

Dive angles for a green turtle (*Chelonia mydas*)

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The depth and swim speed of a green turtle (*Chelonia mydas*) were measured during the interesting period in Cyprus. For dives to the seabed (U-dives) we used these data to determine dive angles. Typically the turtle initially descended at a steep angle ($\sim 60^\circ$) but as the dive continued this angle lessened until the turtle approached the seabed at an average angle of $\sim 15^\circ$. This systematic change in descent angle is consistent with the prediction that the energetic implications of dive angle are most important at the start of the dive when the turtle is fighting to overcome its positive buoyancy. On leaving the seabed, the turtle often seemed to rise passively.

INTRODUCTION

For at least two reasons green turtles (*Chelonia mydas*) are a potentially more tractable diving group than marine mammals and birds, with which to test predictions for optimization of descent and ascent angles. Firstly, this species spends long periods on the seabed, either resting (e.g. Hays et al., 2000) or feeding (Hochscheid et al., 1999) on its primary food sources which are either benthic sea grasses or macroalgae (Bjorndal, 1980). Therefore without the possibility of mid-water foraging, there is an invariant 'goal' (i.e. the seabed) for many dives. Secondly, unlike phocid seals and penguins, turtles typically inhale before submerging and adjust their lung volume so that neutral buoyancy is achieved at the maximum dive depth (Milsom, 1975; Minamikawa et al., 1997, 2000). Thus during the initial stages of descent, individuals will be positively buoyant, but as they descend, their level of buoyancy declines. It would therefore be predicted that, when diving to the seabed, green turtles should initially descend with a steep dive angle in order to travel through the zone of highest buoyancy as efficiently as possible. As the dive continues and positive buoyancy declines, descent angle will become less critical and it may be more important to select a resting or foraging site, consequently descent angles may decrease. The fundamental objective of this study was to test these predictions by measuring the changes in dive angle during benthic dives in green turtles.

MATERIALS AND METHODS

The study was conducted in July 2000 at Alagadi, northern Cyprus ($35^\circ 21'N$ $33^\circ 30'E$), a green turtle nesting beach. A green turtle was fitted with two separate time–depth recorders (TDRs). A MK6 TDR (Wildlife Computers, Redmond, Washington) recorded speed and depth every 5 s (range 0–250 m, resolution 2 m, stall speed 0.05 m s^{-1}) for three days; while a Lotek LTD-100 (LOTEK Marine Technologies, St John's, Newfoundland, Canada) recorded depth every 5 s with a higher resolution

(range 0–100 m, resolution 0.06 m). The 3-d duration of the concurrent depth and speed measurements was simply a consequence of the memory capacity of the Wildlife Computers TDR.

In order to match the swim speed data with the high-resolution depth data, the internal clocks of both instruments were first synchronized, and then a known signal was introduced into both data sets prior to attachment. This was done by simultaneously rotating the speed sensor of the Wildlife Computers TDR while immersing the Lotek TDR in water. In this way it proved straightforward to match up the data-sets from both instruments against a common time scale. Consistency was maintained between the depth data from both instruments throughout the measuring period, showing there was no drift between the clocks of the two TDRs.

Instruments were attached just after the turtle had completed nesting. Both instruments were attached to the second central scute of the turtle's carapace using epoxy resin (Foilfast, SFS Components, Cheltenham), with the swim speed data logger being attached anteriormost so that it was unobstructed to the water flow when the turtle was swimming forward. Instruments were removed when the turtle returned to lay its next clutch 11 days later and the data downloaded to a computer.

Dives to the seabed were evident from their distinctive profile, with descent and ascent separated by a flat bottom profile indicative of the turtle resting on the bottom. Such dives were termed 'U-dives' following previous terminology (Hochscheid et al., 1999). The start of a U-dive was defined as the first reading deeper than 0.5 m. The end of the descent phase, start of the ascent phase and end of the dive were all defined using a threshold vertical speed of 1 cm s^{-1} . We assumed a linear change between consecutive swim speed measurements.

RESULTS

Dive angles were determined for 86 U-dives. These dives were always shallow, with a mean maximum depth

of 4.6 m (Table 1). An example of a bout of U-dives is shown in Figure 1, with the corresponding swim speed readings showing motion on descent and ascent.

Using a procedure used previously (Boyd et al., 1999), the manufacturer's calibration of the swim speed recorder was investigated by examining the ratio (R) of the change in depth to the total distance travelled. This ratio would be expected to have a maximum value of 1, with $R=1$ indicating vertical descent. A high proportion of values >1 might indicate that the calibration of the swim speed recorder needs to be adjusted. On descent, the frequency distribution for values of R showed that most (501 out of 512) values were <1.3 (Figure 2A). Therefore swim speed values were multiplied by a correction factor

Table 1. Mean values (\pm SD) for different dive parameters recorded during 86 U-dives.

