duration with the dive depth has been described in warm-blooded aquatic animals (cf. Wilson et al. 1996) as a strategy to achieve optimal efficiency despite prolonged commuting time. In sea turtles, which have been shown to dive with inflated lungs (e.g. Lutz & Bentley 1985), the connection between depth and duration is enhanced by the need for neutral or negative buoyancy for an efficient benthic stay. For deeper dives a turtle can inspire more air before it submerges and it therefore has a larger oxygen store. If shallow dives are performed, the turtle takes less air and therefore less oxygen. The fact that the slope of the regressions in Fig. 32 are different implies that apart from dive depth there must be another parameter that separates day and night data. I hypothesise that the crucial factor is, again, the difference in metabolic rate, with active dives occurring during day and resting at night. An additional influence might be seen in the temperature differences between night and day of 0.1 to 0.4°C. The detailed effects of temperature on dive performance is discussed later in section 4.5.

No clear diel activity pattern could be found in inter-nesting females, either in dive duration or in the compass output (Fig. 28). Indeed, it could be shown that time of day was of secondary relevance for the level of activity of inter-nesting females. While not much diel variation of activity was found, a characteristic fluctuation of daily activity was found over the course of the inter-nesting interval (Fig. 27). This increase in activity around days 7 and 8 of the inter-nesting interval has not been previously directly addressed in literature. However, in a publication on inter-nesting movements of Loggerhead Turtles by Tucker et al. (1996) the swimming rate of the females was increased above the calculated trend during days 5 to 7. As the average inter-nesting interval of Loggerhead Turtles, ca. 14 days (Limpus & Reed 1985), is slightly shorter than in the Hawksbill Turtles observed here (15 days), the relative timing of the increased activity is strikingly similar. This narrow timing of the phenomenon led to the conclusion that it may be part of the cycle a nesting female undergoes between nestings. Simple feeding behaviour would not be expected to show this kind of timing, however, adult female Hawksbill Turtles have occasionally been observed biting pieces of coral and stomach lavage has revealed such ingested pieces in one case

(van Dam pers. comm.). It has been proposed that this material is ingested to support the development of egg-shells during the inter-nesting intervals. Miller (1985) found that the calcification of sea turtle eggs occurs at days 9 to 10 after the preceding nesting. Therefore, it can be speculated that the endocrine system of Hawksbill Turtles induces enhanced coral-biting activity around the 7<sup>th</sup> and 8<sup>th</sup> day of inter-nesting that aims at ingesting calcium and other minerals needed for the egg shells.

The present data showed that when evaluating the effect of anthropogenic disturbance (such as e.g. SCUBA diving and snorkeling) on reef dwelling Hawksbill Turtles, it is necessary to differentiate between immatures and foraging adults on the one hand and inter-nesting females on the other. Due to the distinctively different diel patterns of activity of these groups, daytime tourism may effect the foraging of immatures and non-nesting adults, while inter-nesting females might be disturbed in their resting behaviour.

### 4.2.4.5 Swim Speed

In the present study direct measurements of swim speed of Hawksbill Turtles were conducted for the first time. While initial trials, using the Prandtl-tube sensor during inter-nesting, mostly failed (see section 4.2.3.2), the enhanced method applied in the 2002 field season (miniature paddles and recording frequencies of 2 to 4 Hz) delivered the desired results, thus enabling the description of swim speeds during the ascent and descent phases. Apart from occasional peaks that were obviously related to flight behaviour (e.g. after release), the pattern of swim speeds was astonishing constant for all individuals, indicating a common physical background. The distinctive maximum after a steep increase at the end of each ascent can be ascribed to the positive (and continuously increasing) buoyancy that appeared to be the prevailing force determining the swim speed during the last meters of ascent. As under the condition of positive buoyancy it is most likely that an ascending turtle ceases active propelling, these finding can be seen as part of an energetic optimisation strategy, comparable to the downward gliding found in pinnipeds and cetaceans (Williams et al. 2000).

In the present study no parameter could be identified that influences the depth at which, implied through swim speed during ascents, positive buoyancy occurs. Further studies with larger sample sizes, more variation in dive depth and experiments of manipulating buoyancy (with weights or floats) are desirable to clarify the factors influencing the dynamics of ascent and descent as well as estimating the energetic significance.

### 4.3 REACTION TO HURRICANE GEORGES

#### 4.3.1 *Introduction*

The peak nesting season of Hawksbill Turtles at Buck Island lasts from July through September (Hillis 1995) and coincides with a period when the likelihood of hurricane occurrence is highest (August through October with the maximum in September, Deutsches Hydrographisches Institut 1967). Several studies deal with storm damage to sea turtle habitat and resulting indirect effects on nesting and hatching, as the effects of storms may hinder access to the beaches, expose eggs, inundate nests and block emerging hatchlings with debris (e.g. Hillis & Phillips 1998, Starbird & Hillis 1992, Milton et al. 1994, Hillis 1995). Given the substantial changes that occur in the environment during hurricanes it seems likely that the behaviour of turtles is altered at such times. To date, to my knowledge, a single sub-adult Green Turtle has been tracked via satellite transmitter while it encountered a hurricane, with no apparent effect from the hurricane on satellite positioning although detailed analyses are still pending (Meylan pers. comm.). In addition some satellite-tagged turtles were recently situated in affected areas when one of the latest hurricanes, Isabel (6 through 19 September 2003), passed through the coastal regions of the western North-Atlantic (Mansfield pers. comm., Meylan pers. comm.), thus possibly delivering more information for future analyses.

In this chapter I present the first and, to date, only detailed data on the behavioural reaction of a sea turtle to a hurricane.

Hurricanes in the Caribbean Sea, as on the whole northern hemisphere, revolve in a anti-clockwise direction. By the time they strike the chain of the Antilles they are usually travelling in a WNW-direction (Deutsches Hydrographisches Institut 1967), as did hurricane Georges (National Climatic Data Center 1999). Georges passed over Buck Island and St. Croix on 21 September 1998. In the morning hours the hurricane arrived with rainfall and wind gusts of 182 km/h (98 kts) from a NNW (338°) direction. After the eye had passed at noon, with a calm period of 30 min, the wind switched to SSW (190°) with maximum speeds of 150 km/h (81 kts). Hurricane Georges caused massive destruction and

numerous deaths in the Virgin Islands and Puerto Rico (National Climatic Data Center 1999).

The objective of this chapter is to determine the reactions of an adult female Hawksbill Turtle to the weather conditions of hurricane Georges. Changes in parameters of dive behaviour are described and discussed as well as aspects of terrestrial nesting behaviour after the storm.

I hypothesised that during the severe conditions of a hurricane sea turtles off Buck Island would use the near drop-off in the sea floor to find shelter at great depths from the wave action at and below the surface. Furthermore, previous experience from the Buck Island Sea Turtle Research Program (BUIS) hinted at a possible influence of hurricanes on the individually-preferred beach sections used for nesting activities (Hillis 1995, Hillis-Starr pers. comm.).

### 4.3.2 Results

#### 4.3.2.1 Data Obtained and General Effects of the Storm

Two female Hawksbill Turtles were equipped with data-loggers to monitor their dive behaviour during the inter-nesting interval when hurricane Georges struck the study area. The device attached to animal QQD 176 failed to record any data during the storm due to a malfunction (see section 4.2.3.1, Tab. 1). This malfunction in the electronics occurred after 13 September for unknown reasons and was not caused by the hurricane. Device number 20, deployed on QQD 148, however, delivered data from 12 through 27 September (see section 4.2.3.1, Tab. 1). All data were sampled at 15 sec intervals. The chronological data of light intensity, water temperature and dive depth are shown in Fig. 43 to give an overview over the complete inter-nesting interval. The time span of extreme winds (as experienced at site and described by Hillis-Starr) is shaded grey. A more detailed view of the course of events during the storm follows in section 4.3.2.2. The overview of the light data clearly documents the unusual condition of overcast skies, already apparent in the morning hours of 21 September and lasting the complete day. The light was back to normal levels on the following day (Fig. 43 top).

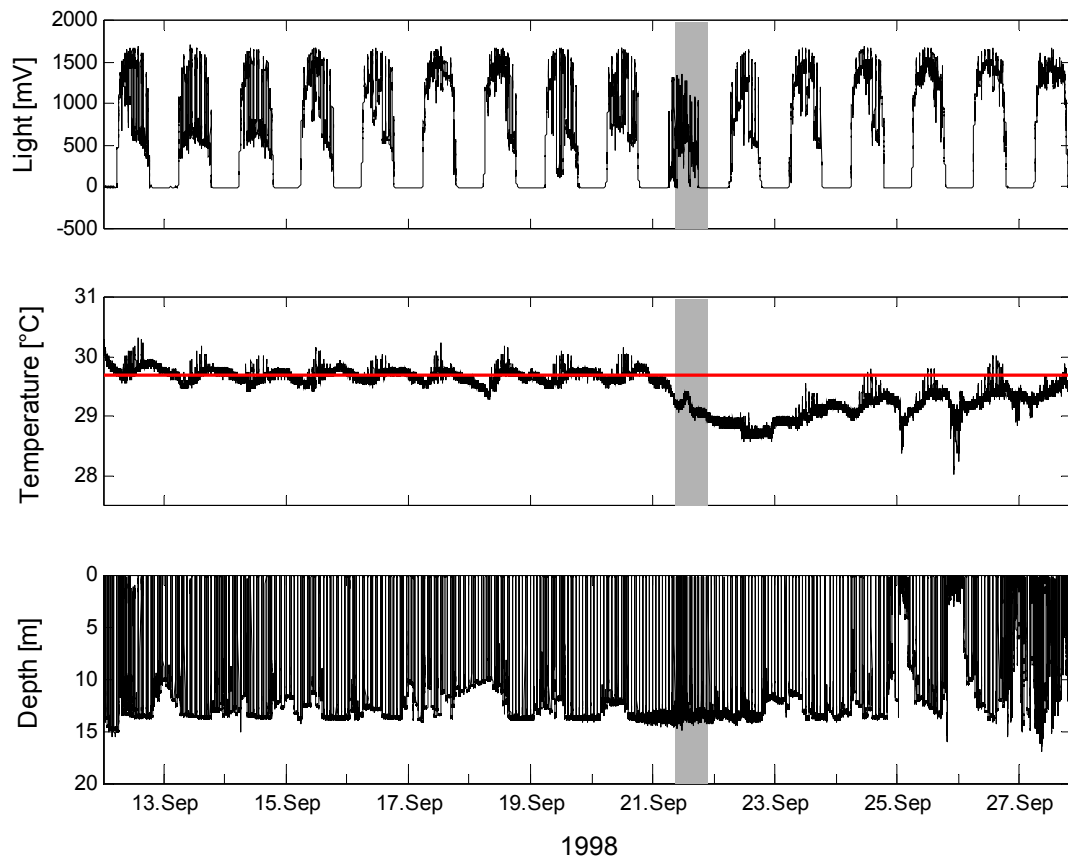


The amplitude of surface waves increased during the storm (see section 4.3.2.2, Fig. 46), the height of the waves being apparent as fluctuations in the dive depth data during periods of unchanged compass output, this latter indicating that the turtle was motionless at the time (see Fig. 46). Waves were increased by the storm from less than 0.5 m to ca. 1.5 m. The intensified wave action reached the study site ca. 12 hrs before extreme winds were observed (Fig. 46) and lasted through 22 September (Fig. 43).

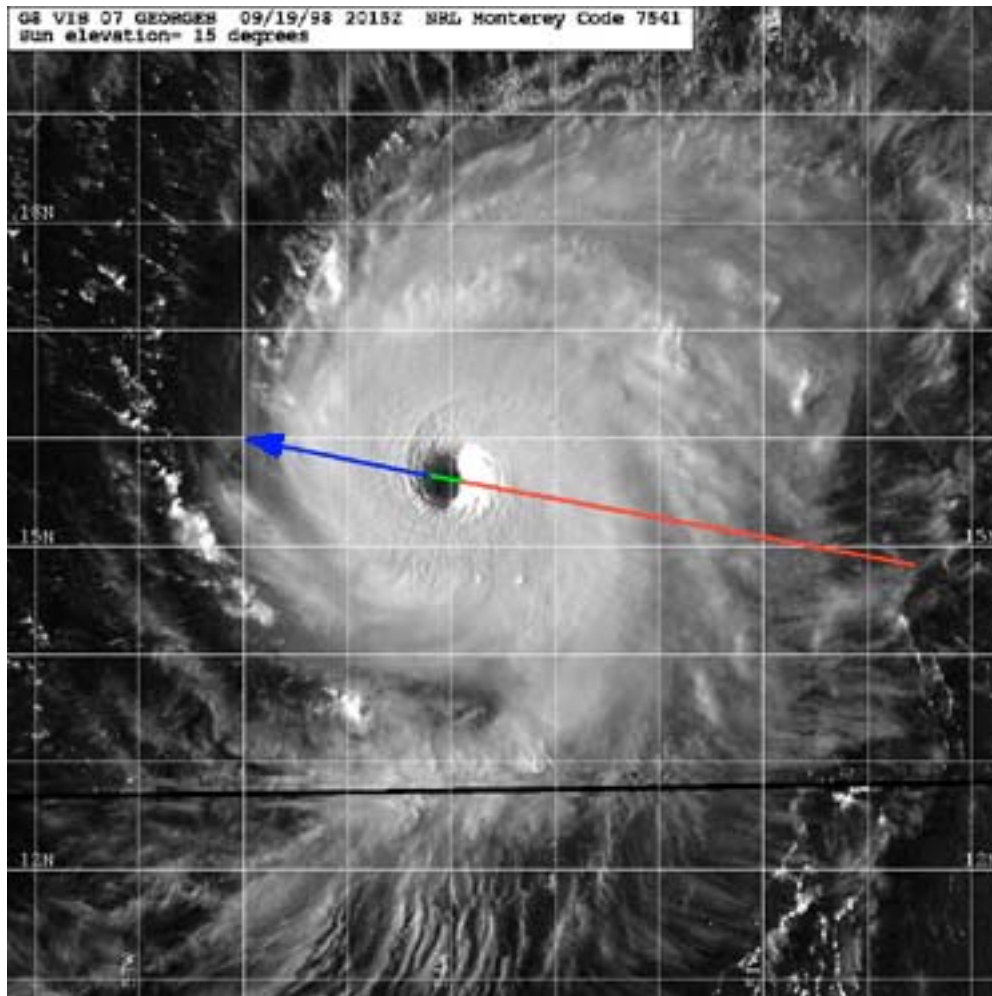
For comparison of pre- and post-hurricane water temperatures the mean temperature between 2:00 h on 12 September (after entering and adapting) and 18:00 h on 20 September (before any influence of the storm was recognisable) was calculated as 29.7°C. With increasing wave action the water temperature started to drop over the last few hours on 20 September, reaching the coldest measured temperature of 28.6°C on 22 September between 11:40 and 22:30 h local time (Fig. 43). The additional sharp decreases of temperature recorded in the dark hours of the early and late 25 September (Fig. 43) are derived from evaporative cooling due to the animal surfacing (note the according shallow depths) and are considered in section 4.3.2.2. The water temperature remained lowered throughout the rest of the inter-nesting interval, i.e. 6 days after the hurricane passed.

#### 4.3.2.2 In-Water Behaviour

As described above, the oceanic effects of the storm appeared to be rather long-term, while the period of extreme winds lasted ca. 12 hrs. In the next section the dives performed by the turtle will be described in relation to the phases of the storm as witnessed on site (Hillis-Starr pers. comm.). The phases are schematically marked in Fig. 44, showing the satellite image of hurricane Georges two days before it reached Buck Island. The phases of extreme winds started with northern winds between approx. 9:00 and 12:00 h local time on 21 September 1998, followed by the passage of the calm eye of the storm (12:00 to 12:30 h) and an extended phase of southern winds from 12:30 to approx. 21:00 h (Hillis-Starr pers. comm.).

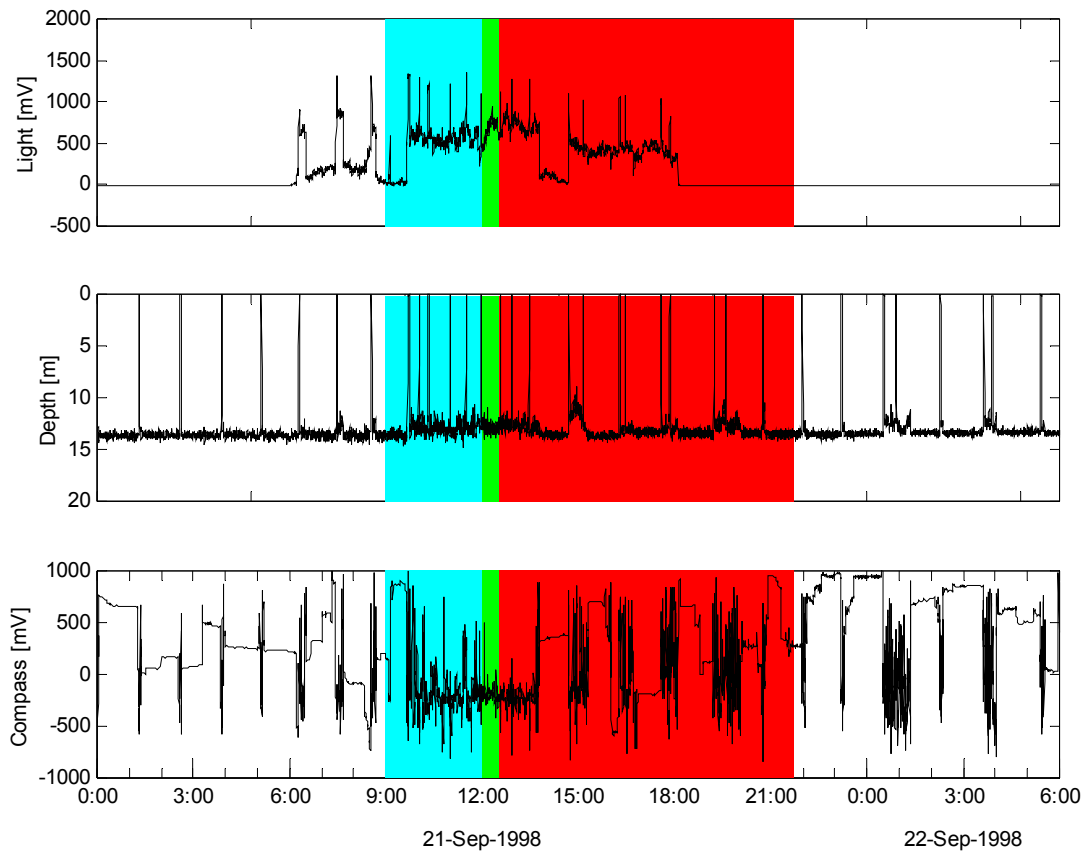


**Fig. 43:** Overview of parallel data of light (top), water temperature (middle) and dive depth (bottom) measurements obtained from QQD 148. The grey patches mark the time hurricane Georges passed over the study area (see text and Fig. 46 for details). The red line marks the mean temperature of 29.7°C calculated over all datapoints obtained before the storm (see text).

