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First records of flipper beat frequency during sea turtle diving

G.C. Hays[a,*], J.D. Metcalfe[b], A.W. Walne[c], R.P. Wilson[d]

[a] *School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP, UK*
[b] *The Centre for Environment, Fisheries and Aquaculture Science,*
Lowestoft Laboratory, Lowestoft NR33 0HT, UK
[c] *Sir Alister Hardy Foundation for Ocean Science, Citadel Hill, Plymouth, UK*
[d] *Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany*

Abstract

Depth and flipper movements were simultaneously measured during 23 dives for a free-swimming green turtle (*Chelonia mydas*) at Ascension Island. A few characteristic dive profiles that have been widely reported in hard-shelled turtles were recorded. Flipper movements revealed that, on dives to midwater, there was generally active swimming, compared to long periods of inactivity on dives to the seafloor. During all dives, there were clear changes in the flipper beat frequency during the descent. On leaving the surface, flippers beats occurred quickly (typically 30–40 beats min^{-1}) and then as the descent continued the frequency declined (typically to about 10–14 beats min^{-1}). These observations match the general pattern reported for other air-breathing divers for increased effort at the start of the descent to overcome initial positive buoyancy.

Keywords: Buoyancy; Dive; Descent; Ascent; *Chelonia mydas*; TDR; IMASU; Penguin; Seal

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1. Introduction

Over the last decade or so, the extensive deployment of dive computers, generally termed Time Depth Recorders or TDRs, has provided a huge amount of information about dive profiles and surfacing intervals for a range of marine species, with mammals and birds being a focus for many studies (Schreer et al., 2001). However, establishing details of the behaviours performed during dives is difficult by using TDRs alone, since the

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* Corresponding author. Tel.: +44-1792-295375; fax: +44-1792-295447.
E-mail address: g.hays@swan.ac.uk (G.C. Hays).

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variety of activities that may potentially be associated with dives, e.g. feeding, travelling or resting, cannot be separated conclusively from information about the dive profile alone. We might consider an analogy with a terrestrial animal: by simply recording the movements in one spatial dimension, it would be impossible to separate movements to find prey, to seek shelter, to search for mates, etc.

In the case of marine divers, more light can be shed on the behaviours performed during dives by measuring other parameters in addition to depth. For example, by deploying visual imaging systems, the behaviours associated with prey capture have been identified in some marine mammals (e.g. Fuiman et al., 2002; Hooker et al., 2002); activity and swim speed sensors have been used to identify whether animals are moving or are motionless during dives (Hochscheid et al., 1999; Minamikawa et al., 2000; Eckert, 2002); instruments that record jaw-opening have been used to identify when penguins attempt to ingest prey during dives (Wilson et al., 2002).

For marine mammals and penguins, the deployment of equipment to measure individual flipper beats has revealed some commonalities in their diving behaviour. Most noticeably, it has been shown that the reduction in buoyancy during descent due to compression of the lungs (and also air trapped in the plumage in birds) is often accompanied by a reduction in the swimming effort (Lovvorn et al., 1999; Skrovan et al., 1999; Williams et al., 2000; Wilson et al., 1992). Generally, the explanation for these observations is couched in terms of divers working harder at the start of dives so that they can descend efficiently through the zone of high near-surface buoyancy (Wilson et al., 1992). If swimming effort during descent is indeed determined by buoyancy state, then we would predict the same pattern of effort versus depth in other divers in addition to mammals and birds. In order to test this prediction, for a free-living green turtle (*Chelonia mydas*), we simultaneously deployed a TDR in conjunction with a movement sensor designed to measure individual flipper beats. By examining the pattern of flipper beats throughout dives, we also shed more light on the function of different dive types commonly exhibited by turtles.

2. Materials and methods

2.1. General occurrence of different dive types

Fieldwork was conducted on Longbeach, Ascension Island (7°57′ S, 14°22′ W), a major nesting site for green turtles (Mortimer and Carr, 1987). In order to assess the relative occurrence of different dive profiles for free-living green turtles at Ascension Island, between 21 March and 26 March 2002, we deployed TDRs to record the diving behaviour of six turtles throughout the entire internesting interval, which lasted between 11 and 13 days. In total, these deployments provided 69 days of dive data. Two types of TDR were used (both manufactured by LOTEK Marine Technologies, St. John’s, Newfoundland): (a) LTD_1200 (weight in air 16 g, weight in seawater 1 g, dimensions 18 × 57 mm), which recorded depth every 5 s with resolution of 4 cm; and (b) LTD_1100 (weight in air 5 g, weight in seawater 2 g, dimensions 8 × 16 × 27 mm), which recorded depth every 52 s with resolution of 30 cm. Dive data were analysed using bespoke software (MultiTrace, Jensen Software Systems, Laboe, Germany). Following the terminology of Hays et al. (2000) and Hays et al. (2001), we assessed the occurrence of U-dives and types 1 and 2 midwater dives. U-dives had a flat bottom phase indicative of dives to the seafloor. Types 1 and 2 dives were both characterized by a gradual ascent during the bottom phase, with gradual ascent commencing at the start of the bottom phase in type 1 dives, while in type 2 dives the gradual ascent was preceded by a brief excursion to deeper water. The distinction between types 1 and 2 dives (i.e. the extent of the brief excursion required before a type 1 dive becomes a type 2 dive) is somewhat arbitrary. In addition, we examined the occurrence of deep V-dives, i.e. dives where there was a direct descent and ascent from the maximum depth with little time spent at this maximum depth. Examples of these different dive profiles will be shown in the results.