Parameter	Mean value (SD)
Dive depth (m)	4.6 ± 2.7
Descent angle ($^{\circ}$)	33.5 ± 15.5
Vertical descent speed (cm s^{-1})	18.3 ± 10.0
Vertical ascent speed (cm s^{-1})	16.0 ± 12.9

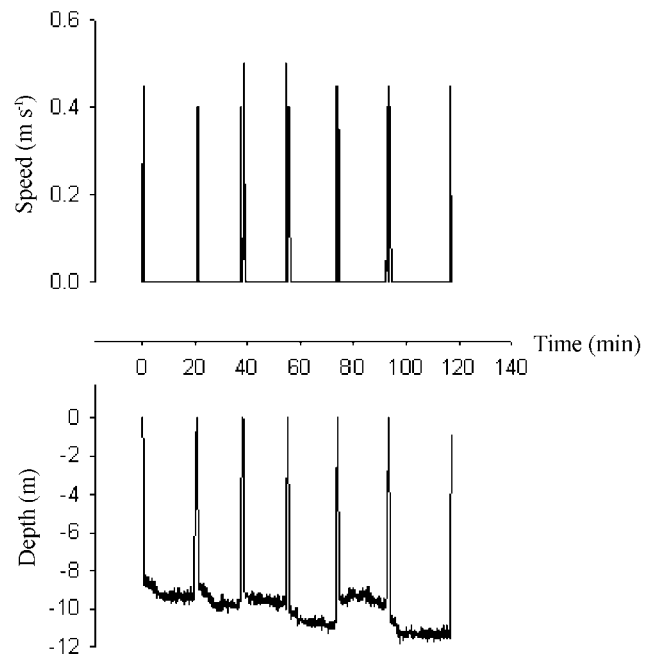


Figure 1. An example of six U-dives, each characterized by a flat-bottomed profile indicating descent to the seabed. Swim speeds are the raw readings supplied by the TDR.