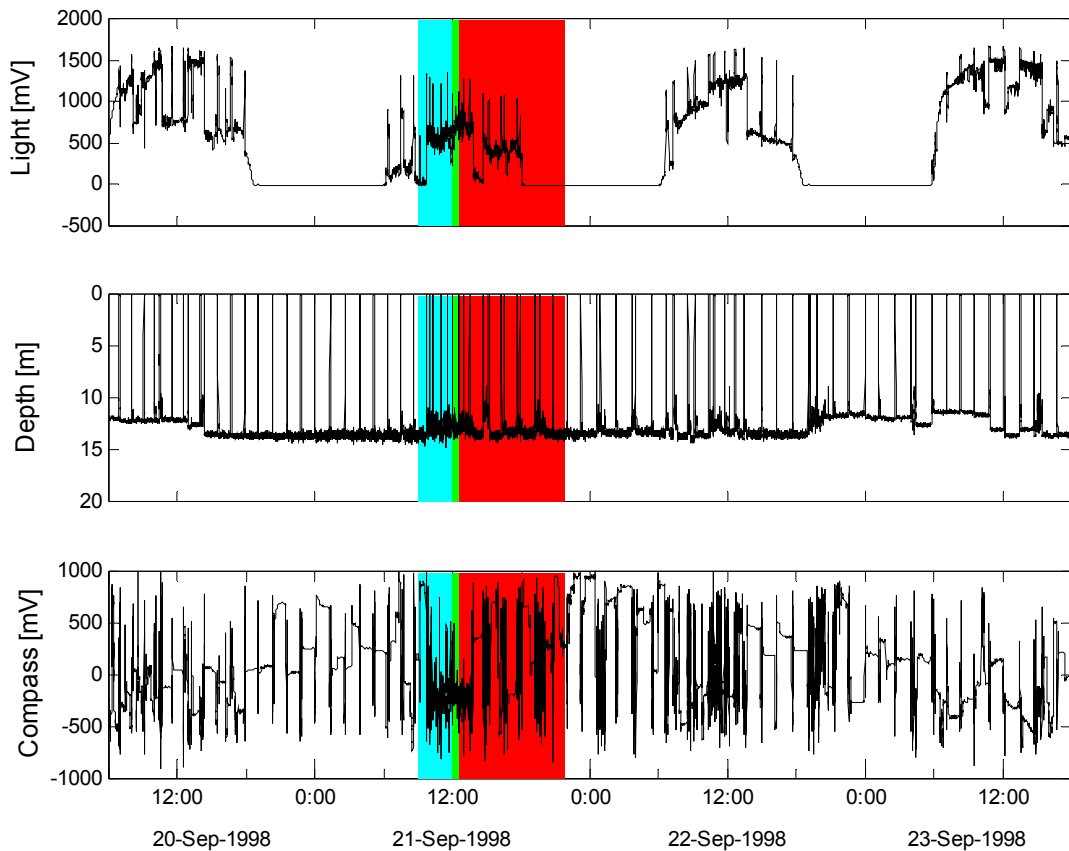


**Fig. 44:** Satellite image of hurricane Georges taken on 19 September 1989 (National Climatic Data Center 1999). The line indicates the direction of travel of the storm. The coloured sections of the line (fitted by eye and not to scale) represent the phases of extreme wind conditions with northern winds (blue), a calm eye (green) and an extended phase of southerly winds (red).

In the dives occurring during periods of high wind speeds the compass signal showed a high level of variability, indicating that the turtle was moving most of the time, even during the bottom phases of the dives (Fig. 45, middle and bottom). During the period of southern winds later in the course of the storm QQD 148 was motionless for some brief periods at a depth of 13.5 m (Fig. 45, red marked phase). The turtle did not show any particular reaction to the short phase of low winds at the eye of the storm (Fig. 45, green marked phase). Overall, the regularity of the dive performance was disturbed during the storm (Fig. 45) and only gradually returned to normal afterwards (Fig. 46).



**Fig. 45:** Chronological data of light intensity (top), depth (middle) and motion (bottom) recorded during hurricane Georges. The phases of the storm, as defined by wind conditions (see text), are coloured according to Fig. 44 as northern winds (blue), calm eye (green) and southern winds (red).



**Fig. 46:** Data recorded over a 4-day period including hurricane Georges (see Fig. 45 for description of axes and colour code). The increase in wave action, beginning in the afternoon before the hurricane passed the island, is visible as fluctuations in dive depths during bottom phases (see text section 4.3.2.1).

Comparison of the dive duration during the hurricane (21 September 9:00 to 21:00 h local time) to the dive duration of the previous day (20 September 9:00 to 21:00 h local time) revealed that the turtle performed significantly shorter dives during the severe storm than at the day before (Tab. 11). The mean dive duration was reduced by 27% from 57.3 min to 42 min, while the difference in the surface interval was even greater (Tab. 11) showing reduction by 50%.

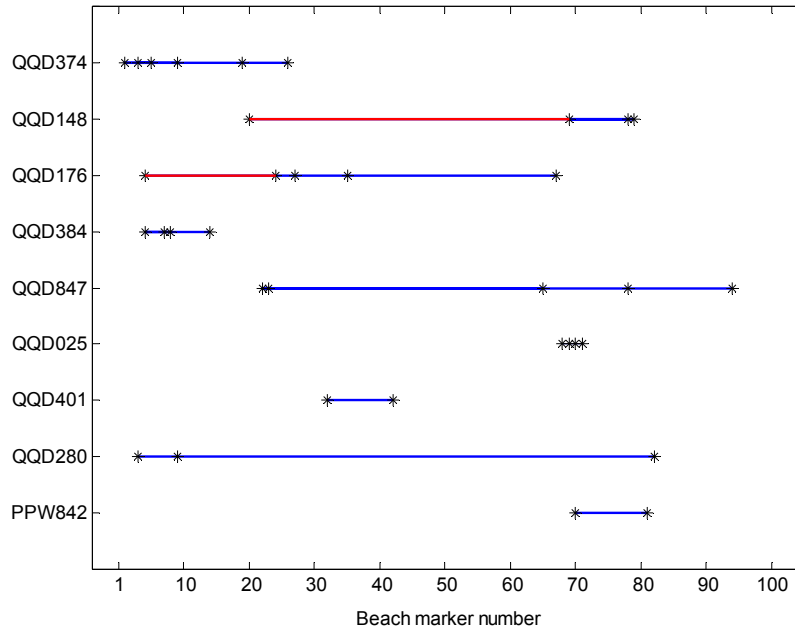
**Tab. 11:** Influence of hurricane Georges (21 September 1998) on dive duration and surface interval of QQD 148. Mean values obtained during the storm (09:00 to 21:00, see text) are compared to data from the previous day (20 September 1998, 09:00 to 21:00). Standard deviations are given in brackets. T-tests and Levene-tests were conducted to test for significant differences.

	<i>Day before hurricane</i>	<i>Hurricane Georges</i>	<i>Comparison of means</i>	<i>Similarity of variance</i>
Dive duration [min]	57.3 (± 20.0) n = 14	42.0 (± 24.6) n = 19	* different T = 1.9 p < 0.05	n.s. difference F = 0.15
Surface interval [min]	1.4 (± 0.2) n = 14	0.7 (± 0.2) n = 19	* different T = 10.4 p < 0.005	n.s. difference F = 2.92

The data from QQD 148 shown in Fig. 43 displays sequences of shallow dives paired with obvious drops in temperature in the last quarter of the inter-nesting interval. These parameters indicate approaches towards the beach with extended surfacing events and probable emerges over three successive nights before the actual nesting, with evaporative cooling causing the measurements of low temperatures.

#### 4.3.2.3 Terrestrial Parameters

Under normal conditions, terrestrial activities of the females (false-crawls as well as nests) occurred within a median distance of 104 m (n = 24, 1<sup>st</sup> quart. = 39, 3<sup>rd</sup> quart. = 150) from the previous observed activity (Tab. 12 and Tab. 13). These observations gave a median beach section of 143 m (n = 9, 1<sup>st</sup> quart. = 130, 3<sup>rd</sup> quart. = 559, Fig. 47) used by an individual within the observed part of the season. After hurricane Georges had passed over the island (21 September 1998) the total stretch of beach used by per individual over the nesting season increased from 130 m to 767 m and from 559 m to 819 m in females QQD 148 and QQD 176, respectively (Fig. 47). The mean distance of the post-hurricane nesting activities considered in this study was 513 m (n = 2) from the previously observed emergence.



**Fig. 47:** Stretch of beach used by individual females observed in this study. Crosses mark location of terrestrial activity, referring to the markers set up on the beach at distances of 13 m from each other (see section 3.3). The lines give the length of the beach section used within the concerning nesting season. The red parts of the lines show the increase of beach section used by QQD 148 and QQD 176 after hurricane Georges.

**Tab. 12:** Distances between the successive observed emergences of 3 female Hawksbill Turtles nesting at Buck Island in 1998. The distances between the terrestrial activities are estimated using the allocated beach markers (see description in section 2.1). Distances are calculated along coastline, not straightline between locations.

<i>Year</i>	<i>Tag Number</i>	<i>Marker Number</i>	<i>Distances between successive emergences [m]</i>	<i>Notes</i>
1998	QQD 374	9		
		1	104	
		5	52	
		3	26	
		19	208	
	QQD 148	26	91	
		78		
		69	117	
	QQD 176	79	130	
		20	767*	* <sup>)</sup> after Georges
		67		
		35	416	
		27	104	
24		39		
PPW842	4	260*	* <sup>)</sup> after Georges	

**Tab. 13:** Distances between the successive observed emergences of 6 female Hawksbill Turtles nesting at Buck Island in 1999. The distances between the terrestrial activities are estimated using the allocated beach markers (see description in section 2.1). Distances are calculated along coastline, not straightline between locations. enl = emerge no lay, i.e. unsuccessful nesting attempt.

<i>Year</i>	<i>Tag Number</i>	<i>Marker Number</i>	<i>Distances between successive emergences [m]</i>	<i>Notes</i>
1999	QQD 384	4		
		14	130	enl
		8	78	
	PPW 847	7	13	
		94		
		78	208	enl
		65	169	
		23	546	
	QQD 025	22	13	
		69		
		68	13	
		71	39	
	QQD 401	70	13	
		32		
		42	130	
	QQD 280	82		
		9	949	
		3	78	
PPW 842	70			
	81	143		



### 4.3.3 Discussion

#### 4.3.3.1 Terrestrial Parameters

Typically, sea turtles are known to show a high nest-site fidelity over a scale of kilometers (see review in Miller 1996), often even returning to the same section of the nesting beach within hundreds of meters of the previous emergence (Carr & Carr 1972, Bosc & Le Gall 1986, Johnson & Ehrhart 1994). The distances between emergences observed at Buck Island in previous studies, and in the present work, both under normal conditions and after a hurricane, have to be seen in relation to the limited length of coastline that is suitable for sea turtle nesting (1.3 km, see section 2.1). This means that only deviations smaller than 1.3 km can be recognised as nest site fidelity, as any greater deviation would result in nesting activities occurring at another island (St. Croix being the only option close by) and thus in a doubling (or tripling) of the interval between observed nestings of the individual in question at Buck Island. Over the years such irregular intervals have been observed in only a minor part of the registered nestings (Hillis-Starr per. comm.).

In this study the maximum distances between all emergences of the two turtles QQD 148 and QQD 176 appeared to increase after the hurricane. However, the total beach sections used by these two animals (767 and 819 m) are still within the range observed in the other seven females that were not influenced by a hurricane (39 to 1027 m). A loosened bond of female Hawksbill Turtles nesting at Buck Island to a certain beach section following a hurricane has been described by Starbird & Hillis (1992), attributing this phenomenon to the changes in beach topography. QQD 148 and QQD 176 both nested on the north shore section of Buck Island after hurricane Georges. A possible reason for a northward shift of nesting activities might be the rocks that are exposed and the steep, sandy embankment that builds up in the other parts of the beach after the storm.

After previous hurricanes in 1989 and 1995 a shift of nesting activities to the West Beach was reported, a section that usually exhibits only a small proportion of the nests laid at this island (Hillis & Phillips 1998). The analysis of track numbers found at the beach of Buck Island in post-hurricane seasons revealed an increase in the number of false-crawls in relation to the number of successful nestings (Hillis & Phillips 1998). Accordingly, the

data obtained from QQD 148 (Fig. 43) indicate several approaches prior to the successful nesting emergence, however, with the single inter-nesting interval reported here the data base on the side of the hurricane-struck turtles is too small for any definitive conclusions. Additional data-logger studies would be needed to determine whether individual turtles repeatedly attempt to emerge within their normal beach section before switching to other, unblocked stretches. Experiences on site have already shown that the beach clean-up activities conducted by the NPS and BUIS after a hurricane are important in helping emerging female Hawksbill Turtles (Starbird & Hillis 1992). Additional chronological hurricane-data at the individual animal level may help conservation efforts to be more efficiently focussed in this regard.

### 4.3.3.2 In-Water Behaviour

The phases of the hurricane as described in the introduction (Hillis-Starr pers. comm.) are based on the atmospheric appearance of the hurricane, i.e. the phases of winds, clouds and rainfall.

During the extreme winds the variability of the compass signal proved that the turtle either actively moved or was moved by wave action. The shortened dive duration during the hurricane can, in this context, be interpreted as an indication of increased metabolism resulting from active swimming behaviour.

The short events of motionlessness during the second half of the storm indicate that the animal was lying on the bottom, probably in the shelter of some rigid structure, at a depth of 13.5 m. This indicates that QQD 148 was still in the shallow area around Buck Island instead of moving over to the close drop off to take shelter at great depth, as previously hypothesised. It can be speculated that either the conditions of the southern winds allowed this motionless resting, contrasting the phase of northern winds with no such events, or the turtle adjusted its behaviour or position to the conditions of the hurricane after approx. 4 hrs of storm.

### 4.3.3.3 Water Temperature

It is desirable to exchange the terrestrial view of the hurricane, as it has been described above, for the necessary aquatic view for considering sea turtles at sea because the time span of oceanic effects of hurricanes is obviously different from the atmospheric. However, measurements of oceanic parameters were not a direct aim of this study and official local oceanographic data are not available. Nevertheless, an increased wave activity could be detected indirectly and the resolution of water temperature measurements was sufficient to prove an appreciable temperature drop.

Although the obvious atmospheric effects of the hurricane (i.e. extreme winds and unusual cloud cover with rainfall) were limited to a relatively short time range (approx. 12 to 24 h, respectively), the oceanic conditions (wave action and water temperature) remained disturbed much longer (several days). The reduced water temperature during the hurricane may have lowered the turtle's metabolism (cf. section 4.5) to a degree that allowed a substantial reduction in surface time despite the hypothesised increased activity (see section 4.3.3.2).

It can further be hypothesised that the decreased water temperature evokes a reduced rate of egg development, thus causing a longer inter-nesting interval. The observed hurricane-influenced inter-nesting interval lasted 16 days, which is longer than mean duration (15 d), but within the range that was observed under normal weather conditions (13 to 17 d). Previous studies (Hays et al. 2002a) revealed such an effect in Loggerhead (*Caretta caretta*) and Green Turtles (*Chelonia mydas*). The authors found the duration of the inter-nesting interval increased by one day in females at an ambient temperature of 27°C (12.3 d) in comparison to turtles experiencing a warmer environment (28°C, 11.1 d).

Conversely it has been reported that the duration of the inter-nesting interval of female Hawksbill Turtles increases with the number of unsuccessful nesting attempts, which again are more likely to occur after a hurricane (Hillis 1995). The observed duration of the inter-nesting intervals is most likely a result of both the developmental status of the eggs and the circumstances of a disturbed beach situation. In the present study it is not possible to separate these two elements in this regard.

While the average pre-hurricane temperature of 29.7°C was typical in representing the warmest water temperatures over the year (see Tab. 16, section 4.5.4.1), the minimum reached during the hurricane (28.6°C) is still well above the usual winter temperatures (25 to 26°C).

It can be concluded that the Hawksbill Turtle observed at sea seemed to be much less affected by the hurricane than expected. However, as the nesting habitat is usually devastated during a hurricane (Cantu 1997) the question remains as to why an ancient species still reproduces in a season that is likely to bring such extreme weather conditions. The answer probably lies in the strategy of the sea turtles to spread their reproductive effort over a long season (Eckert 1987), depositing several clutches at week-long intervals. It is most unlikely that all nests that a female produces in one season are destroyed by a hurricane, so there is still an obvious advantage for an ectothermic aquatic species to produce eggs during times of warmer seas.

The effect of a temporarily-lowered water temperature adds another, to date not considered parameter to be included when discussing the whole complex picture of influences of hurricanes on sea turtle populations (for a preliminary assessment see Agardy 1990).

### 4.4 EXTENT OF MIGRATORY BEHAVIOUR

#### 4.4.1 *Introduction*

Since the 1950s it has been stated in the literature that Hawksbill Turtles do not migrate between foraging and nesting sites, but that these 'virtually sessile' animals nest on the beach next to the reef where they feed and rest (Carr 1952, Bustard 1979). Despite a lack of data this thesis was repeatedly put forward and spread (e.g. Hendrickson 1980) before more recent studies were able to show the migratory character of this species (Parmenter 1983).

Evidence for migration stems from either tag returns or from satellite transmitters (PTTs) (see reviews in Meylan 1982 and Meylan & Donnelly 1999). The Hawksbill Turtles were either shown to nest at a site far from the tag site in the foraging grounds (e.g. Miller et al. 1998) or, more often, left the nesting area where they have been tagged and were recaptured at a distant feeding site (e.g. Carr & Stancyk 1975). These movements were all documented for only one direction, as tag retrievals at the foraging grounds usually involves the demise of the animal or, in the case of satellite tags, monitoring periods were too short due to problems including limited battery power, device loss or antenna damage. The latter often occurs as soon as the animal concludes its pelagic travel and shifts to a benthic habitat use (Schroeder & Balazs 2000, Hickerson 1999). Compared to modern high-tech approaches, the study of sea turtle dispersal through tag-returns, although providing the advantage of being a low-budget method, suffers from the recapture bias, as the likelihood of recapture is dependent on locally different fisheries effort (Cornelius & Robinson 1986).

In the present study data-storing devices were used for the first time to record the travel of three adult female Hawksbill Turtles after they finished their nesting season.

Having described the behaviour of the turtles between nesting seasons (section 4.2.3.3) the present chapter now aims to contribute to the description of the spatial dispersal of the Hawksbill Turtles in the Caribbean.

### 4.4.2 Specific Methodology

The distances of travel ( $D_{\text{travel}}$ ) given in this chapter, referring to own data as well as quoted findings, are minimum distances calculated as the shortest route between two points without crossing land. The actual distances swum by the turtles are thus likely to be greater. The same holds for the speeds of travel given in the present chapter, which are based on the minimum distances.

The travel speed ( $V_{\text{travel}}$ ) presented in this study was estimated as

$$(6) V_{\text{travel}} [\text{km/h}] = D_{\text{travel}} [\text{km}] / \text{MB} [\text{h}]$$

with  $D_{\text{travel}}$  calculated as defined above and MB representing the duration of distinctive migratory behaviour as described later in section 4.2.3.3. Because of the duty-cycle of the devices (two days operating and four days shut-down), MB was given with an uncertainty of several days, unless, by chance, the beginning and the end of MB fell within the operating phase.

As described earlier the accuracy of locations based upon the GLS methodology is not given as the radius of a circle, as in satellite tracking positioning, but, due to the latitudinal errors around the equinox, has greater errors in a north-south than east-west orientation. Accordingly, the latitudinal component of the turtles' locations were provided with a mean expected accuracy of 30 km, while the errors in positions during the calibration procedures were up to 243 km in latitude (see section 3.5).

### 4.4.3 Results

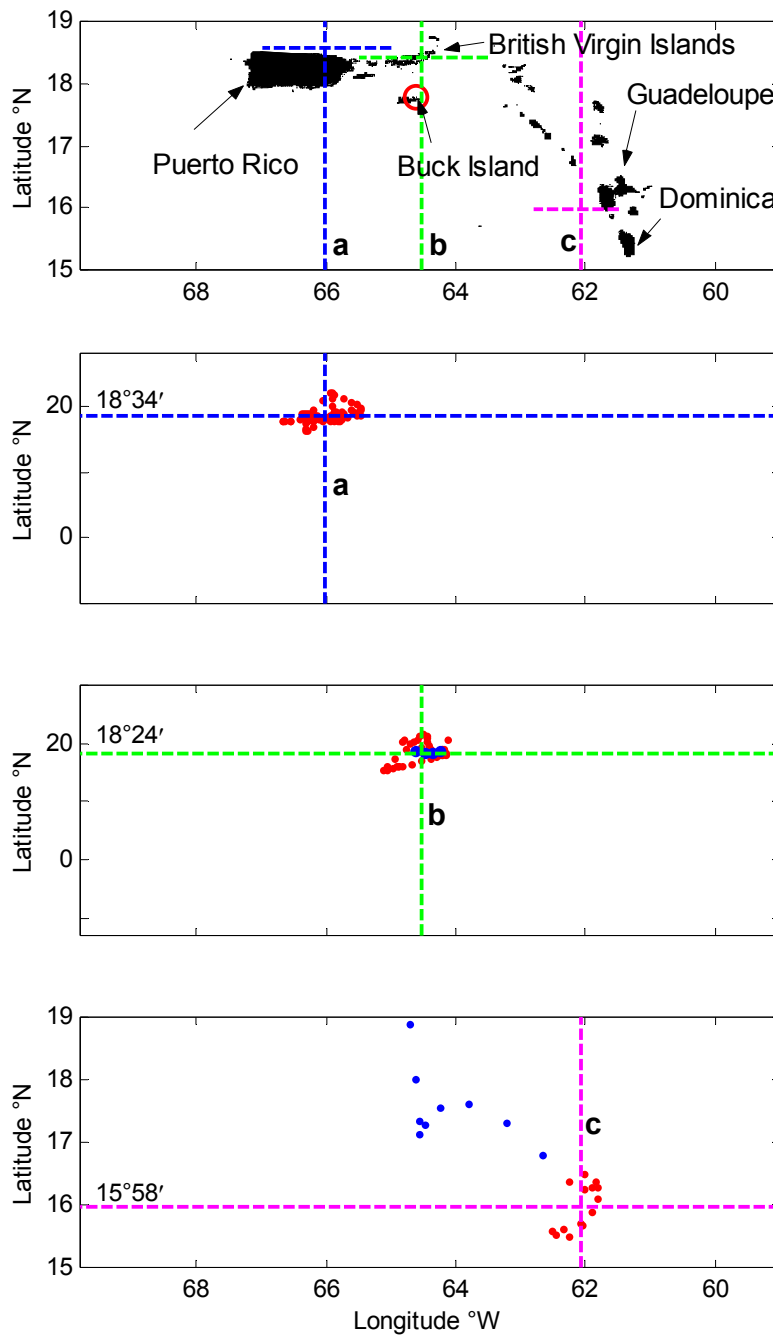
Malfunction of the light sensors ended the recording of light data in all three cases before the memory of the device was complete (see also section 4.2.3.3, *Breeding migration*). Successful recording of data suitable for GLS calculations lasted from 31 October 1999 to 4 February 2001 in turtle QQD 280, from 3 October 1999 to 29 July 2000 in turtle QQD

048 and from 3 September 1999 to 11 February 2000 in turtle QQD 132, resulting in 69, 45 and 23 locations, respectively.