To extract dive parameters for each dive, dives were defined as having a maximum depth of ≥ 5 m for types 1 and 2 dives and U-dives and ≥ 20 m for V-dives, with the start and end of the dive occurring when the vertical descent/ascent rate exceeded 0.3 m s^{-1}. The start and end of the bottom phase was defined by a threshold vertical speed of 0.02 m s^{-1}. Visual analysis of individual dive profiles confirmed that these parameters successfully captured the different profiles.

2.2. Flipper beat records

At 04:00 (GMT) on the 29 March 2002, we located a turtle that had aborted its nesting attempt and was returning to the sea. We attached two instruments to this individual: a TDR (LTD_1100, Lotek Marine Technologies), which measured depth and water temperature and an IMASU (Integrated Movement Assessing Sensory Unit, Driesen and Kern, Bad Bramsted, Germany, weight in air 47 g, maximum dimensions 72 × 33 × 17 mm) to measure flipper movements. For protection, both instruments were placed in a single plastic housing, where they were held in place with stainless steel wire, and attached to the second central scute of the carapace using quick setting epoxy (Foilfast, SFS Stadler). The top of the plastic housing was open to allow water exchange. The TDR measured depth every 14 s, with a resolution of 30 cm. The IMASUs consisted of a data logger attached by a 40-cm lead to a Hall sensor, which measured the local magnetic field. The Hall Sensor and lead were threaded through Tygon™ tubing, to afford protection and allow easy removal of the sensor and lead. The Tygon™ tubing was again attached to the carapace with epoxy so that the Hall sensor was positioned on the leading edge of the carapace on the first marginal scute. A magnet was attached with epoxy and waterproof Duck™ tape to the largest scale on the trailing edge of the front flipper. With this positioning, it was expected that as the flipper moved during swimming the magnet would alternately move towards and away from the Hall sensor, giving an expected sinusoidal output from the Hall sensor associated with each flipper beat. The Hall sensor measured the magnetic field at 10 Hz. We used a neodymium rare-earth magnet that was disk shaped, measuring 38 mm in diameter by 6 mm thick. Trials before deployment showed that, in the optimum alignment (i.e. magnet approaching directly in line with the Hall sensor), the Hall sensor would perceive the magnet at a distance of 15 cm. Aquarium trials (see below and also Wilson and Liebsch, 2003) indicated that our positioning of the magnet and Hall sensor on the free-living turtle were optimized so that the magnet would approach within 15 cm of the sensor on each flipper beat. Attachment of all the equipment took about 40 min, and the turtle was then left to crawl back to the water, entering the sea at about 05:20, i.e. around 80 min after she was first sighted. The turtle was relocated at 20:45 the following evening when she returned to Longbeach to nest successfully and at this time the TDR, IMASU and magnet were removed and the data downloaded to a PC.

Previous aquarium trials have shown the ability of the IMASU to record turtle flipper beats (Wilson and Liebsch, 2003). In order to assess how the IMASU might respond to specific flipper movements, an adult male hawksbill turtle (*Eretmochelys coriacea*) housed in the Stralsund museum (Germany) was equipped on 3 July 2002 with an IMASU. Positioning of the Hall sensor and magnet were the same in both the field trials with the wild green turtle and the aquarium work with the captive hawksbill turtle. In addition in the aquarium work, six fluorescent latex circles were stuck with single drops of cyanoacrylate glue to the left fore-flipper, three being spaced equidistant down the leading edge and a further three down the trailing edge. The animal was then released into its holding aquarium where it swam freely while being filmed through the aquarium glass using a JVC video-recorder at 24 frames/s. The animal was recovered after ca. 30 min and the data downloaded from the logger.

3. Results

3.1. General occurrence of different dive types at Ascension Island

While types 1 and 2 dives, U-dives and V-dives were recorded by all six individuals during their internesting intervals, U-dives were the most common (Fig. 1), accounting for

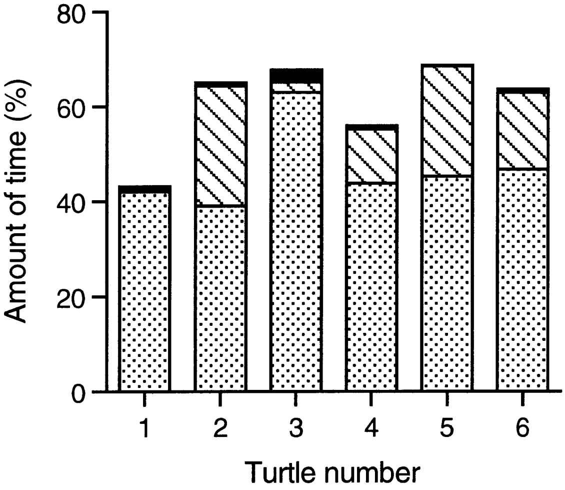

Fig. 1. For six free-living green turtles at Ascension Island equipped with TDRs, the proportion of time spent conducting different dive types during the internesting period. Grey fill, U-dives; hatched fill, type 1; dark fill, type 2.

between 39% and 63% of the time during the internesting interval (mean = 46.6%, $n = 6$ individuals). The occurrence of types 1 and 2 dives was more variable, accounting for between 0.5% and 25.4% of the time during the internesting interval (mean = 13.2%), while deep V-dives were always relatively rare, accounting for < 2.5% of the time for all six individuals.

3.2. Dive profiles during IMASU deployment

The turtle equipped with the IMASU performed a variety of different dive profiles with flipper beats being recorded on 23 dives (Fig. 2). For example, between 05:30–08:40, 09:20–11:25 and 16:55–18:55, types 1 and 2 dives occurred. Between 08:45 and 09:20, three deep V-dives took place, with a maximum depth of 60 m being attained, while between about 13:00 until 16:55 a series of U-dives took place. Consequently, we were able to assess the pattern of flipper movements on all the characteristic dive types performed by green turtles at Ascension Island.