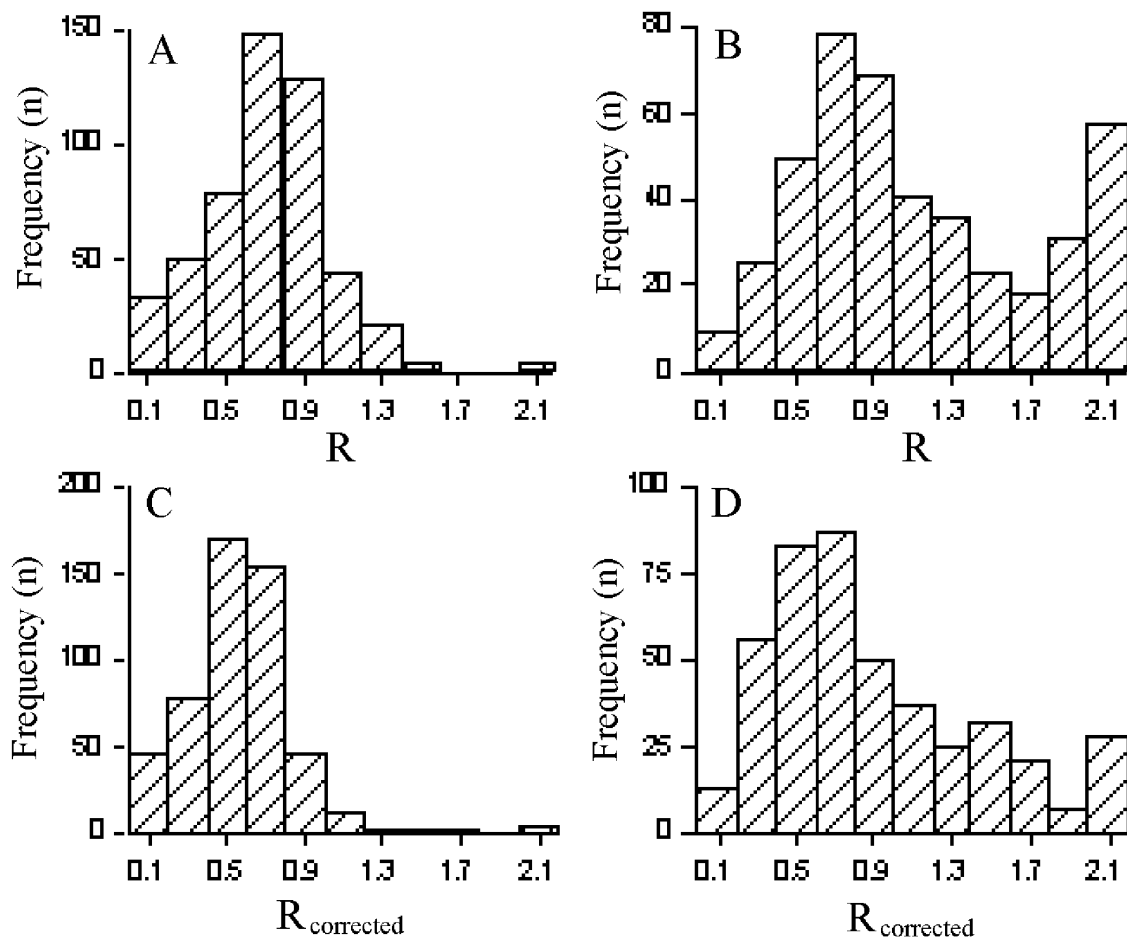


Figure 2. Frequency distribution of the values for R (vertical distance moved divided by total distance covered using the manufacturer's calibration of the swim speed recorder) on (A) descent; and (B) ascent. Values of $R_{\text{corrected}}$ on (C) descent and (D) ascent, determined by multiplying the raw speed values by 1.3 (see text for details). All values >2.1 are pooled in this final bar.

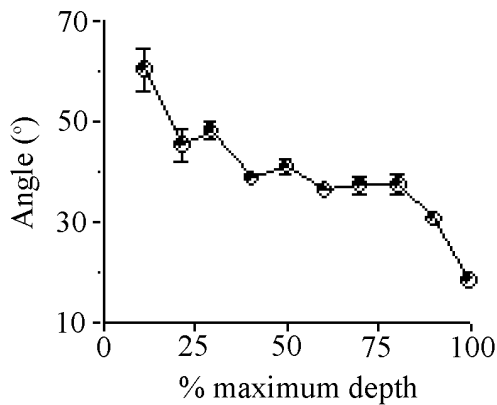


Figure 3. The angle of descent in relation to the percentage of the maximum dive depth. Mean values ± 1 SE are shown. Error bars smaller than the plot symbol are not shown.

of 1.3 in order to determine dive angles. However, interestingly on ascent the frequency distribution of values for R was shifted to the right, with far more values >1.0 (Figure 2B).

Using the calibrated swim speed readings, we repeated the calculation of the change in depth divided by the total distance travelled, terming these revised values $R_{\text{corrected}}$ (Figure 2C&D). As expected the proportion of $R_{\text{corrected}}$ values >1.0 was always low on descent, but on ascent many values were still >1.0 . In particular these high ratios tended to be frequently recorded just after the turtle left the seabed.

Dive angles were determined using simple trigonometry and knowing both the vertical distance and total distance covered between consecutive depth readings. Dive angles were not calculated when $R_{\text{corrected}}$ was >1.0 ($<2\%$ of occasions on descent). Dive angles changed systematically during descent. At the start of dives the turtle tended to descend more steeply and then, as it approached its maximum depth (i.e. the seabed) the angle of descent decreased (Figure 3). Given the high proportion of $R_{\text{corrected}}$ values >1.0 on ascent, ascent angles were not plotted for this phase of the dive. The reasons for these high $R_{\text{corrected}}$ values will be considered in the discussion.

DISCUSSION

By measuring speed and depth, and therefore the angle, we have been able to create a two-dimensional view of the green turtle's dive to the seabed. Although speed recorders can be calibrated in the laboratory, once the instrument is attached to a diving animal the flow of water is modified and so the flow through the speed sensor may not necessarily reflect the speed of the animal through the water (Blackwell et al., 1999). The procedure we adopted here (determining R , the ratio of the change in depth to the measured total distance travelled) has been suggested as a method of checking the calibration of speed recorders (Boyd et al., 1999). On descent there were relatively few values of R much greater than 1.0, suggesting that the raw speed values from the instrument were a fairly accurate reflection of the animal's speed through the water during this phase of the dives. The correction factor that we applied (multiplying raw speed values by 1.3) therefore had only a minor impact on the calculated angles of descent and so will not be crucial to our key findings. In addition, the fact that only a very small percentage (2%) of the $R_{\text{corrected}}$ values were >1.0 suggests that the correction factor was appropriate. We are therefore confident in the accuracy of the reported dive angles.

There was a clear dichotomy in the frequency distribution for the values of $R_{\text{corrected}}$ found on descent compared to ascent. That values of $R_{\text{corrected}}$ were very rarely >1 on descent, suggests the turtle was generally descending with the direction of motion being in line with its major body axis (i.e. anterior–posterior). However, on ascent, values of $R_{\text{corrected}}$ were frequently >1 particularly near the seabed, suggesting that the turtle was often moving upwards while still in a near-horizontal orientation and hence the depth changed without a corresponding measurement by the speed recorder of distance moved. This dichotomy is illustrated schematically in Figure 4. In other words, on ascent the depth often changed while there was little forward motion detected by the speed sensor.