##### 4.4.3.1 Directions of Travelling and Proposed Destinations

Fig. 48 shows the locations obtained from the three female Hawksbill Turtles during their re-migration interval. The GLS-analysis revealed that all 3 equipped females moved in different directions after leaving Buck Island. Locations of turtle QQD 280 were found to be north-west of Buck Island, while QQD 048 travelled north and QQD 132 moved south-east (Fig. 48, top). Based on the date when behavioural patterns changed (see section 4.2.3.3), the positional data were differentiated into foraging migration (Fig. 48 b-c, blue dots) and stationary foraging (Fig. 48 a-c, red dots). Since the long-term study began around the autumn-equinox, no locations could be calculated for the foraging migration of QQD 280 (Fig. 48 a), while 4 and 9 locations could be obtained from QQD 048 and QQD 132, respectively, before the arrival at the foraging grounds. The time at the foraging site was documented by 66, 41 and 14 data-points for QQD 280, QQD 048 and QQD 132, respectively, that were used to calculate the mean location of the foraging area. None of the sensors operated long enough to obtain data on the breeding migration.

The calculated destination was for QQD 280 approx. 13 km off-shore from La Torre, northern Puerto Rico, (18° 34'N, 66° 01'W), for QQD 048 within ca. 2 km of the coasts of the British Virgin Islands between Tortola and Salt Island (18° 24'N, 64° 32'W) and for QQD 132 about 25 km south-west off the coast of Guadeloupe, French Antilles, (15° 58'N, 62° 05'W).



**Fig. 48:** Map of islands within the chain of the Antilles from Puerto Rico to Dominica (top), showing the position of Buck Island (red circle). The mean GLS-locations of the three turtles QQD 280, QQD 048 and QQD 132 are projected into the top map as crosshairs (blue, green and magenta, respectively). The complete sets of locations are shown in lower graphs (a-c). Blue dots indicate locations during the foraging migration (graphs b and c only), red dots mark the positions during the foraging phase. Mean positions are calculated from foraging locations only.



## 4.4.3.2 Distances Covered and Speeds of Travel

The minimum distances covered by the three tracked females between two successive nesting seasons (1999 and 2001) were 340, 140 and 720 km, corresponding to distances of 170, 70 and 360 km between the nesting site at Buck Island and the various individual foraging grounds. These migrations are within the lower range of previously published movements documented for Hawksbill Turtles in the Caribbean (Tab. 14).

**Tab. 14:** Recorded migrations from this study (3 turtles) and previously published data from 12 adult Hawksbill Turtles in the Caribbean crossing international boundaries. Except for one male, the animals were all females that were equipped at the nesting beaches; therefore data refers to the foraging migrations, FM (cf. Tab. 15). Methods used were recovery of flipper tag ('tag'), deployment of satellite transmitters ('PTT') or data recorders ('logger').

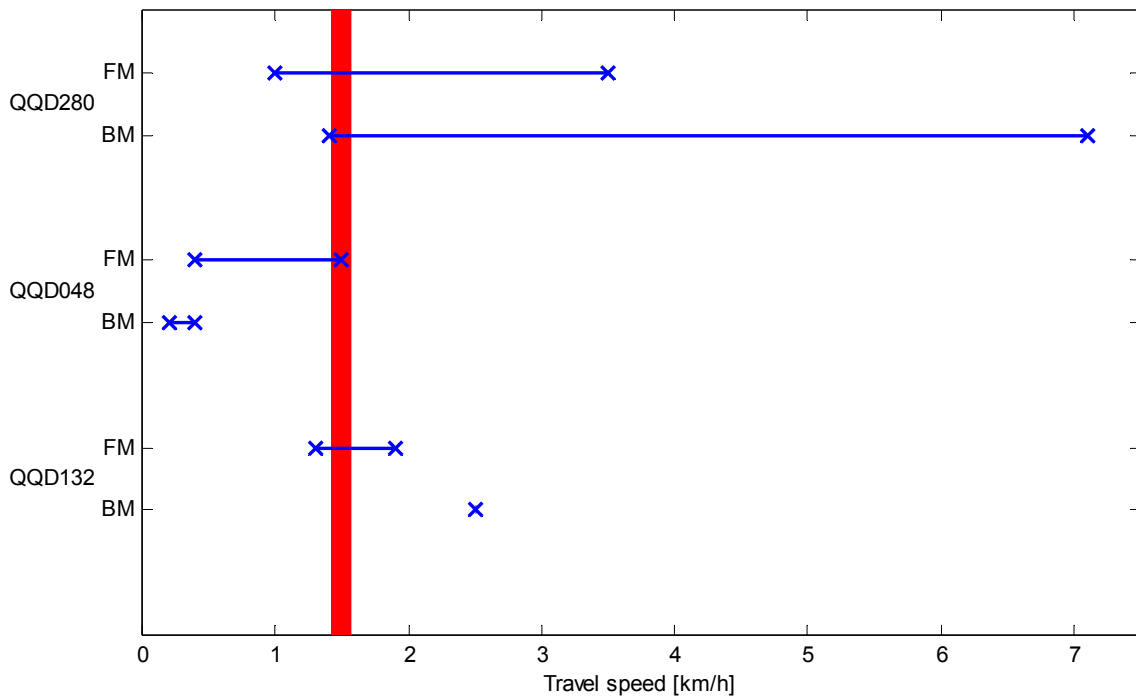
<i>Start and endpoint of migration</i>	<i>One-way distance [km]</i>	<i>Data obtained through</i>	<i>Foraging or breeding migration</i>	<i>Source</i>
Buck Island (U.S. VI) to Puerto Rico	170	logger	FM	this study
Buck Island (U.S. VI) to British Virgin Islands	70	logger	FM	this study
Buck Island (U.S. VI) to French Antilles	360	logger	FM	this study
Buck Island (U.S. VI) to Cuba	1400	tag	FM	Hillis-Starr et al. 2000
Buck Island (U.S. VI) to Nicaragua	2000	tag	FM	Hillis-Starr et al. 2000
Buck Island (U.S. VI) to British Virgin Islands	90	PTT	FM	Hillis-Starr et al. 2000
Buck I. (U.S. VI) to Puerto Rico via St. Thomas (U.S.VI)	170	PTT	FM	Hillis-Starr et al. 2000
Buck Island (U.S. VI) to Nicaragua	1996	tag	FM	Hillis 1994
Costa Rica to Nicaragua	385 (3 turtles)	tag	FM	Carr & Stancyk 1975
Costa Rica to Nicaragua	463	tag	FM	Carr & Stancyk 1975
Nicaragua to Jamaica	650	tag	(male)	Nietschmann 1981
Costa Rica to Nicaragua	459	tag	FM	Carr et al. 1966
Costa Rica to Nicaragua	523	tag	FM	Carr 1966

After the nesting season QQD 280 covered a distance of approx. 170 km to Puerto Rico within 2 to 7 days (the broad range of this and the following estimates is due to the duty-cycle of the devices; see section 3.2). The average travelling speed was therefore between 1.0 and 3.5 km/h. Returning to Buck Island the duration of migration behaviour lasted 1 to 5 days, leading to speed estimates between 1.4 and 7.1 km/h.

QQD 048 apparently travelled towards the British Virgin Islands 70 km north of Buck Island. The period of travelling behaviour could be restricted to a duration of 2 to 8 days, resulting in speeds between 0.4 and 1.5 km/h. During the breeding migration the animal covered the same distance within 8 to 16 days at an estimated speed of 0.2 to 0.4 km/h.

The third female, QQD 132, travelled approximately 360 km along the chain of the Lesser Antilles within 8 to 12 days at 1.25 to 1.9 km/h. Returning to Buck Island in 2001 it swam the distance in 6 days at an approximate speed of 2.5 km/h. The latter estimate for travel duration is more robust than the former ones because the shifts in behaviour occurred while the device was recording instead of taking place during the off-period of the duty-cycle. The most likely travel speed (marked with the red bar in Fig. 49), concluded from the point of maximum numbers of overlapping ranges from the 6 estimates, was 1.5 km/h.

Long-term hydrographic data revealed that the prevailing current in the waters enclosed by the Lesser Antilles flows a WNW direction at a speed of approx.  $\frac{3}{4}$  nm/h or 1.4 km/h (Deutsches Hydrographisches Institut 1967). QQD 280 and QQD 048, both travelling within the shelter of islands, showed no systematic difference in speed of travel between the foraging and the breeding migrations (Fig. 49) that could be correlated with this current. However, the only turtle that migrated substantially through open water, QQD 132, obviously travelled at a lower speed when heading against the current towards Guadeloupe compared to the reverse course of the breeding migration.



**Fig. 49:** Travel speeds over ground from three female Hawksbill Turtles during foraging migration (FM) and breeding migration (BM). Ranges of possible speeds are shown, based on ranges of the durations of the migration (see text). The red bar indicates the most likely typical travelling speed of a Hawksbill Turtle (approx. 1.5 km/h) concluded from the overlaps of the ranges.

#### 4.4.4 Discussion

##### 4.4.4.1 Travel Speeds

Hillis-Starr et al. (2000) found travel speeds of 1.2, 2.2 and 2.5 km/h deriving from minimum distances between satellite locations from three female Hawksbill Turtles, equipped while nesting at Buck Island. Previously, a tag return from the Philippines revealed a Hawksbill Turtle to have travelled at a minimum speed of 0.7 km/h (De Silva 1982).

Meylan (1982) summarised data on the travelling speeds of Loggerhead Turtles (*Caretta caretta*) with a mean of 1.4 km/h (min 1.0, max 1.7, n = 6), Green Turtles (*Chelonia mydas*) with a mean of 1.6 km/h (min 0.9, max. 2.8, n = 12), Kemp's Ridleys (*Lepidochelys kempi*) with a mean of 1.1 km/h (min 1.0, max 1.2, n = 2) and Olive Ridleys (*Lepidochelys olivacea*) with a mean of 1.9 km/h (min 1.2, max 3.4, n = 5), all data derived from tag returns.

The mean speed of travel of five post-nesting Green Turtles equipped with satellite transmitters while nesting at Ascension Island was 2.6 km/h (max 2.7, min 2.1, n = 5) (Hays et al. 1999).

The travel speeds of Hawksbill Turtles and other species of sea turtles based upon tag returns are more likely to under-estimate speeds than the data from satellite transmitters, as the exact time of arrival at the point of capture is unknown. Both methods under-estimate real speeds by assuming straightline distances travelled between two points. Again, the satellite studies have a slight advantage in usually providing several way-points along the route. It may be concluded that it is systematic for more recent estimates of speeds of travel, using modern satellite technology, to result in more rapid migratory speeds than the early reports resulting from tag returns, possibly sometimes observing sprinting rather than average swimming behaviour (Wynecken 1996). However, many studies do not take the sometimes large inaccuracies in satellite locations into account, although their implications on speed estimates are recognised (Hays et al. 2001a).

In this study the speeds of travel for each tracked migration are given as wide ranges of estimates, these being caused by the uncertainty in the duration of the migration (Fig. 49). The most likely typical travelling speed of Hawksbill Turtles is given by the point of most overlaps, occurring at 1.5 km/h (Fig. 49). The concept for a general value for a species is, however, questionable, as sea turtles have considerably inter-individual variation (Hays et al. 1999, this study). It is therefore quite probable that the calculated travelling speed of QQD132 during its breeding migration (2.5 km/h, Fig. 49) is realistic despite its rather large difference to the typical value of 1.5 km/h. Both values are well within the range of previously published data from Green and Loggerhead Turtle as well as Kemp's and Olive Ridley.

The data obtained from QQD 132 appear to reveal the effect of the current on the travelling speed, since travel speed increased from ca. 1.5 km/h (against the current) to 2.5 km/h (with the current at 1.4 km/h velocity).

##### 4.4.4.2 Spatial Dispersal of Observed Animals

This study gave estimates of the destinations of three adult female Hawksbill Turtles that migrated from their nesting site at Buck Island to their individual foraging grounds. The time span over which the calculation of locations based on light-level data was possible ranged from 161 via 299 to 462 days, the latter two representing the longest spatial tracking periods for any species of sea turtle. Longer sets of data have only been achieved from the depth sensors of the same units that, unlike the light sensors, continued functioning until the memory of the units was complete or the device retrieved (see section 4.2.3.3).

The data on the destination of the three females has to be interpreted carefully as large errors are inherent in GLS methodology (Hill 1994). However, the accuracy of the single positions obtained from the three females is good enough to summarise that all turtles travelled in different directions, as data-points did not overlap (Fig. 48). In contrast, the calculated distances from shore might involve a high inaccuracy, especially in turtles QQD 280 and QQD 048, where this measure is oriented in north-south direction and therefore being subject of errors of up to ca. 200 km. However, as these errors are not systematically biased into one direction the calculated means may be a quite accurate estimation of the actual position. An indication for the plausibility of the presented data is the fact that Condado, one of three specifically identified reefs at the northern shore of Puerto Rico, is located at 18° 28'N, 66° 04'W (UNEP/IUCN 1988), that is within approx. 11 km (north-south direction) and 6 km (east-west direction) of the calculated mean foraging site of QQD 280.

Direction and extension of migration seems to be very individual. This findings support previous evidence from tag recoveries from Hawksbill Turtles nesting at Buck Island

(Hillis 1994, Hillis-Starr et al. 2000) as listed in Tab. 14, and, at the same time, add a new south-easterly component to the pattern of dispersed migration.

The previously published international migrations recorded for Hawksbill Turtles in the South Pacific ranged from 713 to 2425 km (Tab. 15). No published data on migrations from other regions than the Caribbean or the South Pacific are available.

**Tab. 15:** Published data on migrations of 7 adult Hawksbill Turtles in the South Pacific crossing international boundaries; obtained through tag returns ('tag'). Data are divided into movements from the breeding to the foraging ground (foraging migration FM) and vice versa (breeding migration BM).

<i>Start and endpoint of migration</i>	<i>One-way distance [km]</i>	<i>Data obtained through</i>	<i>Foraging or breeding migration</i>	<i>Source</i>
Princess Charlotte Bay, Australia, to Vanuatu	2425	tag	BM	Miller et al. 1998
Princess Charlotte Bay, Australia, to Solomon Islands	2369	tag	BM	Miller et al. 1998
Green I. Reef, Australia, to Papua New Guinea	1530	tag	BM	Miller et al. 1998
Milman I., Australia, to Merauke, Indonesia	368	tag	FM	Miller et al. 1998
Torres Strait, Australia, to Solomon Islands	1650	tag	BM	Parmenter 1983
Sabah to Culasi, Philippines	713	tag	FM	De Silva 1982
Solomon Islands to Papua New Guinea	1400	tag	FM	Vaughan & Spring 1980

Based on the data from this study and the previous findings listed in Tab. 14 and Tab. 15 it can be concluded that at least some Hawksbill Turtles conduct long-distance migrations. Particularly the females nesting at Buck Island generally crossed international boundaries, this being partially due to the great extent of the movements but also because of the small size of political territories in the area.

While evidence was found that the travelling speed of migrating Hawksbill Turtles is influenced by currents (see section 4.4.3.2), no general conclusion can be drawn about the

preferred heading of the nesting females from Buck Island. As the direction of the prevailing currents of the North-Eastern Caribbean vary only to a minor degree (between WSW and WNW) throughout the year (Deutsches Hydrographisches Institut 1967), this region does not offer any opportunity of avoiding counter-current by choosing certain directions and times. Data from tag returns from Buck Island's nesting population (Tab. 14) imply a preferred heading towards foraging grounds in the west of Buck Island. However, this is likely to be due to the bias of the methodology where most data come from areas of high fishing effort (such as the mainland coast of Central America). This bias disappears in the information gleaned from satellite transmitters, which fits the pattern of dispersal that is shown in the present study. In summary, the current seems to have influenced the travelling speed of the individual that travelled through open water, as was the case in Green Turtles (Hays et al. 1999), but inter-individual differences in direction of travel imply that there is no common strategy in using prevailing currents. For any further interpretation of the dispersal pattern a higher sample size of unbiased PTT or logger data is urgently needed.

##### 4.4.4.3 Ecology and Conservation of a Migratory Species

The total number of Hawksbill Turtles that has been tagged at the major nesting sites in the Caribbean region over the last 40 years, an estimated 2500 individuals (Meylan 1999), is small compared to other species, when e.g. several thousand Green Turtles can be tagged at just one nesting beach of Tortuguero, Costa Rica, in a single year (Carr et al. 1978). Meylan (1999) reviewed 19 tag returns and calculated that 2% of the turtles tagged at Buck Island were recaptured in neighbouring countries, while the percentage was somewhat lower for Jumby Bay (Antigua) at 1.6% and higher (3.5%) for Tortuguero, Costa Rica. As these percentages are within the range, although at the lower end, that is found in the highly migratory Green Turtles (1%, Solé 1994 to 8.9%, Meylan 1982), Meylan (1999) concluded that the assumption that Hawksbill Turtles are sedentary is incorrect.

Because of the migratory nature of the Hawksbill Turtles and because females from different nesting sites gather at a given foraging ground (cf. Bowen 1982), the local impacts of fisheries, oil spills etc. on Hawksbill feeding habitats have far-reaching

consequences for populations from different regions (Bowen et al. 1996). Conversely, the threat to a specific nesting population due to females being killed at the foraging ground is diluted because other females migrate to different areas during their non-nesting seasons. However, the high nest site fidelity and the spatial-temporal aggregation of large numbers of Hawksbill Turtles make the breeding populations very vulnerable to disasters at the nesting grounds, which furthermore are often used as foraging grounds for other, non-nesting females, males and immatures, as in the case of Mona Island (van Dam pers. comm., own observation).

The migratory nature of the Hawksbill Turtle complicates the management of this endangered species. The risk of a mature female falling prey to fisheries activities during its migration or at the foraging ground is serious, as reflected by the fact that tagging appears to be an effective low-budget method for obtaining data on the extent and direction of movements. The recovery of tags of females away from the nesting sites results from the capture (and death) of the turtle in the vast majority of the cases (see literature cited in Tab. 14).

The well-known example of European migrating songbirds (e.g. Spina 1986, McCulloch et al. 1992) that are protected in Northern Europe while being hunted and consumed on their migration through Middle and Southern Europe, shows that conservation of internationally migrating species is a difficult issue. This is the case especially when traditions of different cultures are involved, in e.g. some Indian tribes which harvest sea turtles (e.g. the Miskito Indians in Nicaragua), or when commercial aspects lure developing countries (e.g. Cuba) to lobby for the opening of the tortoiseshell-trade. Further documentation of the migratory behaviour of these animals is needed as a base for the management of the Hawksbill Turtles in the Caribbean, where they face the jurisdiction of several countries on their journeys between nesting and foraging sites. It is therefore necessary to conduct further studies to elucidate migratory routes and destinations of Hawksbill Turtles using modern technologies such as transmitters or data-loggers because only these methods deliver data independent from the destination or direction the animal takes by avoiding the bias connected to tag returns (see section 4.4.1).