3.3. Individual flipper movements

3.3.1. Free-living turtles

For the free-living turtle, regular beating of the flippers was clearly evident in the data from the IMASU. On the upstroke the magnet attached to the front flipper would move closer to the Hall sensor, giving an increase in the detected magnetic field. Thus, each individual flipper beat was characterized by a peak in the IMASU readings (Fig. 3a). Superimposed on this general pattern, there was some variability in the specific pattern of the regular changes in flipper position detected by the IMASU (Fig. 3b) and this tied in well with that observed in captivity (see below). In the wild, changes in the specific nature of the phasal output from the IMASU often corresponded with shifts in the rate of change of depth (Fig. 4). For each phasal change in flipper position, we defined the time of that flipper beat as the time of the maximum reading from the Hall sensor. Using the interval between

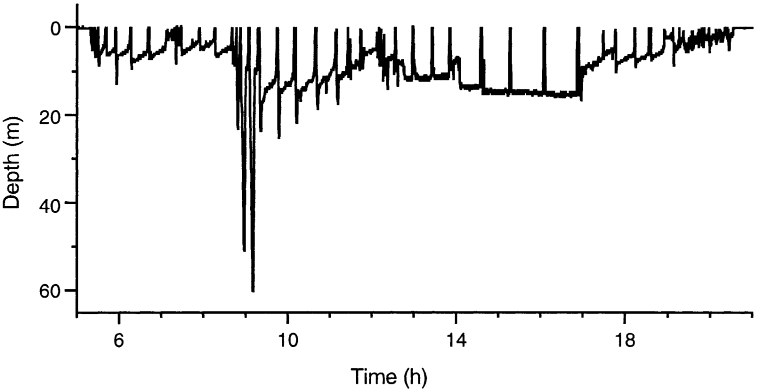

Fig. 2. The complete dive record for a free-living green turtle at Ascension Island during which flipper movements were monitored.

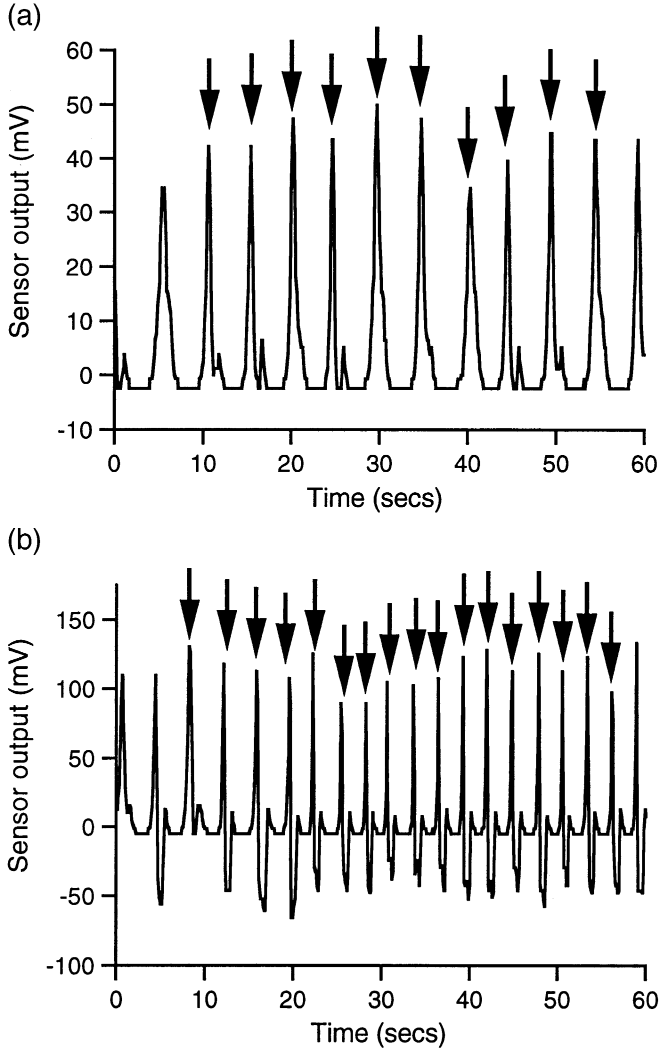

Fig. 3. For a free-living green turtle at Ascension Island, examples of the regular movement of the flippers revealed by the IMASU. Each trace shows 1 min of data. The time of each flipper beat, which we defined as the time of the maximum reading from the Hall sensor, is shown by the arrows.

consecutive flipper beats, we then calculated the instantaneous flipper beat frequency throughout each dive.

3.3.2. Captive turtles

Assessment of the film of the hawksbill turtle swimming in captivity showed two basic patterns: When the animal moved slowly, the fore-flippers were moved essentially dorso-ventrally through a relatively narrow vertical arc. Here, propulsion was gained

