Surfacing Behavior of the Marine Turtle *Eretmochelys imbricata*

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Marine turtles are accomplished divers capable of making extended breath-hold dives (Berkson, 1966) and frequenting great depths (Landis, 1965; Eckert et al., 1986). Because aquatic respiration in non-hibernating turtles is minimal (Lutz and Bentley, 1985), the animals are obliged to periodically rise to the surface to breathe. Adaptations in lung structure (Lutz and Bentley, 1985) and blood properties (Friedman et al., 1985) facilitate a rapid gas exchange in marine turtles. Ventilation in large turtles is completed after taking only a few deep breaths (Tenney et al., 1974), allowing these animals to resume benthic activities with minimal interruption.

The dynamics of surfacing behavior reflect the way in which marine turtles use the surface zone. Several turtle species are known to stay at or near the sea surface for periods well in excess of those necessary for ventilation. Post-hatchlings of all species except the flatback turtle (*Natator depressus*; see Walker and Parmenter, 1990) are thought to stay in close proximity to the ocean surface during their pelagic life phase (Carr, 1986). Adult leatherback turtles (*Dermochelys coriacea*) appear to bask in the Pacific off the coast of Mexico (Eckert et al., 1989). Sightings of olive ridleys (*Lepidochelys olivacea*) in the Eastern Tropical Pacific frequently coincide with the presence of flotsam from which these turtles may obtain food (R. L. Pitman, pers. comm.). In deep water adjacent to the cliffs of Mona Island, Puerto Rico, we have observed juvenile green turtles (*Chelonia mydas*, 30 to 50 cm carapace length) foraging in the surface zone amidst debris for periods up to 45 min. Whereas quantitative data on the surfacing behavior of several species of marine turtles is available (e.g., Eckert et al., 1989; Sakamoto et al., 1990), we know of only one published paper (Kontos and Eckert, 1988) containing information on the surfacing behavior of hawksbill turtles (*Eretmochelys imbricata*).

In this paper we report on the surfacing behavior of hawksbill turtles residing in coral reef and cliff wall habitats along the western coast of Mona Island, Puerto Rico (18°05'N, 67°54'W). Data were collected during the 1992 to 1994 field seasons (July–November). Detailed information on the diving behavior was obtained from time-depth recorders (TDRs) attached to nine hawksbill turtles (Table 1). The electronic TDRs sampled and stored turtle depth every 8 sec for periods of up to 12.1 d. Experimental procedure of the TDR deployments and the habitat characteristics of

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TABLE 1. Size, habitat type and number of surfacings recorded for nine TDR-equipped immature hawksbill turtles (*Eretmochelys imbricata*) at Mona Island, Puerto Rico. Turtle length is straight carapace length measured from nuchal notch to the posteriormost marginal scute.

Turtle ID	Turtle length (cm)	Habitat type	Number of surfacings examined	Number of surfacings after dives to > 5 m depth
94-110	27.1	reef	531	461
94-128	29.3	reef	485	466
92-022	38.5	reef	607	594
93-016	41.8	reef	596	488
92-050	51.6	reef	515	503
94-038	32.0	cliff wall	970	269
93-053	32.1	cliff wall	900	425
94-041	50.5	cliff wall	713	523
94-085	53.4	cliff wall	766	446

the study sites are further described in Van Dam and Diez (1996, 1997). A total of 6083 surfacings were examined. A turtle was considered to be at the surface whenever its TDR registered a depth of less than 1 m. Surface interval duration was calculated as the number of sequential TDR readings yielding depth values <1 m and multiplied by the sampling interval of 8 sec. A subset of 4175 dives to depths greater than 5 m was used to calculate post- and pre-surfacing profiles. Profiles consisted of a 40 sec duration descent (six depth readings taken at 8 sec intervals) starting at descent from the surface and a 40 sec ascent. Ascent and descent rates were calculated from the difference in measured depth between sequential samplings. Mean ascent and descent rates were determined by averaging the five values obtained for each rate per surfacing. Shallow dives (to depths <5 m) were excluded from the profile analysis to avoid the inclusion of non-surfacing-related behaviors in the 40 sec intervals. Additional data on non-instrumented hawksbill turtles were collected by observing surfacing hawksbill turtles from atop the 40 to 70 m high cliffs of Mona Island.

Through the use of TDRs we were able to examine in detail the surfacing behavior of immature hawksbill turtles. Surface intervals varied in length from 8 sec (the time resolution of the recorders) to 216 sec (by turtle 92-050). Mean surface intervals differed significantly by habitat type (see Fig. 1; t-test, $P < 0.001$). Surfacings by hawksbill turtles in the reef habitat had a mean duration of 50.5 sec; along the cliff wall, surface intervals had a mean duration of 32.9 sec. In each of the habitat types, surfacing durations correlated significantly and positively with turtle size (straight carapace length; Pearson product moment, $P < 0.001$: reef r = 0.774, cliff wall r = 0.844).