### 4.5 TEMPERATURE DEPENDENT DIVE BEHAVIOUR

#### 4.5.1 Introduction

Study of the diving behaviour of air-breathing aquatic animals allows insight into the physiological status of the individual. In animals that are highly aquatic and constantly diving aspects of the behaviour, such as the duration of dives, are most likely to be optimised and reveal the physiological limits of the animal. Sea turtles are excellent subjects for such studies because, unlike some species of freshwater turtles (e.g. Girgis 1961, Priest & Franklin 2002), adult sea turtles rely entirely on gas exchange at the water surface. In contrast to most diving endotherms, sea turtles have a time budget that is constantly and extremely biased towards time spent submerged with typically as little as 3 to 6% of their time being spent at the surface of the water (e.g. Lutz & Bentley 1985, own data). Compared to many reptile species, these animals are large and very active (Jackson & Prange 1979, Lutz & Bentley 1985). The extreme body size of the Leatherback Turtle (*Dermochelys coriacea*) and its previously-studied gigantothermy (Davenport 1998, Paladino et al. 1990) make it desirable to differentiate between the families *Dermochelidae* and the smaller *Cheloniidae*. But even species of the latter family are capable of maintaining body temperatures above ambient temperature during activity when the huge pectoralis muscles show temperatures of 7°C above water temperature (Heath & McGinnis 1980, Standora et al. 1982, Spotila & Standora 1985, Sato et al. 1994). Animals the size of sea turtles have high internal heat storage capacities and therefore large thermal inertia. In addition, the Green Turtle (*Chelonia mydas*) is capable of controlling heat exchange with the environment through variable blood circulation in the front flippers (Hochscheid et al. 2002). Although such studies have not been conducted on Hawksbill Turtles to date, it is probable that this species adheres to similar patterns, despite smaller size.

By virtue of their limited contribution to energy expenditure in movement, resting sea turtles can be particularly expected to show clear physiological reactions to different temperatures; to date changes exhibited in blood gas and pH (e.g. Lutz et al. 1989), duration of gastric and intestinal digestion, intestinal glucose transport, frequency of

gastric contractions, likely digestive efficiency (Skoczylas 1978), activity (Moon et al. 1997), duration of inter-nesting intervals (Sato et al. 1998, Hays et al. 2002a) and metabolic rate (Lutz et al. 1989) have been shown. In this context the temperature quotient  $Q_{10}$  is important in describing the response of metabolism to temperature (Rao & Bullock 1954).

Other reactions of reptiles to temperature, such as thermal dependence of sensory functions (Adrian et al. 1938, Patterson et al. 1968), neural function (Andry et al. 1971) and even learning (Krekorian et al. 1968), might also occur in sea turtles.

In this chapter I examine the hypothesis that the dive behaviour of female Hawksbill Turtles in the Caribbean Sea varies over the year, following seasonal temperature fluctuations. This thermal dependence is studied over the two year re-migration interval of turtles nesting at Buck Island. Times of nesting activity and migratory behaviour are excluded due to their divergent diel behaviour pattern previously described in section 4.2. To date, such a long-term study has not been conducted using data-storing devices on sea turtles by any other workers.

### 4.5.2 *Specific Methodology*

The computer program Statistica<sup>®</sup> was used to conduct an iterative search for a breakpoint within a linear fit and to calculate a piecewise linear regression.

### 4.5.3 *Results*

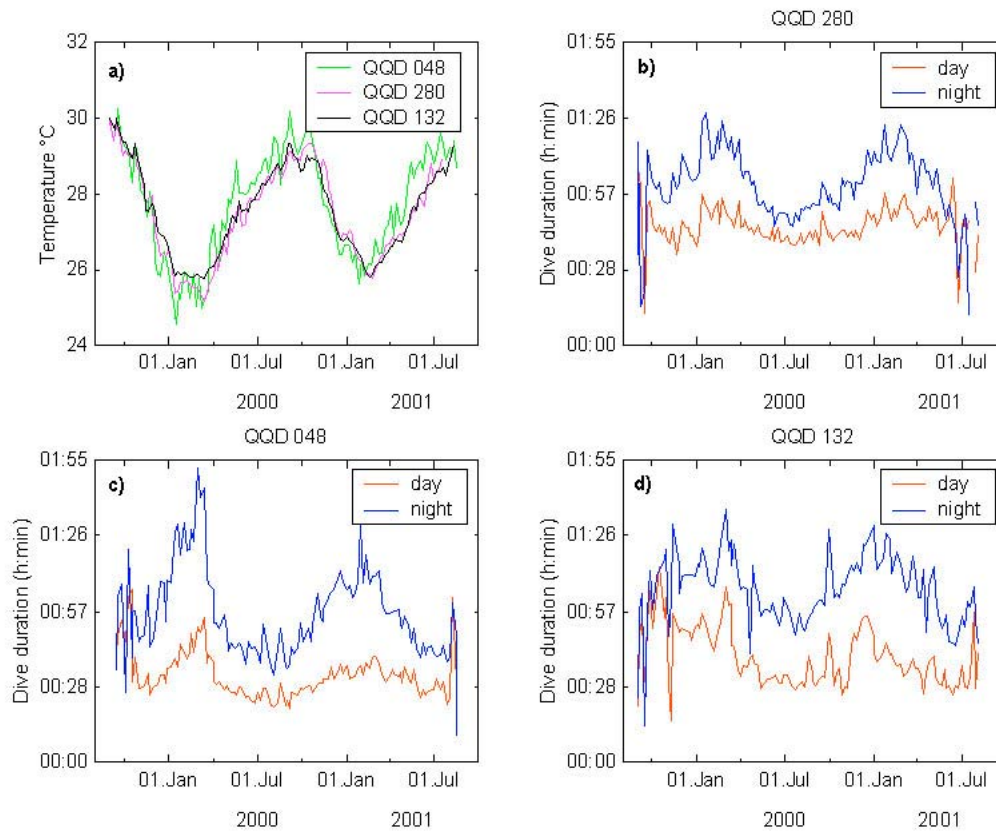
By excluding phases of obvious nesting activity or migratory behaviour (see section 4.2) data series with regular patterns of nocturnal resting and diurnal activity at the foraging grounds were obtained.

### 4.5.3.1 Temperature Fluctuations and Dive Duration

Data from the three recovered MK7 (females QQD 280, QQD 048 and QQD 132) showed seasonal fluctuations in water temperature (Fig. 50a) over the observed period of 22 months. Although the turtles moved off to different feeding grounds after the 1999 egg-laying season (Storch et al. 2003) all three animals experienced parallel temperature changes. The minimum and maximum recorded temperatures were 24.1°C and 31.4°C. As the sampling interval of temperature measurements was long (15 min) it could not be expected to see clear temperature gradients within single dive events. I did, however, occasionally obtain surface temperatures when the turtle happens to be at or near the surface at the time of data recording. These recordings showed an increase of up to 2°C compared with the temperature at depth during day, while the difference was only approx. 0.4°C at night. During the dives the temperature data did not show any trend in relation to the actual depth of the animal (values between 2.6 and 48 m at the deepest point of the dives, see section 4.5.3.3).

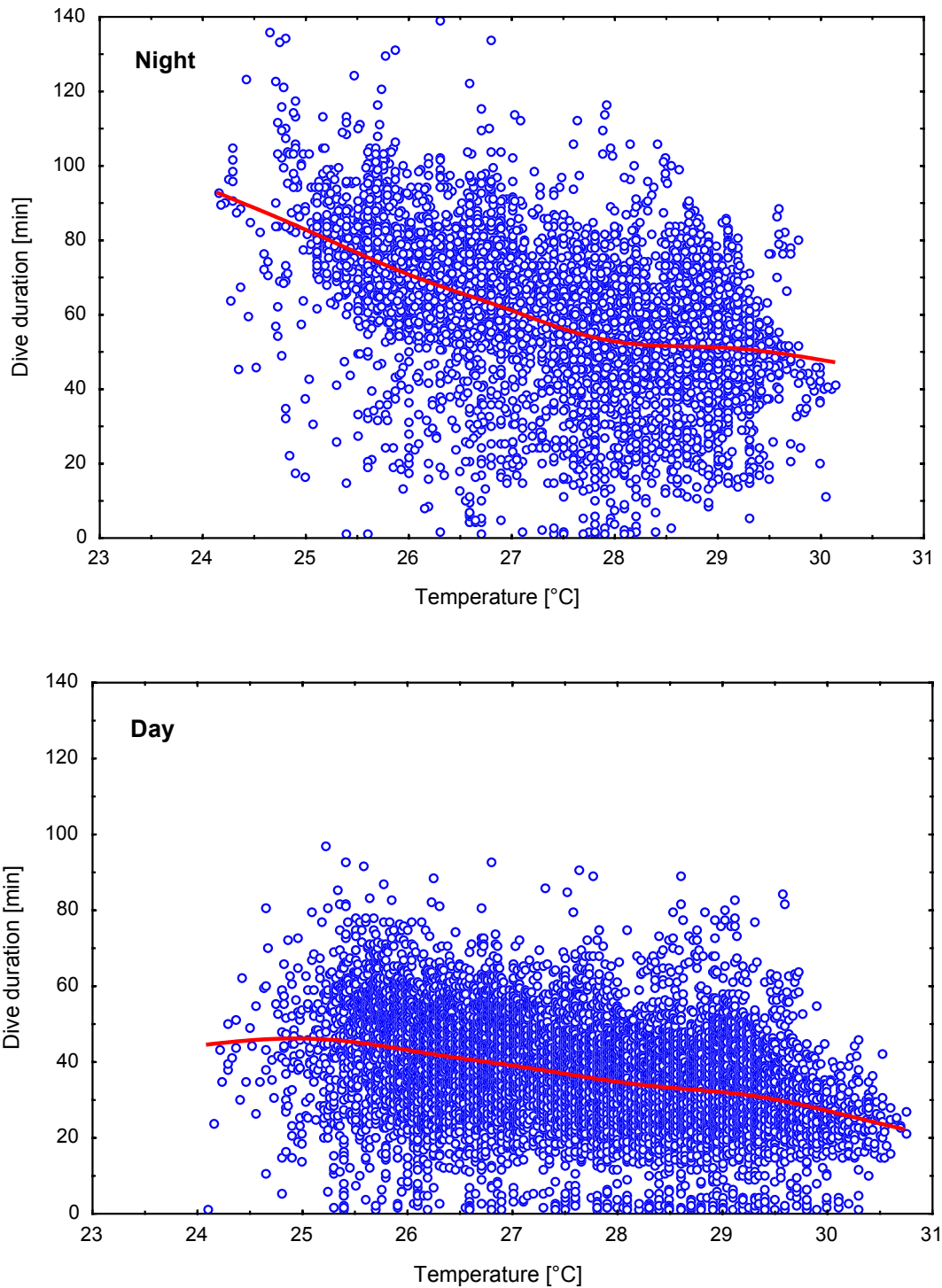
The dive behaviour was very regular and uniform over the period of feeding away from the reproduction site, whereas nesting and migratory behaviour lead to specific behaviour patterns that were much more complex (Storch et al. 2003). For the following analysis I extracted the period of regular activity-resting patterns of each individual, resulting in a total of 18955 dives.

Dive duration was negatively correlated with water temperature, with increased submergence times at lower temperatures (Fig. 50b-d). This change in dive duration between winter and summer conditions was more apparent in nocturnal dives than during the day.



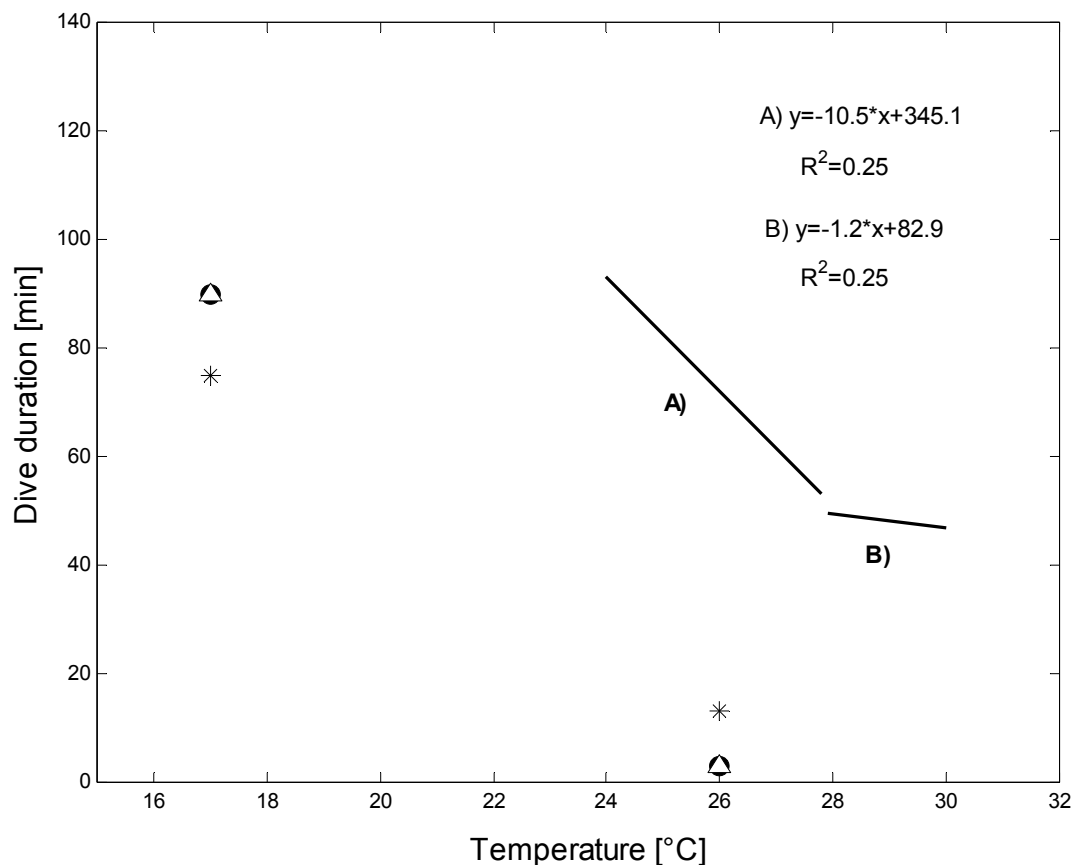
**Fig. 50:** a) Water temperature data (daily mean values shown) recorded by TDRs attached to three female Hawksbill turtles (QQD 280, QQD 048 and QQD 132) over a period of 22 months. b-d) Daily mean dive duration of the three turtles, separated for day and night dives.

The least-squares fit calculated for the dive duration as a function of temperature showed a strong effect of temperature on nocturnal submergence times at temperatures below 28°C (Fig. 51), while at temperatures between 28 and 30°C the curve appeared to level off.



**Fig. 51:** Nocturnal (top) and diurnal (bottom) dive duration in relation to water temperature. The red lines represent the curves fitted to the data using the least squares smoothing procedure, indicating a point of inflection in the temperature dependency of nocturnal dive durations.

The breakpoint, indicated by the point of inflection in Fig. 51 (top), was located at 27.8°C, with corresponding linear regressions at either side of the break point describing the temperature dependency of the nocturnal dive duration.



**Fig. 52:** Piecewise linear regression modelling the temperature-dependency of the dive duration (solid lines). The two sections of the model show the trends for lower temperatures ( $\leq 27.8^{\circ}\text{C}$ ) and higher temperatures ( $> 27.8^{\circ}\text{C}$ ). Additional data-points (triangles, dots and stars) show the dive duration of three Green Turtles in the Mediterranean at pre-wintering ( $26^{\circ}\text{C}$ ) and wintering temperatures ( $17^{\circ}\text{C}$ ) (Godley et al. 2002).

Dive duration as a function of temperature showed a strong effect of temperature on nocturnal submergence times at temperatures up to  $27.8^{\circ}\text{C}$  (Fig. 52,  $F = 1172.7$ ,  $p < 0.0001$ ). At temperatures above  $27.8^{\circ}\text{C}$  changes in dive duration were not significant ( $F = 1.8$ ,  $p = 0.177$ ). Temperature effects on daytime dive duration were significant ( $F = 1782.2$ ,  $p < 0.0001$ ), but much less distinct than at night (Fig. 51, bottom).

The model consists of two separate regressions with a shift in the slope at 27.8°C. Long-term data (up to 293 days) obtained via satellite transmitters from three Green Turtles in the Mediterranean also revealed a seasonal change in dive duration (Godley et al. 2002) and are plotted to enable direct comparison. While most dives were less than 5 min or between 10 and 15 min at temperatures around 26°C, the submergence times increased to more than 90 min or 60 to 90 min, respectively, when the temperatures sank to 17°C (Fig. 52).

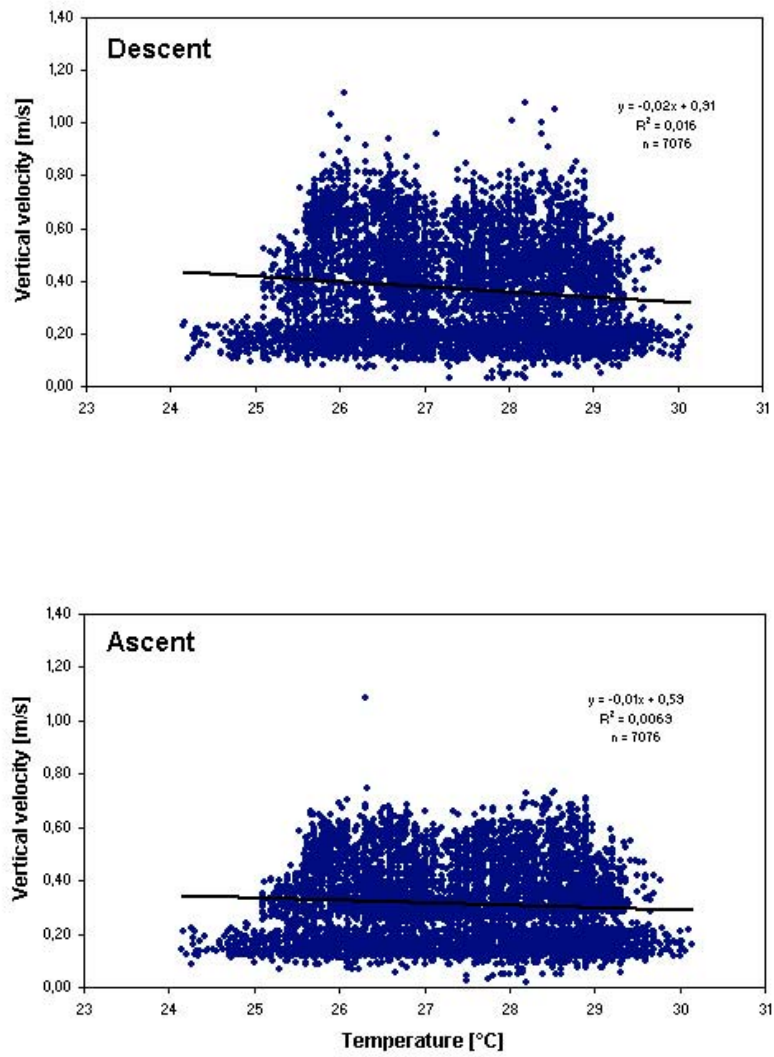
### 4.5.3.2 Q<sub>10</sub>

Assuming that the nocturnal dives of the turtles are resting dives, during which the animals reduce their activity to the necessary minimum of commuting (Storch et al. 2003), dive duration can be used as a relative measure of metabolic rate. I accordingly calculated a resting Q<sub>10</sub> of 4.36 for temperatures below 27.8°C (referred to as R<sub>1</sub>Q<sub>10</sub>), whereas the Q<sub>10</sub> above 27.8°C was 1.16 (referred to as R<sub>2</sub>Q<sub>10</sub>). The Q<sub>10</sub> resulting from the mostly active submergence times during daylight hours was 2.3 (referred to as A Q<sub>10</sub>).