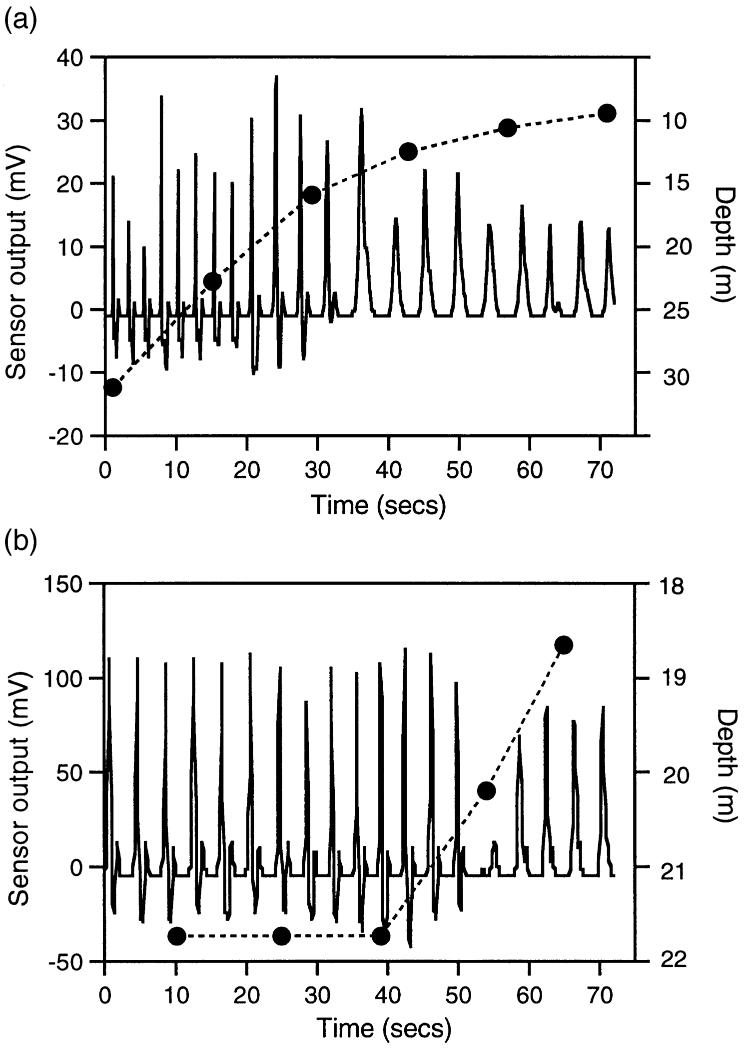

Fig. 4. For a free-living green turtle at Ascension Island, segments of both IMASU (solid line, no points) and depth (broken line connecting filled circles) readings to illustrate a general change in the nature of the phasal output from the IMASU associated with the switch in the rate of change of depth.

from the flippers in much the same way as penguin flippers (Bannasch, 1995) or dolphin flukes (Fish, 1993). The IMASU recorded this movement with a single, relatively small peak when the flipper was raised, followed by a single trough during the downstroke. With increasing speed and/or acceleration, however, the flippers were also moved anterio-posteriorly, with this movement becoming more pronounced with increasing speed or acceleration. In essence, at the end of the stroke, the flippers were moved up and then forward (see Davenport et al., 1984 for diagrams of these movements). The main power stroke took place with the flippers moving back and down, this movement pushing water behind the animal and acting to project the turtle forward. This action took the flipper-attached magnet past the carapace-attached Hall sensor twice during a single stroke cycle,

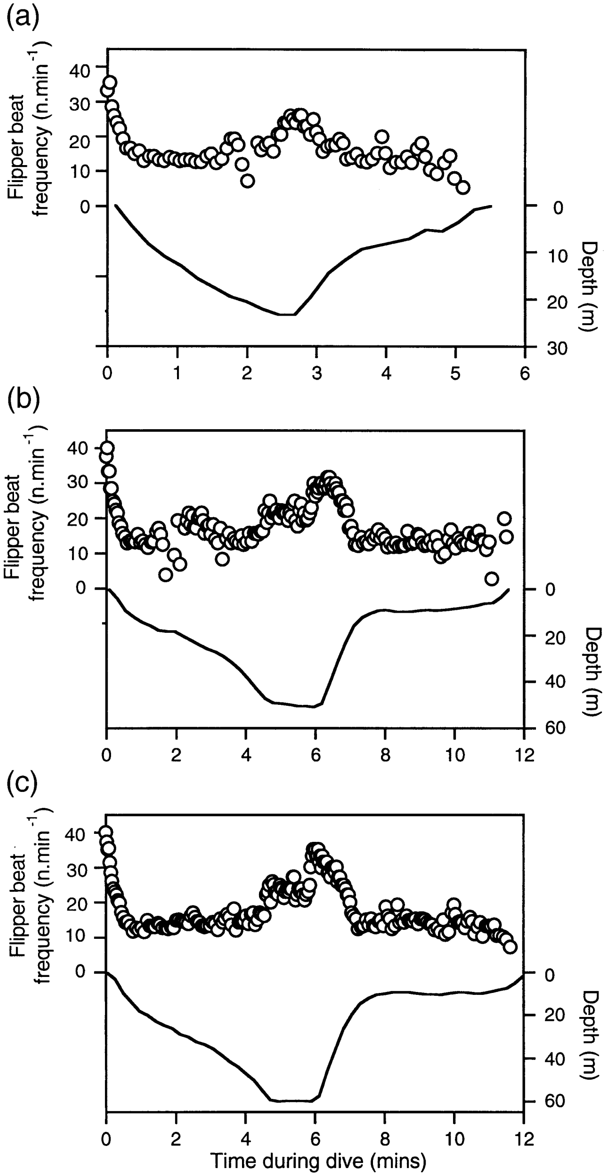

Fig. 5. For a free-living green turtle at Ascension Island, during three V-dives, the depth (line) and flipper beat frequency (circles) throughout each dive. Note the different x-axis scales to accommodate the fact that the dives differed in duration.