In order to decrease the time spent in travel during U-dives, it would seem sensible for the turtle to dive vertically. However, our results show that this rarely

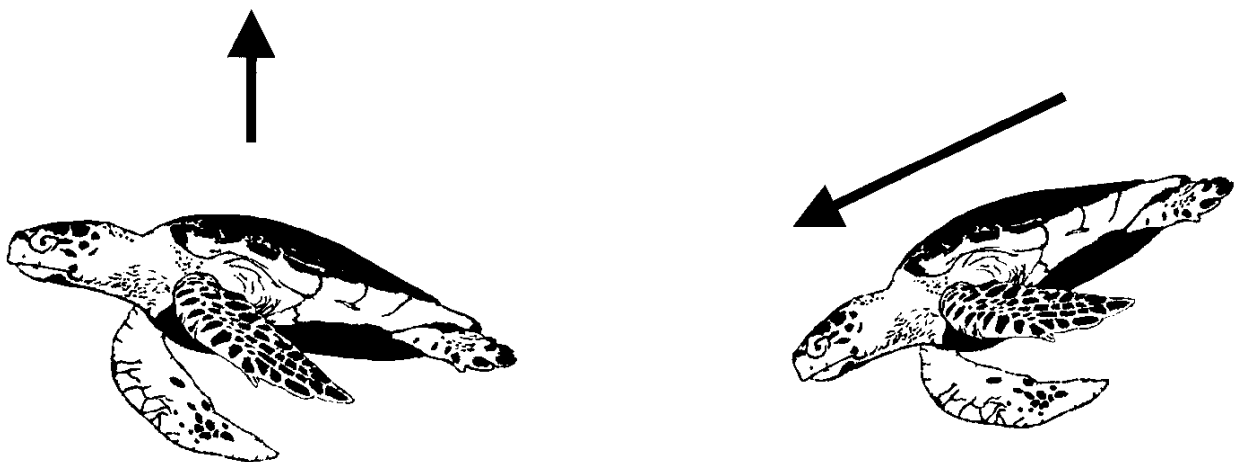


Figure 4. A schematic illustration to show that on descent the direction of motion was probably aligned with the major axis of the turtle, but that on ascent (particularly the initial stages) the turtle often rose through the water while still in a near-horizontal orientation.

happens. This is consistent with findings for other air-breathing divers (Le Boeuf et al., 1992; Chappell et al., 1993; Crocker et al., 1994; Wilson & Wilson, 1995; Radl & Culik, 1999) and suggests there is some common reason why animals do not descend vertically, maybe in order to allow the animal to scan for suitable foraging or resting areas, or to better allow individuals to maintain vigilance against predation threat. For example, descent angles of 40° have been recorded for the northern elephant seal (Crocker et al., 1994; Le Boeuf et al., 1992), while in penguins descent angles tend to increase when individuals dive to greater depths, but again are shallow, with recorded values ranging from 7 to 42° (Adélie penguins, Chappell et al., 1993; African penguins, Wilson & Wilson, 1995; Magellanic penguins, Radl & Culik, 1999). However, consistent with predictions from the reduction in buoyancy with depth, we did find that the descent angle was greatest at the start of the dive. Presumably the energetic implications of dive angle are most important during these initial stages of the dive when the turtle is fighting to overcome its positive buoyancy. Why might the turtle not maintain its initially relatively steep angle of descent? Unlike penguins and seals, green turtles will not be searching for food in the water column during the descent since they feed on the seabed. Instead the turtle may have been searching for a suitable resting or foraging site on the seabed, and by descending at a shallow angle, the turtle may have been able to survey the surrounding area more easily.

On ascent, the energetic implications of angle are less important because a turtle will generally be positively buoyant and so will not need to actively swim to reach the surface. We would therefore not expect the turtle to waste energy by swimming rapidly on ascent. The evidence for passive ascent (Figure 3) is consistent with this prediction.

In conclusion, we have presented the first measurements of dive angle for a marine turtle. For green turtles which dive after inhaling and which feed and rest on the seabed, our results are broadly consistent with the prediction that this species should initially descend at a steep angle. Further deployments of depth and activity loggers will allow us to identify how dive angle varies between individuals, with dive function (e.g. resting or foraging) and with dive depth.

This work was supported by Natural Environment Research Council (NERC) grant GR3/12740 to G.C.H. was carried out as part of the Marine Turtle Conservation Project in conjunction with the Society for the Protection of Turtles in Northern Cyprus.

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Submitted 18 April 2001. Accepted 18 June 2001.