### 4.5.3.3 Vertical Velocity and Dive Depth

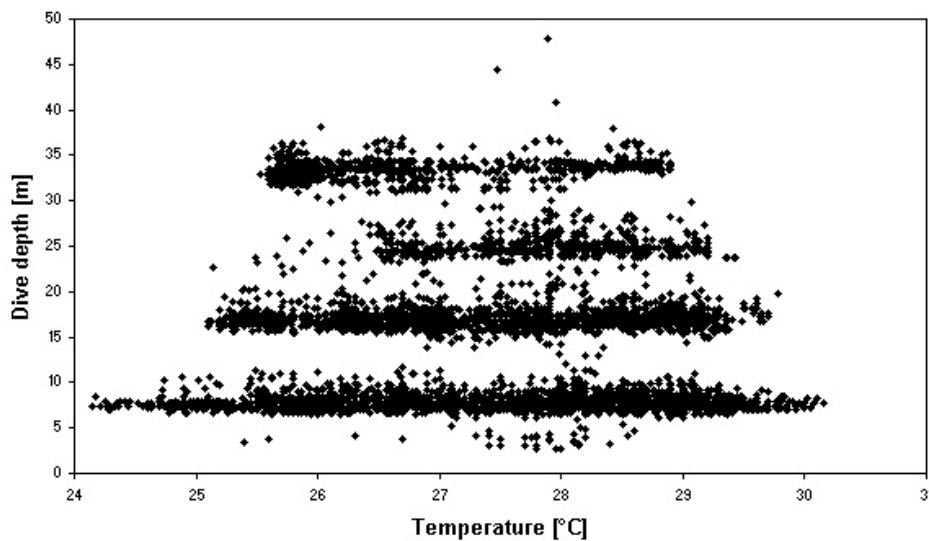
The means of the peak vertical velocities during the descent and ascent were 0.37 m/sec (SD 0.19 m/sec, n = 18997) and 0.31 m/sec (SD 0.15 m/sec, n = 6953), respectively. In the analysed data of the three turtles (nocturnal dives at the foraging grounds) the maximum vertical velocities were not related to water temperature for either the descent or ascent (Fig. 53).

The individual turtles performed resting dives to specific depth levels, however, these depth levels did not show any systematic variation over the temperature range (Fig. 54).



**Fig. 53:** Thermal independence of vertical velocity during descent (above) and ascent phase (bottom) for females QGD 280, QGD 048 and QGD 132.





**Fig. 54:** Thermal independence of dive depth for females QQD 280, QQD 048 and QQD 132. Clusters of data represent preferred depth levels of the turtles during benthic resting dives (n = 7076).

#### 4.5.4 Discussion

##### 4.5.4.1 Temperature Fluctuations and Dive Duration

The temperatures recorded by the TDRs follow the same trends as the official great-scale data for the sea surface temperature in the region of the Antilles published in previous years (Tab. 16) with mostly corresponding values. The maximum temperatures recorded in late summer by the deployed Mk7, however, appear to be 1 to 2° higher than the great-scale temperatures. This is because the equipped turtles tended to reside in shallow areas near oceanic islands, whereas the great-scale data were taken by off-shore ships. The sampling rate used for the long-term recordings was insufficient to describe vertical temperature gradients. However, the devices occasionally recorded an increase of temperature when the turtles were at or near the surface. This increase is likely to be caused by solar radiation rather than by a genuine vertical gradient in water temperature because these differences were not found at night. Because of the short duration of surfacing events of the three turtles at the foraging grounds (mean 2.5 min, Storch unpubl. data) and due to the thermal inertia of the body of large animals (Spotila & Standora 1985),

these differences in ambient temperature are assumed to have no influence on the body temperature of the turtles.

**Tab. 16:** Temperatures recorded by TDRs in 2000 and 2001 and official great scale temperatures for the northern Caribbean Sea (Deutsches Hydrographisches Institut 1956, Deutsches Hydrographisches Institut 1967, Bundesamt für Seeschifffahrt und Hydrographie 1998).

	<i>Water Temperature in °C</i>			
	this study	1956	1967	1998
January	24-26	26	25-26	26
February	25-26	25	25-26	26
March	25-26	25-26	25-26	24-26
April	26-27	25-26	25-27	26
May	27-28	27	26-27	26
June	28-29	27-28	27	26-28
July	28-29	27	27	26
August	28-29	28	27	28
September	29-30	28	28	28
October	29-30	27-28	28	28
November	29	27-28	27-28	26
December	28	26-27	26-27	26

Dives performed during the day were assumed to be associated with active feeding, as they occurred to a variety of depths and showed structured bottom phases (Storch et al. 2002). In contrast, successive nocturnal dives were characterised by a very limited bottom depth range (see also Hays et al. 2000a) and they were longer than dives made during previous and following daylight-periods (Storch et al. 2003). I therefore conclude that the turtles were essentially resting during the dark hours between 18:00 and 06:00, only actively swimming when they commuted to the surface to breathe. A strong relationship between temperature and dive duration was found for the nocturnal resting dives of the turtle.

Unrestrained and undisturbed turtles have been shown to breathe at a fairly constant level of depletion of their oxygen store (e.g. Burggren & Shelton 1979, Lutcavage & Lutz 1991). Assuming a mostly undisturbed nocturnal situation for the equipped free-ranging individuals, submergence times at night are likely to be primarily a function of the metabolic rate and its thermal dependence. In contrast, during the day different levels of

activity may occur that could not be determined in this study. Such activities may substantially influence metabolic rate and consequently oxygen depletion and ultimately dive duration. During the day, when dives are presumed to be mostly active, the relationship between temperature and dive duration has a reduced gradient in the slope (Fig. 51). This enhanced independence probably stems from active sea turtles being able to maintain a body temperature that exceeds the water temperature due to muscular heating and thermal inertia (Sato et al. 1995, Hochscheid et al. 2002), which would tend to dampen the dependence of the dive duration on the water temperature.

### 4.5.4.2 Q<sub>10</sub>

The data indicate that there is a point of inflection in the thermal dependence of the preferred submergence times, leading to a high R<sub>1</sub>Q<sub>10</sub> value of 4.36 at temperatures below, and a low R<sub>2</sub>Q<sub>10</sub> of 1.16 above 27.8°C (Fig. 52). The thermal dependence of this overall Q<sub>10</sub> represents the sum of the Q<sub>10</sub> values of the different tissues of the sea turtle's body. Some exemplary tissues of the Green Turtle have been shown to have temperature-sensitive metabolic rates, with Q<sub>10</sub> values decreasing at higher temperatures (Penick et al. 1996). Studies of tissues of other reptiles revealed that metabolic rate increased dramatically with increased temperature within the lower experimental temperature range (4-20°C, Q<sub>10</sub> of 6.5), but reach a metabolic plateau at the upper range (20-34°C, Q<sub>10</sub> approx. 2.0) (Hoskins & Aleksiuik 1973). These findings correspond with the descriptive model (Fig. 52). The R<sub>1</sub>Q<sub>10</sub> and R<sub>2</sub>Q<sub>10</sub> values in this study frame the Q<sub>10</sub> value of 2.4 calculated from the oxygen consumption of unrestrained, captive Loggerhead Turtles kept in water between 10 and 30°C (Lutz et al. 1989). Typical Q<sub>10</sub> values found for reptiles are between 2 and 3 (Glass & Wood 1983). The AQ<sub>10</sub> = 2.3 found during the daytime is well within this range.

However, cognisance must be taken of the fact, that the relatively elevated body temperature of an active turtle during daylight does not equal that of the water (as reviewed in Spotila et al. 1996), which is the case in a resting turtle at night. Therefore the temperature data included into the calculation of the AQ<sub>10</sub> are likely to be incorrect with regards to body temperature.

Satellite telemetry, as used by Godley et al. (2002), does not reveal the chronology of the depth data, but integrates data from 6-h periods into a histogram. Therefore the data from Godley et al. (2002) is not given with respect to day- or night-time and flat bottom dives cannot be separated from obviously active dives. However, the data obtained from the three Green Turtles included in Fig. 52 for comparison shows a trend that supports the proposed model, although, as it has been reported before (Hays et al. 2000b, Hays et al. 2002b), the routine dive duration of Green Turtles is shorter than the submergence durations of the Hawksbill Turtles.

### 4.5.4.3 Vertical Velocity and Dive Depth

Although a decrease in environmental temperature has been shown to lead to a decrease in the agility of an ectotherm (Hirano & Rome 1984, Du et al. 2000) and vertical velocity is a measure of the degree of active power-stroking during ascent and descent (cf. Skrovan et al. 1999), the data obtained here failed to show a corresponding temperature dependent change in maximum vertical velocity of the sea turtles (Fig. 53). While these findings contrast expected results, previous studies of submaximal performance have shown cases of thermal independence of muscle output in cold-blooded animals (Rome 1982, Rome & Loughna 1983). The conclusion of the results found in running lizards and swimming carp is that at low temperatures a higher number of muscle fibres and a selection of faster fibres contributes to the fact that locomotion speeds were found to be the same at 10 and 20°C (Rome & Loughna 1983).

Fig. 54 clearly shows clusters of levels of dive depth, representing depth preferences of the individual turtles. Hawksbill Turtles are known to dive serially to habitual sites within the reef (van Dam & Diez 1997a). The absence of any influence of water temperature on depth selection (Fig. 54) supports the model shown in Fig. 52, and thus essentially discounts the possibility that a relationship between dive depth and dive duration causes the observed thermal dependence of submergence times.

### 4.5.4.4 Effects of Temperature Changes

Although sea turtles should be able to mostly avoid unacceptable temperatures through migration, they still experience water temperatures which fluctuate over several degrees C. This has been shown to be the case even for the most tropical of all species, the Hawksbill Turtle.

The lowest and highest confirmed temperatures experienced by Hawksbill Turtles are 15 and 32°C (Seminoff, Moore pers. comm.). Assuming that the two-phase linear models presented in Fig. 52 were valid throughout this temperature range dive durations of ca. 180 min at 15°C and 50 min at 32°C would be predicted. Recordings of dive behaviour under maximum and minimum temperature conditions could be used to refine the model. However, at higher temperatures Hawksbill Turtles have to surface more often, thus exposing themselves to a greater risk of e.g. being affected by human impact (fishery, boating) or being attacked by Tiger Sharks (*Galeocerdo cuvier*) (Stancyk 1995), this being the only shark species that is specialised in taking large cheloniid turtles (Witzell 1987). Compared to warm-blooded animals the metabolism of cold-blooded animals like reptiles is particularly low (Schmidt-Nielsen 1990) which probably contributes to the longevity of these animals (Jonsson 1991). Full torpor or hibernation, as discussed or observed in other species (e.g. Felger et al. 1976, Carr et al. 1980) are irrelevant for the Hawksbill Turtle as this species neither experiences temperatures around or below 10°C nor a seasonal shortage of food.

Overall, the long-term data presented here indicate that a substantial change in water temperature would influence sea turtles. Levitus et al. (2000) found an increase in ocean temperature of 0.31°C over the last 45 years, this signal referring to the upper layer (0 - 300 m). However, it was not possible to allocate the extent of the anthropogenic component from the effect of natural variability in the observed temperatures (Levitus et al. 2000). Based on the model shown in Fig. 52 this warming should shorten the resting dive duration by about 3 min at water temperatures below 27.8°C, while at higher temperatures the effect would be much less (15 sec). Although this species seems to be quite sensitive to temperature changes, the full consequences are hard to foresee. Certainly,

as longevity seems to be related to metabolic rate (Jonsson 1991), small increases in water temperature may decrease life expectancy and hence the number of breeding attempts. In the context of climate changes the effects of sea level rising and increased incubation temperatures might lead to an even more serious disturbance to the life cycle of Hawksbill Turtles, with effects being cumulative. The fairly substantial changes in water temperature associated with the phenomenon of El Niño (e.g. Elliott et al. 2001) may provide good conditions for further studies.

## 4.6 SCALING OF DIVING CAPACITIES

### 4.6.1 Introduction

Various studies have attempted to investigate or model animal behaviour patterns with regard to optimisation (see Krebs & Davies 1997 for review). A key aspect of optimality models is the assumption about the parameter that is to be optimised (Krebs & Davies 1997). For air-breathing, diving animals, such as seabirds, the typical parameter usually considered optimised is foraging, i.e. success in capturing prey underwater (e.g. Ydenberg & Clark 1989). However, in this chapter that deals with an animal that is a 'surfacers' by Kramer's (1988) definition (see section 4.2.1) the percentage of time spent underwater will be in the focus of attention.

It can be hypothesised that an animal that routinely dives such as the sea turtle optimises its behaviour to such a degree that patterns of submergence might reflect the physiology of the individual. Furthermore, a relation between the size of the animal and its physiology can be expected and external and internal factors, e.g. habitat characteristics or level of activity, will modify this relation.

While most diving mammals exhale before submerging (Kooyman et al. 1983), sea turtles dive with inflated lungs (Lutcavage & Lutz 1996). However, the differentiation into inhalers and exhalers is not based on phylogenetic groups (see review by Lutcavage & Lutz 1996). The key to the differentiation rather seems to be the depth range of routine dives: in contrast to deep divers, shallow divers in coastal or freshwater habitats, such as the Hawksbill Turtle, Sea Otter (*Enhydra lutris*), Manatee (*Trichechus manatus*), Duck-Billed Platypus (*Ornithorhynchus anatinus*), inhale prior to submergence (Kooyman et al. 1981, Gallivan & Best 1980, Evans et al. 1994), regardless of the phylogenetic group. Animals specialised for deeper dives tend to carry the major part of their oxygen store in blood and tissue (Kooyman 1989). A Loggerhead Turtle, on the other hand, carries 72% of the oxygen supply for a dive in its inflated lung (Lutz & Bentley 1985).

Understanding and ultimately predicting the dive behaviour of sea turtles requires knowledge about the aerobic dive limit (ADL), which is basically dependent of the oxygen store and the metabolic rate. Kooyman (1989) defined the ADL as "the maximum breath-

hold that is possible without any increase in blood lactate concentration during or after the dive". In this study no measurements of blood parameters were undertaken. Instead estimations of ADL are based on dive data in combination with data from literature.

The aim of this chapter is to model chelonid diving capacities and to reveal patterns that indicate the assumed optimisation. For this purpose, resting behaviour under water is analysed separately from active dives. Data on immature Hawksbill Turtles as well as from nesting and non-nesting females are used to unveil the relation between dive behaviour and body size.

### 4.6.2 Specific Methodology

While most physiological studies on sea turtles have been conducted on Loggerhead (*Caretta caretta*) and Green Turtles (*Chelonia mydas*), no such data exist for the Hawksbill Turtle. Assuming the data listed in Tab. 17, derived from various turtle species, are also valid for Hawksbill Turtles, the oxygen store at the onset of a dive was calculated for the individuals observed in this study using

$$(4) \quad \text{O}_2 \text{ store [ml]} = \text{blood vol. [ml]} * \text{O}_2 \text{ capacity[\%]} * \text{saturation[\%]} + \\ \text{muscle mass [kg]} * \text{O}_2 \text{ in muscle [ml/kg]} + \text{lung vol. [ml]} * 18\% \text{ O}_2 \text{ in air}$$

Based on the metabolic rate (MR) given by Prange & Jackson (1976), see Tab. 17, the size-dependent ADL based on literature data ( $\text{ADL}_{\text{lit}}$ ) was also calculated using

$$(5) \quad \text{ADL}_{\text{lit}} [\text{min/kg}] = \text{O}_2 \text{ store at onset of dive [ml]} / \text{MR [ml O}_2\text{/kg*min]}$$



The relationship between ADL, MR and oxygen store was also used to calculate the observed MR ( $MR_{obs}$ ) using

$$(5) \quad MR_{obs} [\text{ml O}_2/\text{kg}\cdot\text{min}] = \text{O}_2 \text{ store at onset of dive [ml]} / ADL_{obs} [\text{min/kg}]$$

where  $ADL_{obs}$  equals the observed dive duration.

**Tab. 17:** Elements for calculation of oxygen stores and  $ADL_{lit}$  taken from literature.

	<i>Value</i>	<i>Species</i>	<i>source</i>
<i>Blood volume</i>	6.5 - 6.7%	Aquatic + terrestrial	
	of body mass	chelonians	Thorson 1968
<i>O<sub>2</sub> capacity</i>	10.8%	Green Turtle	Berkson 1966
	10.7%	Green Turtle	Jackson & Prange 1979
<i>Saturation of blood</i>	93% arterial	Loggerhead Turtle	
	70% venous		Lapennas & Lutz 1982
	Average 81.5%		
<i>Muscle volume</i>	22.4% of body mass	Loggerhead Turtle	Lutz & Bentley 1985
<i>O<sub>2</sub> content muscle</i>	0.8 ml/kg muscle mass	Loggerhead Turtle	Lutz & Bentley 1985
<i>Lung volume</i>	6.5 - 17%	Loggerhead Turtle	Lutcavage et al. 1987, 1989
	12%	Green Turtle	Tenney et al. 1974
	11.5% (7.8 - 18.7%)	Green Turtle	Berkson 1966
	5-15%	Loggerhead Turtle	Minamikawa et al. 2000
	Average 11.3%		
<i>O<sub>2</sub> content in lung</i>	18% of lung volume	Green Turtle	Berkson 1966
<i>Metabolic rate</i>	$x = 0.058 \cdot y^{-0.174}$	Green Turtle	Prange & Jackson 1976
<i>(O<sub>2</sub> consumption)</i>	with $x = 1 \text{ O}_2/\text{kg}\cdot\text{h}$ $y = \text{body mass in kg}$		

During the inter-nesting intervals females perform short, shallow dives related to the surface-oriented behaviour prior to nesting (see section 4.2.3.2). These dives do not have benthic resting behaviour components and were excluded from analysis in this chapter by only considering dives that lead to depths of more than 8 m. Four sets of inter-nesting data obtained from four different individuals in 1999 were suitable for the analyses in this chapter, as the body mass of the turtle needed to be known and a whole inter-nesting interval needed to be recorded without failure of the depth sensor.

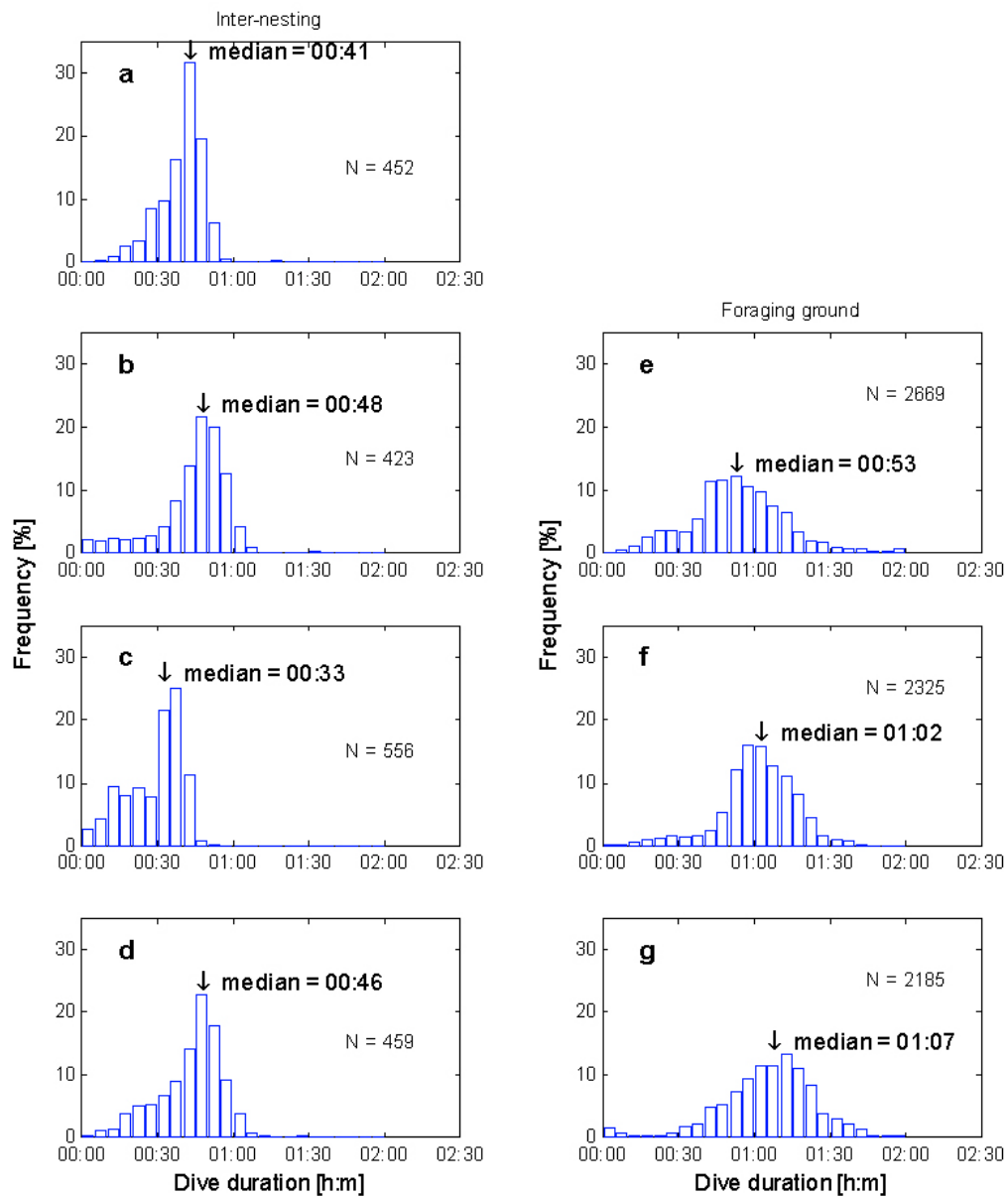
The Kolmogorov-Smirnov test was used to test for normality of distribution of dive durations.