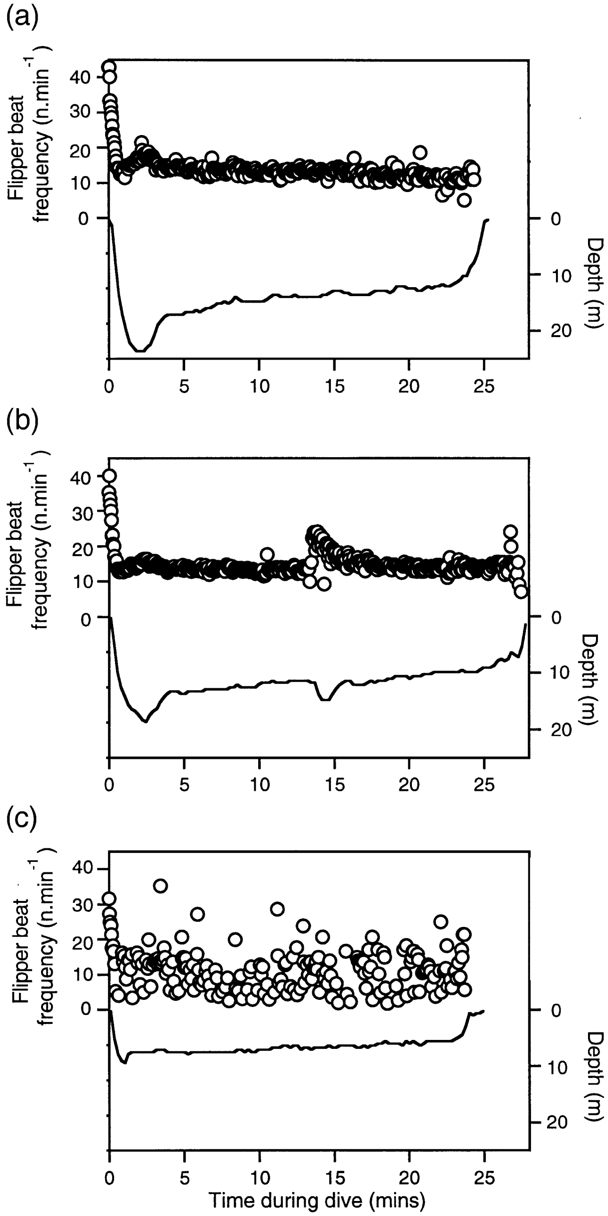

Fig. 6. For a free-living green turtle at Ascension Island, examples of the depth (solid line) and flipper beat frequency (circles) during types 1 and 2 dives. (a and b) Dives with continuous and regular beating of the flippers. (c) A dive with a more erratic pattern of flipper beats.

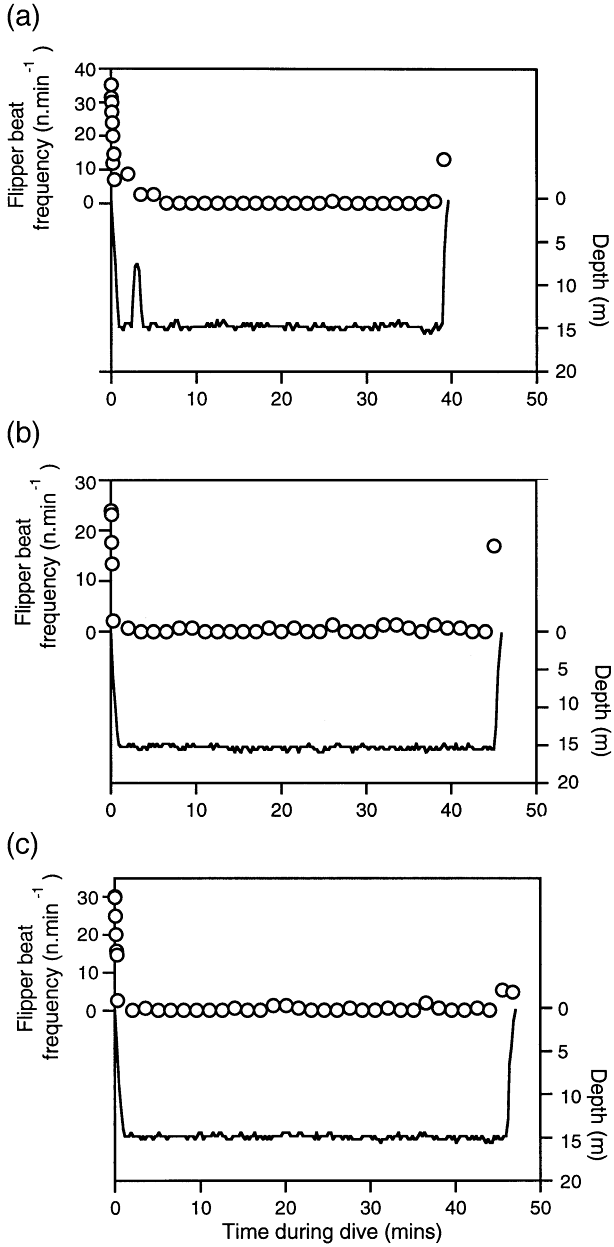

Fig. 7. For a free-living green turtle at Ascension Island, examples of the depth (solid line) and flipper beat frequency (circles) during three U-dives. Due to the very infrequent occurrence of flipper movements once the bottom phase commenced, after the initial descent we calculated the flipper beat frequency for 90-s intervals rather than between consecutive flipper movements. Note this approach reduces the number of data points on the ascent compared to when the interval between all the individual flipper beats is examined (see Fig. 10).

once during the recovery where the distance was minimal and the sensory output correspondingly high, and once during the power stroke where the distance between the magnet and sensor was greater, resulting in a second, lesser peak. Thus, pairs of unequal, double peaks characterized single stroke cycles when the animal increased swimming effort. These two patterns of flipper stroking were also seen in the IMASU records from the free-living green turtle (Figs. 3 and 4).

3.4. Patterns of flipper beats on different dive types

3.4.1. V-dives

During V-dives, there was near continuous beating of the flippers throughout the dive (Fig. 5). However, there was not a constant flipper beat frequency. At the start of these dives, the flipper beat frequency was initially high, approx. 35–40 beats min^{-1}, and then declined to about 12–18 beats min^{-1} during the descent. Then towards the end of the descent and the start of the ascent the flipper beat frequency increased to about 25–30 beats min^{-1} and stayed relatively high during the initial stages of the ascent before declining again to about 12–18 beats min^{-1} as the turtle approached the surface.

3.4.2. Types 1 and 2 dives

During some of these dives, there was continuous flipper beating throughout the dive (Fig. 6a,b). In these cases, flipper beat frequency was high, around 40 beats min^{-1}, at the start of the dive and then declined as the descent progressed. At the end of the descent, flipper beat frequency was relatively low, around 12 beats min^{-1}, and then briefly increased to around 20 beats min^{-1} during the rapid ascent immediately preceding the long gradual ascent phase. Then during the gradual ascent phase, flipper

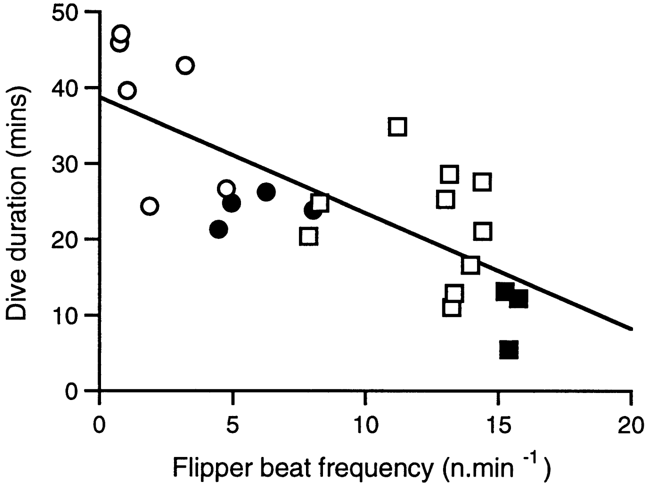

Fig. 8. For a free-living green turtle at Ascension Island, the variation in dive duration as a function of the mean flipper beat frequency (calculated simply as number of flipper beats divided by dive duration). ○ = U-dives, ● = type 1, □ = type 2 dives, ■ = V-dives. For all 22 dives, $F_{1,21} = 24.5$, $r^2 = 0.54$, $P < 0.001$.

beat frequency remained around 10–14 beats min^{-1} except on one occasion (Fig. 6b) when there was a brief break from the gradual ascent about 15 min into the dive and an associated increase in flipper beat frequency. In some other examples of types 1 and 2 dives, there was a more erratic pattern to flipper beats, with a much more variable rate during the dive (Fig. 6c).

3.4.3. U-dives

During the bottom phase of U-dives, there was no regular beating of the flippers and, instead, there were only occasional isolated flipper movements (Fig. 7). In short, there were marked variations between the extent of active swimming on different dives types, with almost no active swimming on U-dives but continuous active swimming on V-dives and some types 1 and 2 dives. This difference in active swimming was related to the

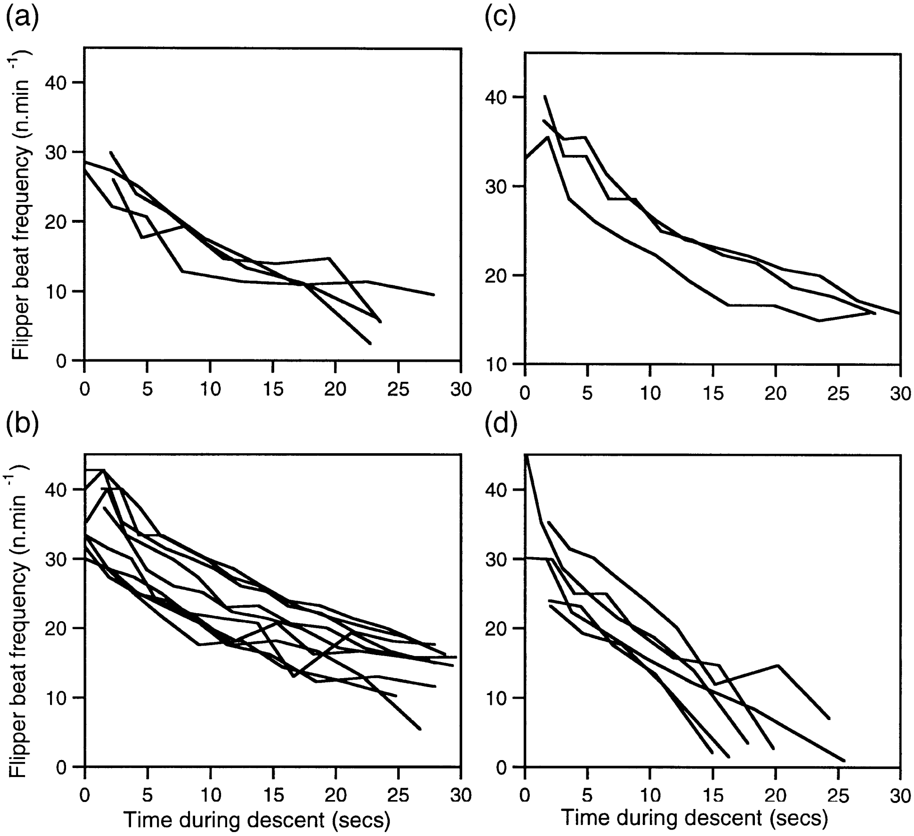

Fig. 9. For a free-living green turtle at Ascension Island, the variation in the flipper frequency during the first 30 s of dives for (a) type 1 dives, (b) type 2 dives, (c) V-dives and (d) U-dives. In each plot, lines connect the values recorded on individual dives. The reduction in stroke frequency during descent is highly significant in all dives (linear regression, $P < 0.001$).