### 4.6.3 Results

#### 4.6.3.1 Resting Dive Duration

The dive behaviour of the four females observed during the inter-nesting interval was characterised by the lack of a clear diel pattern, with resting dives occurring at all times of the day (see section 4.2.3.2). The vast majority of dives lasted less than 1 hr. The dive duration data were not normally distributed, therefore the median dive duration for each individual (marked with an arrow in Fig. 55) was calculated. The median dive duration of females during the inter-nesting interval ranged from 33 to 48 min.

The data of the three adult females in the foraging grounds was characterised by a strong dimorphism in dive behaviour during day and night (see section 4.2.3.3). Only nocturnal, i.e. resting dives, are considered here to avoid the influence of activity on the dive duration. The median resting dive duration of these turtles ranged from 53 to 67 min.



**Fig. 55:** Frequency distribution of dive duration of four females during the inter-nesting interval off Buck Island (a-d: QQD 025, QQD 384, QQD 401 and PPW 842, respectively) and three females in the foraging grounds at night (e-g: QQD 048, QQD 280 and QQD 132, respectively). Dive duration is given in classes of 5 min. The median dive duration of each individual is marked with an arrow. N gives the number of dives considered in each graph.

The distribution of the nocturnal dive duration of the immature Hawksbill Turtles (Tab. 18) followed a normal distribution. The mean dive duration ranged from 33 to 76 min.

**Tab. 18:** Mean duration of nocturnal resting dives of the five immature Hawksbill Turtles equipped off Mona Island. Kolmogorov-Smirnov test was conducted for normal distribution.

<i>Turtle (file name)</i>	<i>121a</i>	<i>121b</i>	<i>123b</i>	<i>123c</i>	<i>128b</i>
<i>Mean nocturnal dive duration [min]</i>	40	76	48	33	42
<i>SD</i>	± 6.1	± 7.5	± 11.5	± 7.7	-
<i>N</i>	15	8	25	19	1
<i>K-S test (D)</i>	0.18	0.20	0.20	0.18	-

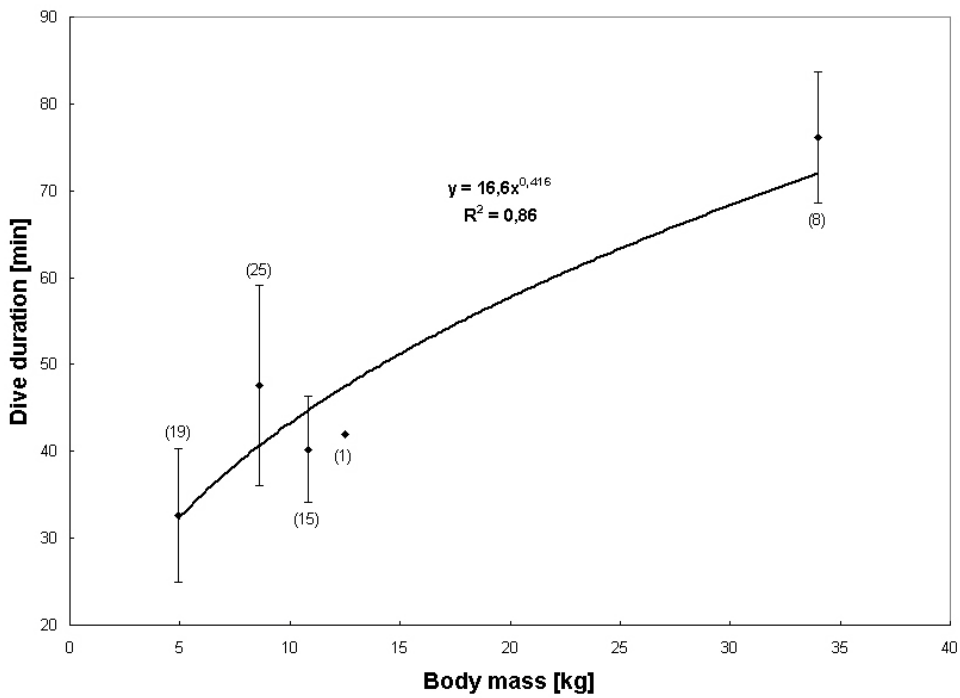
#### 4.6.3.2 Size-Dependent Dive Behaviour

The five immature Hawksbill Turtles (file names 121a, 121b, 123b, 123c and 128b) that were caught, weighed and equipped off Mona Island varied in body mass from 4.9 kg to 34 kg (Tab. 19). Four female Hawksbill Turtles that were equipped for the duration of an inter-nesting interval at Buck Island weighed between 49 kg and 95 kg (Tab. 19). The three females equipped with long-term devices to monitor behaviour at the foraging grounds had a body mass between 72.5 and 80.5 kg (Tab. 19).

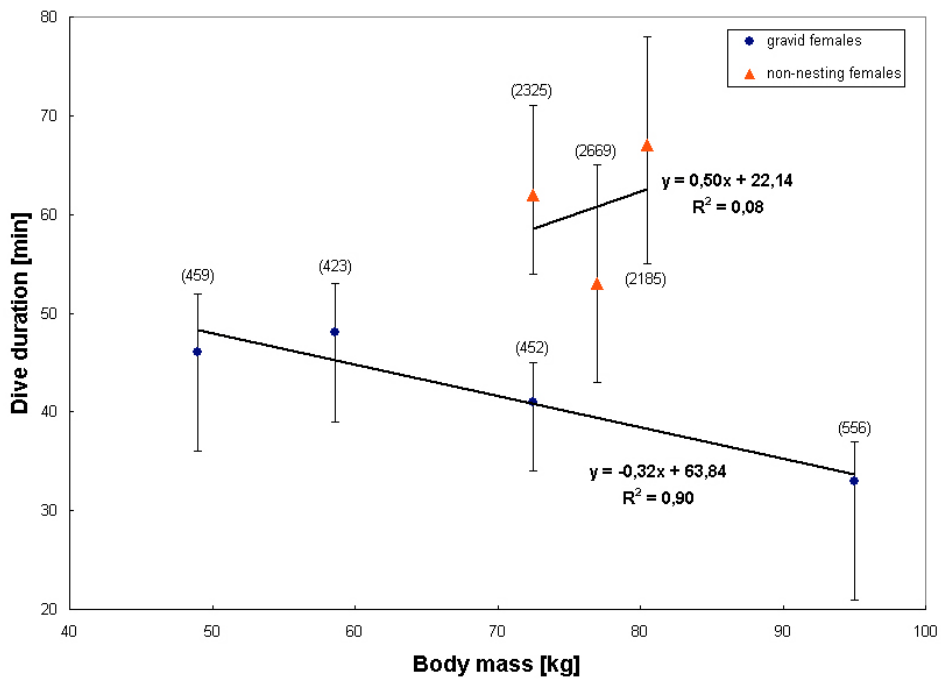
**Tab. 19:** Body mass of the Hawksbill Turtles considered in this chapter.

<i>Turtle</i>	<i>Status</i>	<i>Body mass [kg]</i>
121a	immature	10.8
121b	immature	34.0
123b	immature	8.6
123c	immature	4.9
128b	immature	12.5
PPW 842	adult, gravid	49.0
QQD 025	adult, gravid	72.5
QQD 384	adult, gravid	58.6
QQD 401	adult, gravid	95.0
QQD 280	adult, foraging ground	72.5
QQD 048	adult, foraging ground	77.0
QQD 132	adult, foraging ground	80.5

A strong correlation was found between the dive duration of the immature turtles and their body mass, shown in Fig. 56 ( $p < 0.01$ ,  $F = 47.1$ ,  $n = 68$ ). The submergence duration increased with the size of the animals. In contrast, the median dive duration of gravid females shown in Fig. 57 was negatively correlated with the body mass of the animals ( $p < 0.001$ ,  $F = 505.8$ ,  $n = 1890$ ). No significant correlation could be found between the body mass and the dive duration of non-nesting females.



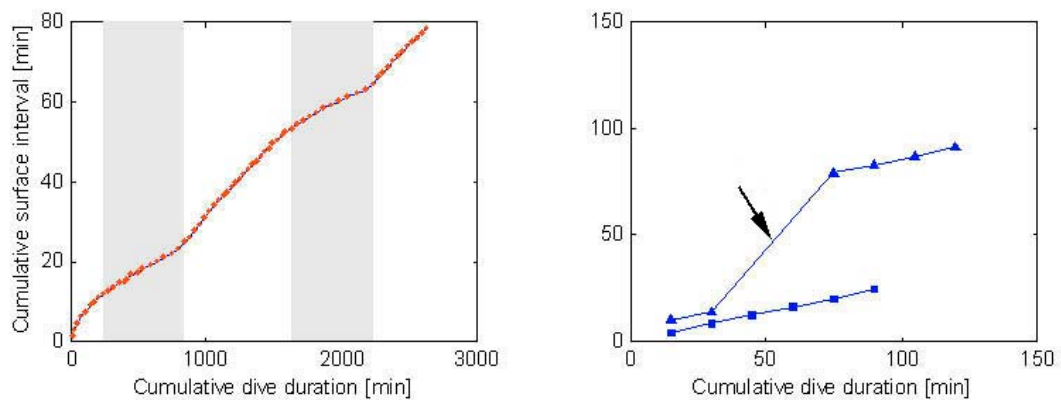
**Fig. 56:** Relationship of mean dive duration to body mass in immature Hawksbill Turtles. The regression line, equation and standard deviation (error bars) are given. Sample sizes are shown in brackets.



**Fig. 57:** Relationship of median dive duration to body mass in gravid females (solid circles) and in adult females in the foraging grounds (triangles). Error bars give first and third quartiles. Sample sizes are shown in brackets. Linear regression lines are given separately for each group (see text).

## 4.6.3.3 Estimation of ADL

Sea turtles show constant diving behaviour. Fig. 58 (left) shows an example of an immature Hawksbill Turtle, that was monitored over 46 hrs. Each dive (mean duration 48 min, SD = 11.5, n = 25) is followed by a short surface interval (mean duration 55 sec, SD = 9.3, n = 25). The relation between dive duration and surface interval is characterised by the slope of the curve (0.03 overall). For comparison, the right hand graph of Fig. 58 shows two exemplary dive series of a Weddell Seal (*Leptonychotes weddelli*) as described by Kooyman et al. (1980). The slope (i.e. the relation between dive and surface times) of a series of dives of 15 min duration (squares) is altered from 0.27 to 1.4 when a single 45 min dive occurs (triangles and arrow). Characteristic points of inflection occur along with the change in the dive/pause ratio, marking a change between aerobic and anaerobic diving (see section 4.6.4.3).



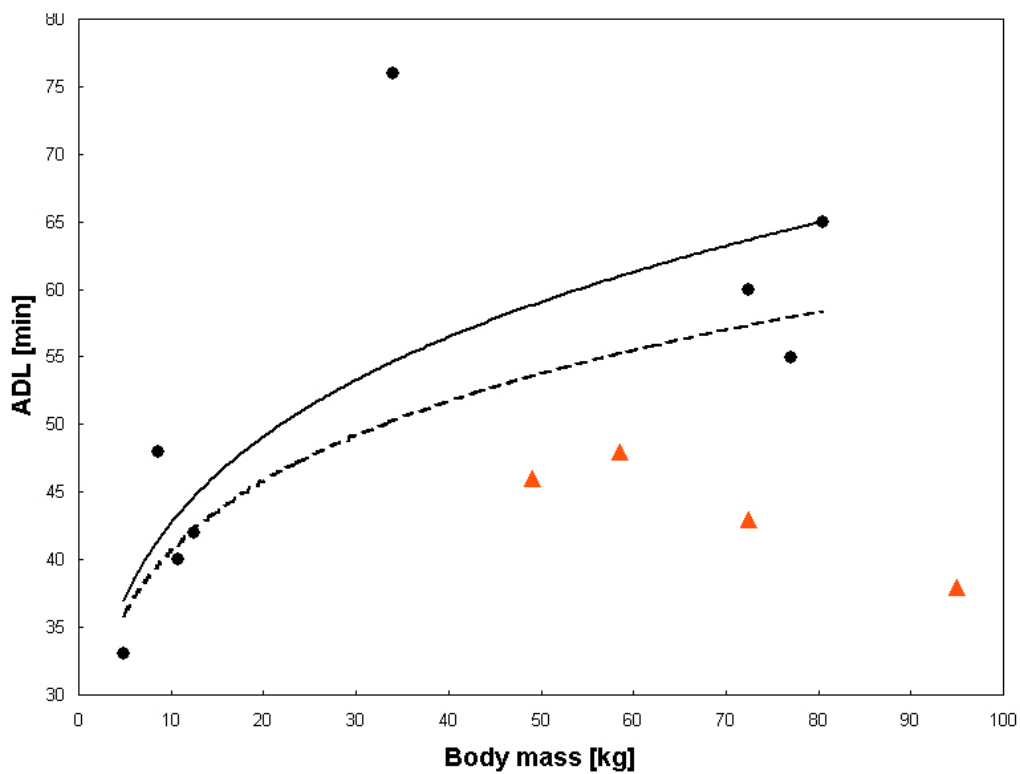
**Fig. 58:** Left: Continuous dive behaviour of immature Hawksbill Turtle over 46 hrs. Grey shading represents night hours. Right: Two exemplary series of dives of a Weddell Seal (after Kooyman et al. 1980). Squares mark series of constant aerobic dives, triangles give the course of aerobic dive series interrupted by one single anaerobic dive (arrow). See section 4.6.4.3 for the discussion of the different slopes of the curves.

No such drastic changes in slope occur in the data of the Hawksbill Turtles, indicating that they perform exclusively aerobic diving, although differences in the dive/pause ratio between day (slope 0.04) and night (slope 0.02) as well as a steep initial slope (0.06) are distinguishable. These differences reflect different levels of activity, with long resting dives at night, shortened active dives during day and escape behaviour with shortest, stressed-induced dives after release. Slopes are always far below a threshold value of 1 that was exceeded in the Weddell Seal in connection with the anaerobic dive.

Based on the observations of continuous dive behaviour it can be assumed, that the duration of resting dives is a good approximation of the ADL of the animal. Accordingly, the observed ADL,  $ADL_{obs}$ , was defined by the resting dive duration of the considered animal. During reproduction adult Hawksbill Turtles showed a strongly reduced  $ADL_{obs}$  compared to non-nesting conspecifics of the same body mass (Fig. 59). Due to their gravid status the data from these individuals were not included into the following model. The significant regression line fitted to the data of immature animals and females in the feeding grounds, however, is slightly above the  $ADL_{lit}$  (dashed line) calculated from literature data as described in section 4.6.2. While  $ADL_{lit}$  and  $ADL_{obs}$  fit closest in small-sized turtles, the gap between the two increases to 7 min at a body mass of 80.5 kg (Fig. 59).

Four of these animals (two immatures weighing 10.8 and 12.4 kg and two females of 72.5 and 77 kg) show ADLs below the values predicted by the model (solid line). These individuals performed resting dives to shallower depths than the other turtles (Tab. 20).





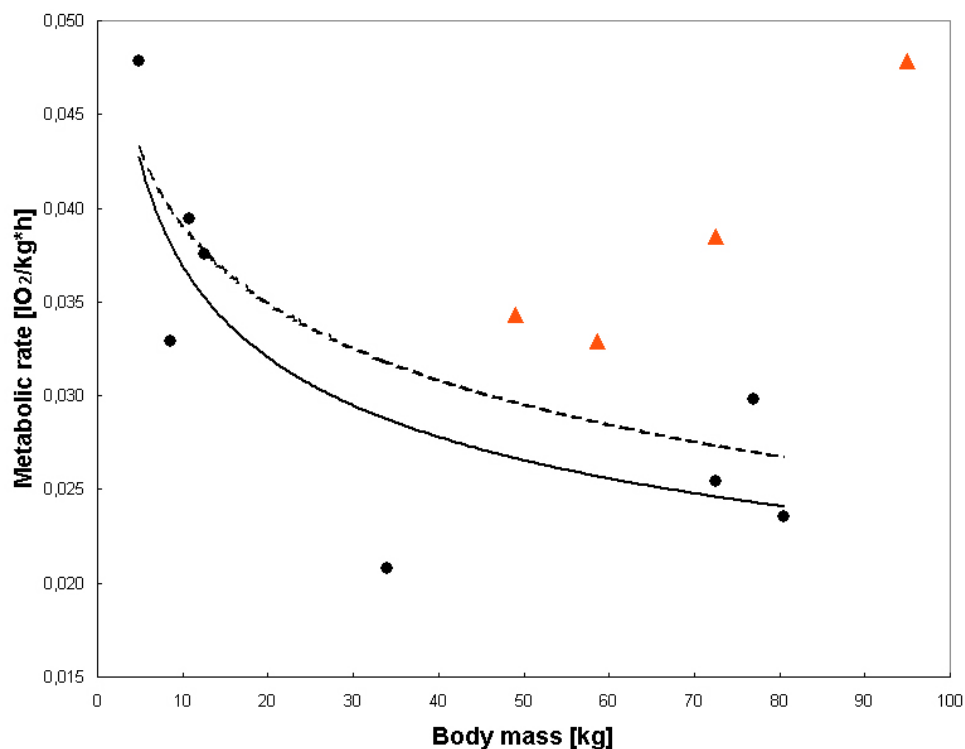
**Fig. 59:** Scaling of aerobic dive limit (ADL) to the body mass of the turtles.  $ADL_{lit}$  (dashed line,  $y = 27.2x^{0.174}$ ) is derived from the literature data in Tab. 17.  $ADL_{obs}$  (solid line,  $y = 26.9x^{0.202}$ ,  $R^2 = 0.66$ ,  $F = 11.8$ ,  $p < 0.05$ ) is calculated from observed dive durations (dots). Data points from gravid females (triangles) were excluded from the regression (see text).

**Tab. 20:** Body mass and resting dive depth of immature and non-nesting Hawksbill Turtles. Bold numbers refer to individuals that show short ADL (see Fig. 59).

	<i>Immature turtles</i>					<i>Adults</i>		
<i>Body mass [kg]</i>	4.9	8.6	10.8	12.5	34.0	72.5	77.0	80.5
<i>Resting depth [m]</i>	16.0	15.0	<b>10.8</b>	<b>12.5</b>	17	28.6	<b>7.8</b>	17.1

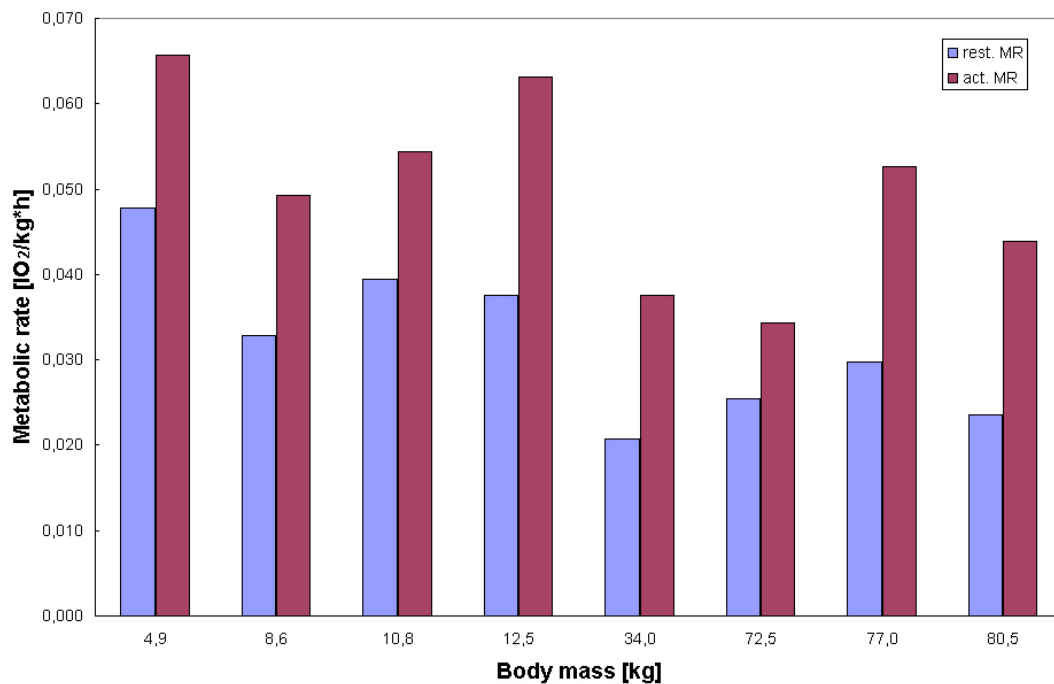
## 4.6.3.4 Estimation of Metabolic Rate

$MR_{obs}$ , the metabolic rate derived from the observations on free-living animals, was calculated as described in section 4.6.2 using the observed dive duration (as  $ADL_{obs}$ ) and the calculated oxygen stores. The results are shown in Fig. 60 in relation to the metabolic rate found by Prange & Jackson (1976) in Green Turtles (Tab. 17).  $MR_{obs}$  represents the average oxygen consumption during a resting dive, i.e. from the moment of leaving the surface until surfacing again. It therefore represents not only resting metabolism but includes swimming activity during the short ascent and descent phase. Over the whole size range the significant regression for  $MR_{obs}$  shown in Fig. 60 as a solid line is lower than the metabolic rate calculated using the regression given by after Prange & Jackson (1976) with a deviation that increases with body mass for turtles less than 30 kg. The curves are parallel for turtles with a body mass of 30 to 80 kg (Fig. 60), diverging by ca.  $0.003 \text{ lO}_2/\text{kg}\cdot\text{h}$ .