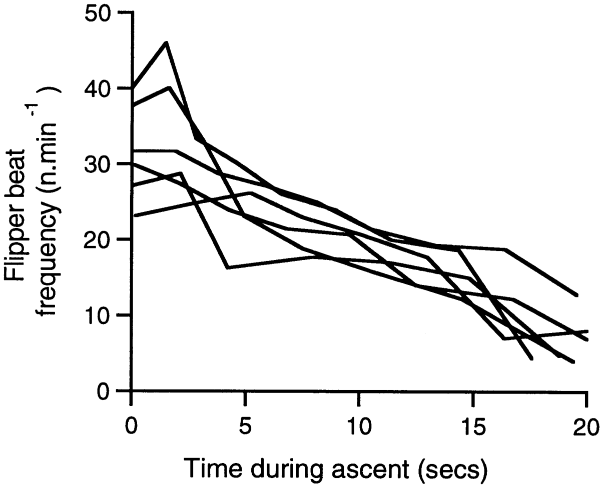

Fig. 10. For a free-living green turtle at Ascension Island, the variation in the flipper beat frequency during the first 20 s of the ascent at the end of U-dives. Lines connect the values recorded on individual dives. The increase in stroke frequency during ascent is highly significant in all dives (linear regression, $P < 0.001$).

duration of dives: as the mean flipper beat frequency on a dive increased so the dive duration decreased (Fig. 8).

3.5. Flipper beat frequency during descent and ascent

There was a general tendency for the flipper beat frequency to be initially high at the start of a dive and then to decline during the descent. This general pattern occurred in every dive regardless of dive type (Fig. 9a–d). During ascent, the general pattern was for flipper movements to either cease altogether as the turtle approached within a few metres of surface, or else to become much more infrequent. The clearest way to illustrate this general pattern is to examine the pattern of flipper movements on the ascent phase of U-dives. On these dives, there was an initial burst of flipper beats as the turtle left the seafloor and then as the ascent progressed the flipper beat frequency declined (Fig. 10).

4. Discussion

Although a number of characteristic dive profiles have been identified in sea turtles, we are only just starting to explore the rudiments of the function of these dives and to examine the strategies that turtles adopt to optimize their diving performance. U-dives to the seafloor and three types of midwater dive, V-dives and types 1 and 2 dives, have been widely reported in loggerhead turtles (Houghton et al., 2002; Minamikawa et al., 2000), hawksbill turtles (van Dam and Diez, 1996) and green turtles (Hays et al., 2000). Here, we showed that all four of these characteristic dive profiles are performed by green turtles at Ascension Island, reinforcing some previous observations made with first generation TDRs (Hays et al., 2000). Having identified the characteristic dive profiles performed by marine turtles, one of the next steps in teasing apart the details of their free-living behaviour is to record whether they are actively swimming during dives. Measuring the flipper beats is one way to distinguish between periods of active swimming versus passive resting, and this technique has been applied to a number of marine mammals using camera systems (Davis et al., 2001; Williams et al., 2000). The approach we used here, using a Hall sensor linked to a data logger to record the movement of a magnet attached to a flipper, has been recently described in detail (Liebsch, 2002; Wilson and Liebsch, 2003). This technique clearly revealed regular flipper movements in the free-living green turtle, showing the utility of this technique for this group. There were some differences in the specific nature of the regular phasal changes in flipper position detected by the IMASU, with, sometimes, secondary peaks within each flipper beat. The observation that these phasal changes in the IMASU output often corresponded with shifts in the rate of change of depth, presumably reflected the turtle modifying the extent of the power stroke during each flipper beat in order to, for example, change dive angle or rate of change of depth via changes in speed. This change in stroking action depending on the swimming effort has been noted before during filming of turtles held in tanks (Davenport et al., 1984) and so may be widespread in hard-shelled turtles. While our existing data provides accurate values for flipper beat frequency, the variable pattern of flipper movements seen in the aquarium suggests that further work is required to extract good estimates of the power generated from each flipper stoke during swimming of free-living turtles.

While we only recorded the pattern of flipper movements in a single individual, it is important to note that this turtle performed all the characteristic dive profiles shown by green turtles at Ascension Island and elsewhere. Hence, this data set allows us, for the first time, to examine how the pattern of flipper beats varies between dive types in a marine turtle, as has been done recently for some marine mammals. For example, during the descent phases of dives in a range of marine mammals, even though the number of individuals examined is always relatively small because of the inherent difficulties with making these measurements (e.g. Williams et al. (2000) reported results for three Weddell seals (*Leptonychotes weddellii*), one northern elephant seal (*Mirounga angustirostris*), one bottlenose dolphin (*Tursiops truncatus*) and one blue whale (*Balaenoptera musculus*)), very consistent patterns of gliding and flipper beating have been reported during different parts of the descent and ascent. In these deep diving marine mammals, periods of non-swimming (“gliding”) have been associated with the descent phase of dives after individuals have attained negative buoyancy and so can sink passively (Williams et al., 2000). On these deep dives, gliding helps to reduce the cost of transport and so allows deep diving marine mammals to extend their aerobic dive limit. For sea turtles, there is another reason why animals may not actively swim during a dive, namely the primary function of the dive may be to rest. Resting may occur during U-dives to the seafloor, i.e. the animal attains slight negative buoyancy and so can sit passively on the sea floor. In some locations, turtles might potentially also forage during U-dives. However, this is unlikely to be the case at Ascension Island since there is a lack of forage for green turtles at this island and hence during their residence at this location during the nesting season green turtles probably do not feed (Hays et al., 2002). The wide occurrence of U-dives for green turtles at Ascension Island, their predominantly nocturnal nature (Hays et al., 2000), and the lack of forage at this site, suggest that these U-dives probably function as periods of rest and, as such, there is probably very little variability in behaviour between U-dives of different individuals at Ascension Island. This conclusion of resting during U-dives is supported by our results, which showed almost no flipper movements during the bottom phase of these dives.

It has been suggested that during the gradual ascent phase of types 1 and 2 dives, turtles may not actively swim but rather may hang motionless in midwater. The evidence for this suggestion comes from loggerhead turtles during the internesting period fitted with an impeller type flowmeter that generally failed to record movement during these dives except on descent and ascent (Minamikawa et al., 2000). However, turtles perform types 1 and 2 dives in quite different phases of their life history. For example, while Minamikawa reported types 1 and 2 dives during the internesting period, we have also shown that these are the dominant deep dive types while green turtles are conducting trans-oceanic migrations (Hays et al., 2001). Our flipper beat records extend the previous observations of Minamikawa et al. (2000) by showing that there may be variation in the extent of active swimming on types 1 and 2 dives. While we recorded irregular and relatively infrequent flipper movements during some of these dives, consistent with the general conclusions of Minamikawa et al. (2000), on other types 1 and 2 dives, we recorded continuous flipper beats, showing active swimming throughout these dives. Essentially our results, when combined with those Minamikawa et al. (2000) suggest that, while turtles are close to neutral buoyancy during the gradual ascent phase of types 1 and 2 dives, they show inter-dive variation in their extent of active swimming.

We also recorded flipper movements during a number of deep V-dives. Deep V-dives are only occasionally recorded in green turtles, presumably because for a herbivorous animal that feeds and rests at shallow depths there is little reason to dive deeply (Hochscheid et al., 1999). While animals that routinely dive deeply, such as some seals, dolphins and whales, may glide during the descent phase of deep dives (Williams et al., 2000), this was not the case during the V-dives we recorded, with continuous flipper beating occurring throughout these dives. The clear changes in beat frequency during these V-dives suggests that, in common with marine mammals, the changing level of buoyancy during these deep dives has implications for the diving strategy of green turtles. During descent, any gas filled spaces will be compressed and hence diving animals will tend to lose buoyancy as the descent progresses (e.g. Wilson et al., 1992). Consequently, if the animal dives sufficiently deeply to attain negative buoyancy, then at the beginning of the ascent it will need to work against this negative buoyancy. Thus, deep diving marine mammals switch from gliding on descent to active swimming on ascent (Williams et al., 2000). On deep dives in the green turtle, the start of the ascent was accompanied by a marked increase in the flipper beat frequency, in line with expectations for increased effort being required to overcome negative buoyancy (Wilson et al., 1992). As the ascent continued, and hence as the lungs were expanding and increasing the buoyancy of the animal, the flipper beat frequency declined. We can use these same arguments about the level of buoyancy during dives to predict that at the end of a U-dive to the seafloor, a turtle will be slightly negatively buoyant (see also Hochscheid et al., 2003) and so will initially need to actively swim to begin its ascent, but then as it ascends, the expanding lungs will provide buoyancy allowing a more passive ascent closer to the surface. This prediction was matched by our empirical findings of an initially rapid rate of flipper beats at the start of the ascent on U-dives.

In order to overcome initial positive buoyancy at the start of the dive, we would predict that regardless of the dive type, in hard-shelled turtle active swimming is required at the start of the descent. This pattern of initial active swimming was confirmed by the measurements of flipper movements, with regular flipper beats at the start of all dives. However, the frequency of flipper beats was not constant. Rather there was initially a high frequency of flipper beats and then this frequency declined as the descent progressed. Similarly in penguins, positive buoyancy near the surface may be overcome by an increase beat frequency (van Dam et al., 2002) as well as an increase in the amplitude of the flipper movements (Wilson and Liebsch, 2003, cf. Sato et al., 2002).

While a number of factors may influence the duration of dives, all other things being equal, dive duration would be expected to be shorter when metabolic rate is higher because of the faster utilization of oxygen stores. Flipper beat frequency may provide a crude proxy for the metabolic rate during sea turtle diving and, as such, the negative relationship between dive duration and flipper beat frequency is expected. What remains perplexing is why turtles at Ascension Island, in the absence of food, do not simply conduct U-dives to rest on the seafloor, but instead show more active dive types as well. In contrast, for the leatherback turtle (*Dermochelys coriacea*) which may feed and move long distances during the internesting period, active swimming is more readily explained (Eckert, 2002).

In summary, by simultaneously measuring flipper movements and depth, we have started to tease apart the details of the extent of active swimming both within and between different dive types for green turtles. Broadly speaking, these first results suggest that green turtles at Ascension Island either swim actively in midwater or rest on the seafloor. Highly repeatable variations in flipper beat frequency during descent and ascent can be explained on the basis of the expected changes in buoyancy during dives due to gas compression in the lungs.

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