**Fig. 60:** Size-dependent metabolic rate,  $MR_{obs}$ , calculated from observed dive durations of immature and non-nesting females (dots) and the calculated regression (solid line,  $y = 0.06x^{-0.202}$ ,  $R^2 = 0.66$ ,  $F = 11.5$ ,  $p < 0.05$ ). Gravid females (triangles) are excluded from regression. The dashed line shows the metabolic rate after Prange & Jackson (1976), as given in Tab. 17.

The data obtained from immature turtles and from non-nesting adult females enabled calculation of the metabolic rate during active dives (Fig. 61). On average the metabolic rate appears to be elevated by 59% (range 35 to 86%) over the oxygen consumption during resting dives.

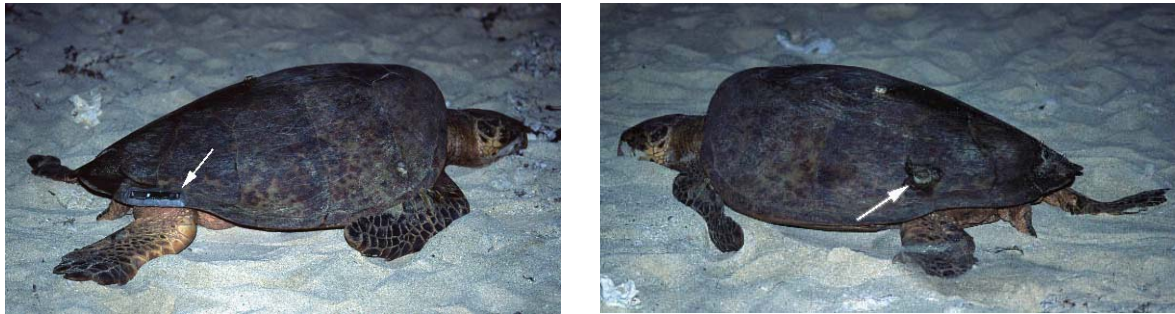


**Fig. 61:** Metabolic rate calculated using equation (5) for resting (blue) and active dives (red) of immature turtles (4.9 - 34.0 kg) and adult females in the foraging grounds (72.5 - 80.5 kg).

#### 4.6.4 Discussion

##### 4.6.4.1 Device effects

The influence of devices can be assumed to be minimal in the case of the adult females due to the small size of the Mk7 and the DK600 in relation to the size of the animal. Adult Hawksbill Turtles often carry (groups of) barnacles that reach, or sometimes even exceed the size of the attached devices (own observation, Fig. 62).



**Fig. 62:** Mk7 attached to an adult nesting female (left, arrow) and barnacle on the other side of the carapace (right, arrow).

Device effects might have occurred in the small immatures, however, the effect of additional drag of devices attached to aquatic animals increases exponentially with increasing swim speeds but is very low at swim speeds below 1 m/s (cf. Prange 1976, Wilson unpubl. data), such as occurred in the observed animals (see section 4.2.3.4, text and Fig. 41).

For a study of device effects Watson & Granger (1998) used a model of a juvenile Green Turtle (47.8 cm carapace length), that would approximate a 14 kg Hawksbill Turtle (van Dam & Diez 1998). The device tested by Watson & Granger (1998) was much larger (13.7 x 6.6 x 4.4 cm) than the data-recorders used in this study and had a box-like housing instead of a streamlined shape. The authors found the drag of the animal being increased by up to 30%, resulting in either a reduction of swim speed of 13% or an increase of 27% in energy used for power stroking. Such device effects would be greater in smaller animals because the relative size of the device is increased. Accordingly, the difference between resting and active metabolic rate in the data presented here would be greater in smaller animals. This is not the case, as the maximum gap between the oxygen consumption rate in resting and active dives was found in the largest of the immatures. It therefore can be assumed that the findings of this study are not influenced by the devices attached to the animals.

### 4.6.4.2 Validity of Literature Data

In the determination of  $ADL_{lit}$  from the literature data, the value used for metabolic rate is least robust as it is partially based on observations from a sea turtle resting on land (Prange & Jackson 1976). Therefore, any physiological adaptations to submergence (such as intra-cardiac shunt, bradycardia etc.) are not considered. Prange & Jackson (1976) also give a value for metabolic rate during activity derived from activity on land which, for a sea turtle, is, at best, a poor substitute for swimming behaviour. Consequently, it does not seem justified to use this metabolic rate to estimate energy expenditure for the time the turtles were actively commuting between sea floor and surface. However, by including data from previous studies, Prange & Jackson (1976) were able to give an equation for minimum metabolic rate that considers the body mass of the animals, which made this data most suitable for this study.

### 4.6.4.3 ADL

Anaerobic dives are inefficient for two main reasons; a) because the breakdown of anaerobic metabolites, such as lactate, requires long surface periods and b) less ATP is produced than during aerobic conditions (cf. Kooyman et al. 1980, Ydenberg & Clark 1989). The example of a Weddell Seal (Kooyman et al. 1980) shown in Fig. 58 (right graph) reveals that when serially submerging for 15 minutes the animal requires 4 min to replenish oxygen stores between the dives. While all of these dives are within the ADL of the seal (20 - 25 min, Kooyman et al. 1980), resulting in a continuous slope of 0.27, a dive of 45 min duration was considered to increase the blood lactate level due to anaerobic metabolism. The processing of these metabolites, which is slower than the oxygen uptake, necessitates a surface pause of 65 min (Kooyman et al. 1980). This changes the relationship between submergence and surface time, leading to a slope of 1.4 in Fig. 58 (right, arrow). In this example, the oxygen debt was completely paid back within one surface pause so that the seal could return to the previous pattern of aerobic diving.

Therefore, assuming that animals optimise for time, un-forced anaerobic dives should only occur when the animal gains substantially by executing them e.g. via foraging success that would not be achieved with aerobic dives (Ydenberg & Clark 1989). It is therefore little surprising that the vast majority of natural (un-forced) dives of different of aquatic animals are aerobic (Kooyman et al. 1981, Butler 1982). In the case of the Hawksbill Turtle a gain in foraging success through anaerobic diving is not to be expected, as this species feeds on sessile prey in relatively shallow coastal waters (Meylan 1988), which is readily available through aerobic dives.

The data from this study show that the turtles do not perform single dives or dive bouts that are separated by long periods of resting at the surface. Indeed, any switch from aerobic to anaerobic dives would result in a distinct break in the continuity of the line of the dive/pause ratio shown in Fig. 58. The lack of any such break and the fact that it is extremely unlikely that all the dives observed over a period of 46 hrs would be anaerobic, lead to the conclusion, that the turtles performed all dives within their ADL. Earlier studies on sea turtles support this assumption, despite the immense tolerance of sea turtles to hypoxia (Lutz et al. 1980, Lutcavage & Lutz 1996).

The aerobic dive limit derived from literature data corresponds reasonably well with the observations in immature turtles (Fig. 59). The smaller slope in the regression of  $ADL_{lit}$ , derived from Prange & Jackson's (1976) equation given in Tab. 17 causes  $ADL_{lit}$  and  $ADL_{obs}$  to diverge in higher size classes. Conversely,  $ADL_{lit}$  seems to bend more towards the data points of the gravid females, that were excluded from the regression of  $ADL_{obs}$  due to their different physiological status (see section 4.6.4.4). This is probably caused by the fact that part of the data used by Prange & Jackson (1976) was obtained from females caught on the beach after nesting. These individuals might not have been suitable for calculation of an allometric model, indicated by a slope that differs from a general allometric model for poikilotherms (Peters 1983) (see section 4.6.4.5).

## 4.6.4.4 Factors Influencing ADL

During the inter-nesting intervals the ADL of a gravid female can be influenced e.g. through its different hormonal status (cf. Keiver & Hochachka 1991). Furthermore, allometric parameters used in the calculations are not valid in gravid females, as lung volume per kg body mass is probably reduced due to the great volume of eggs and developing follicles within rigid body cavity and body characteristics (specific density and buoyancy at depth) might be changed. Therefore, the shortened  $ADL_{obs}$  that is clearly visible in Fig. 59, might not only be a result from hormonally increased metabolic rate (as indicated in Fig. 60) but rather from a combination of factors mentioned above.

Hawksbill Turtles rest on the bottom, in contrast to the Loggerhead Turtles, which, at least occasionally, rest within the water column by achieving neutral buoyancy (Minamikawa et al. 2000). Therefore, the depth of resting dives of Hawksbill Turtles is likely to be preconditioned by the habitat. A Hawksbill Turtle resting at a specific spot must avoid being positively buoyant at that given depth. Following Boyle's law, negative buoyancy is achieved when the turtle a) dives to a depth at which the fully-inflated lung is compressed enough so that the upthrust is smaller than the weight or b) the turtle only partially inhales so that negative buoyancy occurs at a lesser depth. The ability of sea turtles to adjust lung inflation to conform with the projected dive depth has demonstrated before (Jacobs 1940, 1942, Minamikawa et al. 2000). Since the major part of the oxygen supply at the onset of a dive is stored within the lungs (Lutcavage & Lutz 1996 in Lutz & Musick 1996), adjustment of lung volume to allow at least neutral buoyancy at a shallow resting place would reduce the ADL and should therefore be avoided under the aspect of optimising (resting) dive behaviour, i.e. when the rate of trips made to the surface is to be minimised.

On the other hand, resting spots below the level of slightly negative buoyancy would increase the energy involved in commuting. However, the resting depth might be preconditioned by habitat characteristics, something that might explain some data points in Fig. 59 where  $ADL_{obs}$  is relatively low. While the reason why QQD 280 and QQD 048 rested in shallow waters is difficult to assess due to the unknown characteristics of their foraging grounds, a link can be made between data set 121a and 128 b and the known underwater topography off Mona Island. While the other three immature turtles resided off

Sardinera on a wide plateau with a shallow slope, the two turtles performing shorter dives were caught off Carabinero where suitable resting spots might be limited to the depth range of 8 to 10 m due to the steep drop-off.

However, care must be exercised due to individual differences in physiology resulting in variable ADL; different fitness or diseases can alter the relation between oxygen stores and rate of depletion (Lutcavage & Lutz 1996). The extraordinary long dive duration of one of the immature turtles (No. 121b) is an example of these possible variations. Effects of buoyancy adjustments in Hawksbill Turtles should be further investigated by experimentally attaching weights and floats to change the buoyancy of one individual, as has been done on pelagic resting Loggerhead Turtles (Minamikawa et al. 2000).

#### 4.6.4.5 Metabolic Rate

The calculated metabolic rates of the Hawksbill Turtles during resting dives, based upon the observed  $ADL_{obs}$  and ranging from 0.021 to 0.048 l O<sub>2</sub>/kg\*h, are below those given for adult Leatherbacks (0.066 l O<sub>2</sub>/kg\*h), Olive Ridleys (*Lepidochelys olivacea*) and Green Turtles (both 0.072 l O<sub>2</sub>/kg\*h), derived from calculations of body heat production (Mrosovsky & Pritchard 1971). Measurements for the latter study were taken during egg-laying and therefore obviously referred to highly active animals. The highest values obtained in the present study for oxygen consumption during active dives (0.034 - 0.066 l O<sub>2</sub>/kg\*h) are close to this previously published metabolic rates. This is surprising because Leatherback Turtles, being very different from the species of the family *Cheloniidae*, are reputed to have an unusually high metabolic rate (Spotila et al. 1996) and in addition nesting activity on land should put a much higher energetic demand onto sea turtles than swimming. However, maximum values of the Hawksbill Turtles observed here stem from the smallest of the immature turtles and therefore likely represent the size-dependency of metabolic rate, decreasing with animal size (Peters 1983). As expected, the maximum metabolic rate of the adult turtles in the foraging grounds, 0.053 l O<sub>2</sub>/kg\*h, was less than the rates found by Mrosovsky & Pritchard (1971). Estimates of metabolic rate derived from  $ADL_{obs}$  are maximum metabolic rates, as it is unlikely that turtles would completely deplete their oxygen store during a routine dive. The model for  $MR_{obs}$  declining



with increasing body size compares well with the findings from Prange & Jackson (1976) as shown in Fig. 60. The power term under which the  $MR_{\text{obs}}$  decreases (-0.202) is close to the value of -0.249 given by Peters (1983) concerning allometric scaling in energy expenditure of poikilotherms.

### 4.6.4.6 Dive Duration

The observed difference in dive duration at night and day in non-nesting females and immature turtles reflects the trade off between distance actively covered during a dive and time spent submerged. A sea turtle searching for food during day appears to sacrifice on average 36% (SD = 8.6, n = 8) of the dive duration for the benefit of active foraging, along with an increased metabolism.

The dive duration in immature turtles increased with body size (Fig. 56). This trend is expected since it corresponds to the effect of mass-specific metabolic rate (see Peters 1983 for review), so that depletion of oxygen stores is slower in larger animals. However, this is also dependent on the lung volume being linearly related to the body mass. To date, no study has investigated the relative growth of sea turtle lungs during ontogenesis. As the growth rate of immature Hawksbill Turtles as well as their size at maturity appears to vary with extrinsic factors such as food availability (Diez & van Dam 2002) it might be possible that the growth of inner organs relative to body size of immature turtles shows a high individual variability as well.

Such individual variation could explain why no correlation between dive duration and body mass could be found in the non-nesting females. A higher sample size would help to clarify the issue. In addition, unquantified differences in the habitats away from nesting grounds make interpretations of size-dependent dive duration in non-nesting females impossible.

The decrease of the dive duration with increasing body mass in gravid females (Fig. 57) is surprising, as it contrasts the findings in immature turtles as well as the expected trend. One speculative reason could be differences in clutch size as a larger number of eggs would expand further into the space usually available for inner organs such as the lungs.

Again, further studies would be desirable to enhance the sample size and verify or correct this trend to eventually elucidate factors influencing dive duration.

In the present study the attempts to obtain inter-nesting data as well as inter-seasonal data from the same individuals failed in four cases due to a) malfunction of a inter-nesting device, b) loss of a long-term device, c) failed re-migration of equipped animal and d) pending recovery of data from the long-term logger. Further studies are needed to investigate the intra-individual differences between submergence behaviour in the inter-nesting interval and diving at the foraging ground to obtain data where the seasonal differences can be differentiated from individual variations.

## 5 CONCLUSIONS AND OUTLOOK

When applying expensive telemetric techniques to large free-ranging animals, in particular to endangered species, special attention must be given to the well-being of the animals, and small sample sizes are, unfortunately, generally inevitable.

Despite this, the present study succeeded in investigating the at-sea behaviour of Hawksbill Turtles over different phases of the life cycle using data-recording devices. It was possible to address a number of factors that influence their dive performance; body size, reproductive status, storm conditions and seasonal fluctuations of water temperature. The complexity of this matter was elucidated in this work, offering new insights as well as starting points for future investigations.

The speed sensors used in this study did not function as expected, so that calculations of the 3-dimensional routes proved problematic. However, the latest generation of speed sensors shows promise to further enhance the accuracy of the dead-reckoning methodology for slow swimming animals. With regards to the estimates of activity, the use of compass signals was found to be more promising than measurements of swim speeds.

Overall it appeared that Hawksbill Turtles have a distinctive diel pattern of daytime activity and nocturnal resting for the major part of their life, demonstrated here for both immatures and adult females at the foraging grounds. This pattern changed markedly during the inter-nesting interval. While activity is not dependent of daytime for most of the time between nestings, the turtles even switch over to nocturnal activity for the duration of the nesting restlessness, beginning 13 days after the previous egg laying.

Some areas serve as inter-nesting habitat for the females of one population, while other females, nesting elsewhere, may use the site as a foraging ground. Mona Island is an example of such a combined feeding and nesting ground. With the patterns described within this study it would be possible to determine the stock (breeding or otherwise) of an unknown female simply by recording its dive behaviour over ca. 24 hrs. Thus far, the only way this has been achieved is by invasive laparoscopy used to evaluate the status of the ovaries (Wood et al. 1983).

## 5 Conclusions and Outlook

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The use of modern telemetry, including the present study, delivered evidence that the dispersal pattern of Buck Island's nesting Hawksbill Turtles radiates more than previously concluded from tag returns, the latter mostly occurring to the west of Buck Island. This emphasises the need for methods of tracking that are independent from the different local chances of turtles being caught. Apart from a future increase in sample size repeated long-term studies of individual female Hawksbill Turtles it would be desirable to investigate a possible feeding ground fidelity over the lifespan. For a completion of the picture data from adult male Hawksbill Turtles is still needed that due to technical problems could not be obtained in the course of this work. The use of compass units for all such studies would greatly enhance the insight into activity patterns which would otherwise be inaccessible in that accuracy.

In the past it has been shown to be difficult to maintain a device attached and operational on a free-ranging sea turtle over several months. In this regard this study was a great success also, especially because the return of the females to Buck Island and their successful nesting seasons can be taken as a proof for their well-being.

A fourth long-term device was retrieved shortly before this thesis was finished, with data download still pending. Therefore, the desirable enlargement of sample-sizes is currently been worked on.

## 6 SUMMARY

Despite the popularity of all species of sea turtles little is known about the at-sea-behaviour of these marine reptiles. While early studies focussed on the biology of the females and hatchlings at the nesting beaches, modern technology now enables the study of sea turtles in their aquatic environment where females spend most of their time, while juveniles and are exclusively aquatic.

This thesis deals with the behaviour of adult female and juvenile Hawksbill Turtles, analysing aspects of diving performance under various conditions. The fieldwork was carried out at Buck Island Reef National Monument (U.S. Virgin Islands) and Mona Island (Puerto Rico). Data-loggers were deployed on the turtles to record water temperature, light intensity, velocity, depth, compass heading and position in space. The intervals of data sampling varied between 0.25 and 15 sec.

An attachment method was developed that allows repetitive data-logger deployments on sea turtles during successive inter-nesting intervals with minimal handling times (15 min for the first deployment and 2 min for successive attachments) and with minimal stress for the nesting animal.

During the nesting seasons of 1998 and 1999, complete recordings of the whole inter-nesting interval were obtained from seven individuals, covering a total of ten intervals (mean duration 15 d). On average the turtles spent 95% of their time submerged at a median dive duration of 35.9 min and a median surface interval of 1.2 min. Within the inter-nesting intervals three phases of behaviour could be distinguished on the basis of the depth profiles: a) irregular post-nesting behaviour, b) very regular dive behaviour with long submergence times and little variation and c) nesting restlessness prior to next egg-laying. The ratio between dive duration and surface times was found to decrease during the first and the last phase of the interval, while it was high in the long central phase. The benthic dive pattern demonstrated that the females usually stayed within the shallow reef

area (mostly < 20 m), except for two turtles that performed few exceptional dives (2 and 11 dives, respectively) to depths of up to approx. 70 m.

The sequences of low and high variability of compass data revealed, on the one hand, the prevailing resting status of the inter-nesting turtles, on the other hand it characterised, as expected, short periods of increased activity after egg-laying (cf. Phase a) as well as prior to the next nest (days 13 and following, cf. Phase c). An unexpected, formerly not described, peak of activity was found at days 7 and 8 of the interval.

In 2001 a new generation of short-term devices was used to record the diving behaviour of five immature Hawksbill Turtles (122 hrs in total) off Mona Island with high temporal resolution (2 Hz and 4 Hz sampling frequency). Spending 97% of their time under water, the juvenile turtles performed shorter dives during the day than at night, combined with an inverse pattern in surface duration. The compass signal revealed strict shifts of diurnal activity and nocturnal resting. The mean swim speeds during ascent and descent phases were 0.1 to 0.4 m/sec, the maximum observed velocity was 2.1 m/sec.

One of the females equipped in 1999 experienced a hurricane during the inter-nesting interval. The recorded data showed that during the storm the animal virtually completely lacked the typical resting periods during the bottom phase of the dives. However, the turtle did not, as expected, move to the deeper water close by, but rather stayed in the shallows. Apart from the long-known effect of destruction of nesting habitat, the storm-induced drop in water temperature of up to >1°C measured over several days is assumed to have a non-negligible influence on inter-nesting sea turtles.

To conduct a long-term study, six female Hawksbill Turtles were equipped at the end of the peak nesting season in 1999 with recorders monitoring water temperature, light intensity and dive depth over time (temperature at 15 min, light and depth at 30 sec intervals) for the duration of the re-migration interval (approx. 2 years). Three data sets of up to 24 months were obtained, again showing discrete phases of behaviour over time; a) foraging migration, b) stationary foraging, c) breeding migration and d) pre-nesting. While

the observed Hawksbill Turtles usually showed a clear behavioural pattern of daytime-activity, a switch towards a diel indifferent pattern occurs at the onset of the nesting season and finally high nocturnal activity around the time of nesting.

Analysis of recorded light intensity data using the geo-location system (GLS) methodology revealed the direction of migration of the three females successfully equipped for the long-term study. The Hawksbill Turtles moved to individual foraging grounds that were 70, 170 and 360 km away from the nesting site. All animals migrated for several days (estimates between 2 and 12 d) in different directions. The typical travel speed was estimated to be 1.5 km/h. Currents did not seem to influence the direction taken by the animals. However, where animals encountered currents they appeared to influence the speed of travel.

The three long-term data sets showed fluctuations in water temperature over the seasons (24 to 30°C). In nocturnal resting dives during the months of the stationary foraging phase the dive duration of the turtles was negatively correlated with water temperature, i.e. during the winter, when the water temperatures dropped, the submergence events lasted longer than during the warmer periods. Resting dive duration was used as a relative measure of metabolic rate, resulting in a  $Q_{10}$  of 4.36 for temperatures below 28°C. For active daytime dives a  $Q_{10}$  of 2.3 was calculated.

Data were collected from Hawksbill Turtles of a very broad size range (4.9 to 95.0 kg), i.e. from animals with very different theoretical aerobic dive limits. The recordings of dives and surface periods proved that dives were performed within these individual limits. Based upon these results, models are provided describing the size-dependency of the aerobic dive limits (e.g. 60 min for a medium sized 50 kg turtle) and of the metabolic rate (e.g. 0.027 lO<sub>2</sub>/kg\*h for a body mass of 50 kg). During active dives the metabolic rate appeared to be elevated by 59% (range 35 to 86%) above resting-dive rates. Effects of additional drag caused by the devices attached to the studied animals are extremely unlikely due to the similar size of the devices and the barnacles frequently found attached to the carapace, as well as due to the rather slow swimming speeds.

# 7 ZUSAMMENFASSUNG

Trotz der allgemeinen Popularität von Meeresschildkröten ist wenig bekannt über das Verhalten dieser marinen Reptilien in ihrem eigentlichen Lebensraum, auf See. In den ersten Jahrzehnten der Meeresschildkrötenforschung waren die Untersuchungen auf das Verhalten der Weibchen und der schlüpfenden Jungtiere am Niststrand ausgerichtet, obwohl adulte Weibchen fast ausschließlich und Männchen sowie Jungtiere völlig aquatisch leben. Erst in jüngster Zeit ermöglicht der technische Fortschritt Studien an schwimmenden Schildkröten.

Die vorliegende Arbeit beschäftigt sich mit dem Verhalten sowohl adulter Weibchen als auch juveniler Karettschildkröten und analysiert die aufgezeichneten Tauchgänge in Abhängigkeit von unterschiedlichen extrensischen und intrensischen Bedingungen. Die zugrundeliegenden Freilandarbeiten wurden zum einen im Gebiet von Buck Island Reef National Monument (Amerikanische Jungferninseln), zum anderen vor Mona Island (Puerto Rico) durchgeführt. Die an den Karettschildkröten befestigten Geräte zeichneten Wassertemperatur, Lichtintensität, Schwimmgeschwindigkeit, Tiefe, Himmelsrichtung und Lage im Raum in Messintervallen zwischen 0.25 und 15 sek auf.

Es wurde eine Befestigungsmethode entwickelt, die das wiederholte Ausrüsten von Meeresschildkröten zwischen mehreren aufeinanderfolgenden Eiablagen ermöglicht. Die neue Methode vereint eine schnelle Befestigung mit einer sehr schonenden Behandlung des Tieres.

Während der Nistperioden der Jahre 1998 und 1999 konnten erfolgreich zehn vollständige Nistintervalle von sieben Weibchen aufgezeichnet werden. Die mittlere Dauer dieser Intervalle zwischen zwei Eiablagen betrug 15 Tage. Im Durchschnitt verbrachten die untersuchten adulten Karettschildkröten 95% ihrer Zeit unter Wasser, wobei die Tauchgänge und die Oberflächenintervalle im Mittel 35.9 min bzw. 1.2 min dauerten.



Innerhalb der Nistintervalle konnten, basierend auf den Tauchprofilen, drei Phasen unterschiedlichen Verhaltens charakterisiert werden: a) unregelmäßiges Verhalten nach Verlassen des Niststrandes, b) regelmäßiges Muster von langen Tauchgängen und c) Nist-Unruhe vor der folgenden Eiablage. Das Verhältnis von Tauchdauer zur Dauer der Oberflächenphase war in der mittleren Phase, die den größten Teil des Intervalls ausmacht, sehr hoch, während es sich in der Anfangs- und Endphase verringerte. Aufgrund ihres benthisch-orientierten Tauchverhaltens konnte ermittelt werden, daß sich die weiblichen Karettschildkröten zwischen den Eiablagen im flachen Riffbereich (meist < 20 m) aufhielten. Zwei Individuen zeigten kurzzeitig abweichendes Tauchverhalten, indem sie 2 bzw. 11 Tauchgänge in größere Tiefen von bis zu 70 m durchführten.

Zeitliche Abschnitte mit niedriger bzw. hoher Variabilität in den Kompassdaten wiesen einerseits die charakteristischen Ruhephasen im Nistintervall nach, andererseits ergaben sie, wie erwartet, ein typisches Muster an verstärkter Aktivität unmittelbar nach der Rückkehr ins Wasser (entsprechend Phase a) sowie kurz vor der folgenden Eiablage (nach dem 13ten Tag, entsprechend Phase c). Ein unerwarteter, zuvor so noch nicht beschriebener Anstieg der Aktivität wurde um den 7ten und 8ten Tag des Intervalls nachgewiesen.

In der Freilandsaison 2001 wurden verbesserte Datenspeicher für Aufzeichnungen des Tauchverhaltens von fünf juvenilen Karettschildkröten vor Mona Island eingesetzt. Über insgesamt 122 Stunden wurden Daten in hoher zeitlicher Auflösung (2 bzw. 4 Hz) gespeichert. Insgesamt verbrachten die Jungtiere 97% ihrer Zeit unter Wasser, wobei sie nachts längere Tauchgänge und kürzere Oberflächenpausen zeigten als während der hellen Tageszeiten. Die Kompassdaten verrieten einen strikten Wechsel zwischen aktivem Tag- und ruhendem Nacht-Verhalten. Die mittlere Schwimmgeschwindigkeiten beim Auf- und Abtauchen lagen zwischen 0.1 und 0.4 m/sek, maximal wurden 2.1 m/sek gemessen.

Während der Nistsaison 1999 traf ein Hurrikan das Untersuchungsgebiet. Bei einem der ausgerüsteten Weibchen konnten erstmalig kontinuierliche Daten während eines Wirbelsturmes aufgezeichnet werden. Die Auswertungen ergaben, daß die Schildkröte während des Hurrikans nicht ihr normales Muster an Ruhetauchgängen aufrecht erhielt,

sondern fast ständig in Bewegung war. Jedoch suchte sie nicht, wie erwartet, die in unmittelbarer Nähe liegenden größeren Tiefen auf, sondern blieb im flachen Wasserbereich. Die Meßdaten lassen vermuten, daß nicht nur der häufig diskutierte Effekt der Niststrand-Zerstörung durch Wirbelstürme, sondern auch die Verringerung der Wassertemperatur (hier um bis zu  $>1^{\circ}\text{C}$ ) über mehrere Tage hinweg einen nicht unerheblichen Einfluß auf Meeresschildkröten im Nistintervall haben kann.

In einer Langzeit-Studie wurden gegen Ende der Nistsaison 1999 sechs weibliche Karettschildkröten mit Geräten ausgerüstet, die Wassertemperatur, Lichtintensität, und Tauchtiefe (Temperatur alle 15 min, Licht und Tiefe in 30 sek Intervallen) über die Dauer der Re-Migrationsphase (ca. 2 Jahre) aufzeichneten. Es konnten drei Datensätze über einen Zeitraum von bis zu 24 Monaten gewonnen werden, in denen wiederum im zeitlichen Verlauf deutlich unterschiedliche Phasen erkennbar waren: a) Wanderung zu den Freßgründen, b) stationäre Phase im Freßgebiet, c) Wanderung zum Fortpflanzungsgebiet, d) Vorläufer des Nistverhaltens. Diese Studie zeigt, daß Karettschildkröten trotz ihrer grundsätzlich deutlich ausgeprägten Tagesaktivität mit Beginn der Nistsaison diesen klaren Rhythmus verlieren. Die Tage unmittelbar vor und nach der Eiablage sind sogar von starker nächtlicher Aktivität geprägt.

Die Analyse der aufgezeichneten Lichtintensitäten mit Hilfe des Geo-Lokations Systems (GLS) zeigte, daß alle drei erfolgreich ausgerüsteten Weibchen das Gebiet um Buck Island in unterschiedliche Richtungen verließen. Die Karettschildkröten wanderten zu verschiedenen Freßgründen, die jeweils 70, 170 bzw. 360 km von der Nistinsel entfernt lagen und benötigten dafür mehrere Tage (die Abschätzungen liegen zwischen 2 und 12 Tagen). Die typische Reisegeschwindigkeit wurde auf 1.5 km/h geschätzt. Die vorherrschenden Strömungen hatten offenbar keinen Einfluß auf die Wahl der Schwimmrichtung, beeinflussten aber die Reisegeschwindigkeit.

Die drei Langzeit-Datensätze wiesen jahreszeitliche Schwankungen in der Wassertemperatur nach, die sich zwischen 24 und  $30^{\circ}\text{C}$  bewegte. Bei den nächtlichen Ruhetauchgängen während der stationären Monate in den Freßgebieten konnte eine

negative Korrelation der Tauchdauer mit der Wassertemperatur nachgewiesen werden, d.h. im Winter dauerten die entsprechenden Tauchgänge länger als im Sommer. Die Dauer der Ruhetauchgänge wurde als Grundlage zur Berechnung relativer Stoffwechselraten verwendet, woraus ein  $Q_{10}$  von 4.36 für Temperaturen unter 28°C resultierte. Für aktive Tagestauchgänge wurde ein  $Q_{10}$  von lediglich 2.3 berechnet.

Die Daten in dieser Studie stammen von Tieren sehr unterschiedlicher Körpermasse (4.9 bis 95.0 kg). Bedingt dadurch weist auch die theoretische Größe der aerobischen Tauchdauer ein breites Spektrum auf. Die aufgezeichneten Daten von Tauchdauer und Oberflächenzeiten zeigen, daß die Tauchgänge jeweils innerhalb dieses Tauch-Limits durchgeführt wurden. Darauf basierend wurden Modelle errechnet, die die Abhängigkeit der aerobischen Tauchdauer (z.B. 60 min bei 50 kg) sowie der Stoffwechselrate (z.B. 0.027 lO<sub>2</sub>/kg\*h bei 50 kg) von der Körpermasse beschreiben. Bei aktiven Tauchgängen ergab sich im Mittel eine Erhöhung der Stoffwechselrate um 59% (zwischen 35 und 86%) gegenüber den als 'ruhend' eingestuften Tauchereignissen. Geräteeffekte durch die befestigten Datenspeicher konnten als extrem unwahrscheinlich eingestuft werden, da häufig Gruppen von Seepocken in ähnlicher Größenordnung auf den Panzern der Karettschildkröten gefunden wurden und zudem die Schwimmgeschwindigkeiten bei diesen Tieren relativ niedrig sind.



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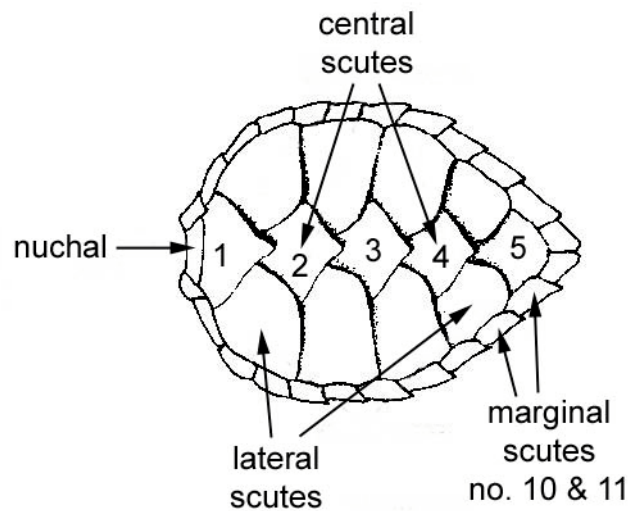
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## 10 DEFINITIONS AND ABBREVIATIONS

- central scutes (No 1-5): syn. vertebral or neural scutes, scutes aligned along the spine (see Fig. 63); ≠ plates of the bony carapace
- marginal scutes (No 1-11): scutes bordering the keratinous carapace (see Fig. 63); ≠ plates of the bony carapace
- SCL: straightline maximum carapace length, taken from nuchal to longest tip of posterior marginal scute (see Fig. 63)



**Fig. 63:** Keratin scutes of a Hawksbill Turtle's carapace.

- inter-nesting interval: time between two successive ovipositions within a single nesting season
- re-migration interval: time between two successive nesting seasons, Hawksbill Turtles at Buck Island typically re-migrate after 2 to 4 years (Hillis-Starr pers. comm.)
- false crawl: unsuccessful nesting attempt
- day: defined here as time between 06:00 and 17:59 local time
- night: defined here as time between 18:00 and 05:59 local time

- pitch: angle of body position, head-up or head-down
- dive depth: maximum depth reached during dive event considered
- depth: instantaneous depth of the turtle
- DSR: dive/surface ratio, quotient of the time spent submerged divided by the duration of a complete dive cycle (dive time plus surface interval)
- BUIS: Buck Island Sea Turtle Research Program
- NPS: National Park Service
- DRNA: Departamento de Recursos Natuales y Ambientales
- GLS: Geo-Location System
- ADL: Aerobic dive limit





## APPENDIX

**Tab. A 1:** Sample size (n) and interquartile range (IQR) of dive duration recorded during the 3 phases (rows) of 10 inter-nesting intervals (columns), separated for day and night.

<i>Interv.</i>	1		2		3		4		5		6		7		8		9		10		
	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	
ph 1	n	18	17	13	15	10	12	14	9	16	16	17	14	13	17	34	24	16	10	20	17
	IQR	14	16	22	38	38	27	20	16	18	16	8	18	35	25	12	9	32	24	7	22
ph 2	n	272	263	156	147	168	153	191	174	295	229	209	207	307	181	378	285	190	179	204	194
	IQR	21	23	19	27	22	22	12	13	42	12	8	10	47	14	29	18	26	19	10	11
ph 3	n	53	89	82	77	68	66	104	95	110	82	16	13	41	92	144	183	46	18	120	132
	IQR	30	8	53	23	39	32	37	28	40	16	20	18	55	6	18	13	15	20	53	29

**Tab. A 2:** Sample size (n) and interquartile range (IQR) of surface intervals recorded during the 3 phases (rows) of 10 inter-nesting intervals (columns), separated for day and night.

<i>Interv.</i>	1		2		3		4		5		6		7		8		9		10		
	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	d	n	
ph 1	n	18	17	13	15	10	12	14	9	16	16	17	14	13	17	34	24	16	10	20	17
	IQR	0.3	0.3	1.0	0.4	0.7	0.7	0.4	1.0	0.7	0.1	0.6	0.4	1.0	0.6	0.7	1.0	0.9	1.2	0.4	0.7
ph 2	n	272	263	156	147	168	153	191	174	295	229	209	207	307	181	378	285	190	179	204	194
	IQR	0.7	0.3	0.7	0.4	0.4	0.3	0.3	0.3	1.2	0.4	0.6	0.3	1.0	0.1	1.0	0.3	0.7	0.3	0.3	0.3
ph 3	n	53	89	82	77	68	66	104	95	110	82	16	13	41	92	144	183	46	18	120	132
	IQR	1.0	2.4	1.3	5.2	1.3	11	1.0	1.0	1.2	4.8	0.6	0.6	1.4	5.0	0.9	1.9	1.6	2.2	1.2	1.3

**Tab. A 3:** Mann-Whitney statistics to test for significant differences in dive duration between phase 2 and 3. Cases of significant differences are marked with asterisks (\*\*  $p < 0.001$ , \*  $p < 0.05$ ).

<i>Interv. No.</i>	<i>SI day</i> <i>Z</i>	<i>SI night</i> <i>Z</i>	<i>DD day</i> <i>Z</i>	<i>DD night</i> <i>Z</i>
1	0.387	1.779	1.368	9.761**
2	2.651*	1.101	4.631**	9.384**
3	1.294	1.539	4.652**	9.626**
4	0.052	4.072**	6.521**	10.566**
5	2.310*	0.474	2.312*	10.507**
6	2.588*	1.366	2.678*	5.416**
7	1.933	1.159	3.842**	12.997**
8	3.040**	0.415	1.974*	13.362**
9	3.269*	2.913*	8.049**	5.534**
10	0.872	1.350	2.855*	10.492**

## PUBLIKATIONEN

Teile der vorliegenden Arbeit wurden mit Genehmigung des Dekans der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel bereits publiziert:

Storch S, Hillis-Starr ZM, Wilson RP (2000) Turtles in the Reef: A Closer Look at the Activities of Hawksbill Turtles in a Caribbean Internesting Habitat. In: Kalb HJ, Wibbels T (eds) Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce, NOAA Tech Memo NMFS-SEFSC-443: 32-35

Storch S, Wilson RP, Hillis-Starr ZM (2000) Sub-surface movements of Caribbean hawksbill turtles (*Eretmochelys imbricata*) during the nesting season elucidated through archival tags. *Zoology*, 103: 36

Storch S, Hillis-Starr ZM, Wilson RP (2002) Things to Do, Places to Be: Inter-Nesting Diving Behavior of Caribbean Hawksbill Turtles elucidated through Archival Tags. In: Mosier A, Foley A, Brost B (eds) Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce, NOAA Tech Memo NMFS-SEFSC-477: 34-36

Storch S, Hillis-Starr ZM, Wilson RP (2003) Caribbean round-trip ticket: the migration behavior of female Hawksbill Turtles recorded using data loggers. In: Seminoff JA (ed) Proceedings of the Twenty-second Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce, NOAA Tech Memo NMFS-SEFSC-503: 54-55

Storch S, Zankl S (2003) Repetitive Data-Logger Attachments to Sea Turtles Using a New Quick-Release Method. *Chelonian Conservation and Biology* 4(3): 717-720

Storch S, Wilson RP, Hillis-Starr ZM, Adelung D (subm. to Marine Ecology Progress Series) Cold-blooded Divers: Temperature-dependent dive performance in free-living Hawksbill Turtles *Eretmochelys imbricata*.



## LEBENS LAUF

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## **Erklärung**

Hiermit erkläre ich, daß die vorliegende Dissertation nach Inhalt und Form - abgesehen von der Beratung durch meine wissenschaftlichen Lehrer - meine eigene Arbeit ist. Es wurden keine anderen als die angegebenen Hilfsmittel verwendet.

Die Arbeit hat weder ganz noch zum Teil zuvor einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen.

Kiel, den 18.12.2003