The recorded surfacing ascent and descent profiles of turtles diving to depths greater than 5 m are summarized in Fig. 2a and 2b. Hawksbill turtle ascent rates (Fig. 2d) increased gradually until shortly before surfacing. The maximum attained ascent speed was 0.77 m/sec by turtle 94-085 during the time segment
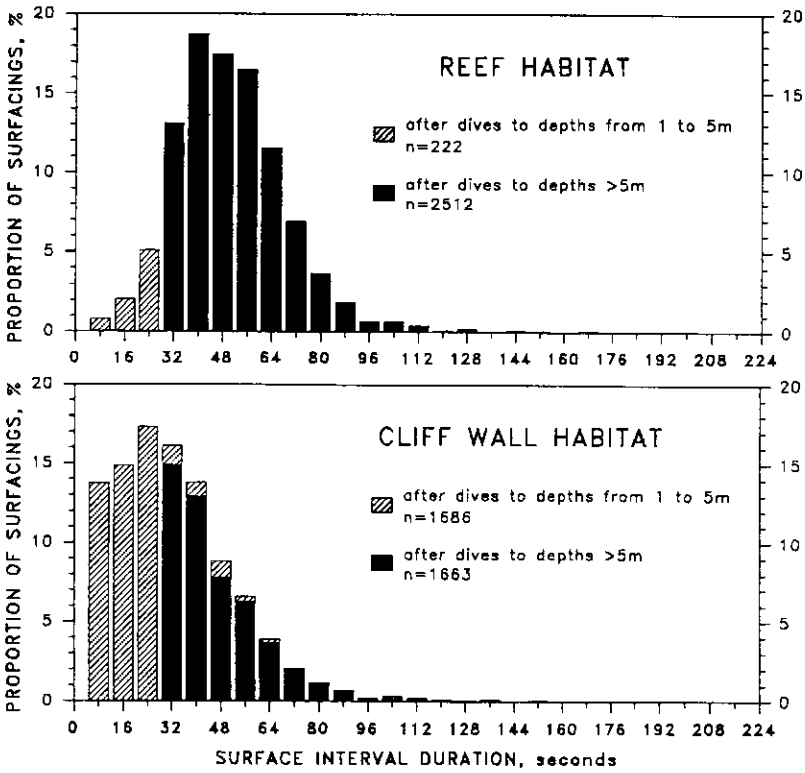
FIG. 1.   Frequency distribution of hawksbill surface interval durations measured using time-depth recorders.

between 8 and 16 sec prior to surfacing. Mean vertical descent velocities (Fig. 2c) tended to be greater during the 16 sec period after departing the surface than the mean speeds observed during the surfacing ascent. The maximum registered descent rate was 1.54 m/sec in the time segment between 16 and 24 sec after submergence of turtle 94-085. Correlations between mean absolute descent and ascent rates (calculated over 40 sec periods) for individual dives were significant (r = 0.785; Pearson product moment, P < 0.001). Surface
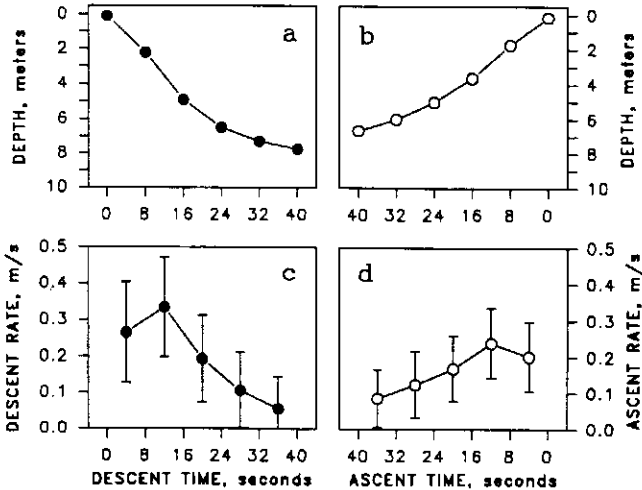

FIG. 2.   Profiles of immature hawksbill post-surfacing descent (a) and pre-surfacing ascent (b). Descent (c) and ascent rates (d) were calculated from the depth profiles. Rates are shown ± standard deviation. Sample size is 4175 for all data points.

interval durations were weakly but significantly correlated with mean pre-surfacing ascent rates ($r = 0.269$; Pearson product moment, $P < 0.001$). Mean absolute descent and ascent rates were not significantly correlated with turtle size (straight carapace length; Pearson product moment, $P > 0.03$ and $P > 0.15$, respectively).

Direct observations by us of hawksbill turtle surfacings in the deep waters (depth >25 m) adjacent to the cliffs of Mona Island provide additional behavioral information. Eleven immature hawksbill turtles (with estimated carapace lengths between 30 and 60 cm) took on average 3.2 breaths per surfacing (range 2 to 5; N = 18 surfacings). Adult male hawksbill turtles (with estimated carapace length >70 cm and protruding tails) were also observed on numerous occasions. These males were alert and remained at the surface without effort for periods of between 1 and 2 min, taking breaths at 11 to 16 sec intervals. Surfacing ascents of all turtles were made nearly horizontally, with the head and carapace breaking the surface simultaneously. Descents were started immediately following the last respiration, with turtles submerging head first and using powerful flipper strokes on a steep descent path.

The recorded hawksbill turtle surfacings reflect highly purposeful, respiration-oriented behavior. Surfacings after dives to depths >5 m lasted a minimum of 32 sec, indicating the turtles made several respirations per surface interval. Hawksbill turtle surfacing durations were substantially longer than the 10 sec or less noted for comparably-sized green turtles taking single breaths in a shallow (1–2 m) seagrass pasture at Mona Island (Van Dam and Diez, pers. obs.). Furthermore, Kontos and Eckert (1988), who also observed hawksbill turtles at Mona Island, saw juvenile animals taking 3.51 breaths per surfacing, whereas adults breathed 5.85 times (total N = 6 turtles). Surfacing adult males observed by us did not appear to engage in any other activity than respiration while at the surface. In all cases, the measured surfacing times were too short for foraging or meaningful basking to take place.

The surfacing profiles of immature hawksbill turtles obtained by using TDRs indicate that the animals did not linger in the near-surface zone on either ascent or descent. On average, less than 40 sec per dive was spent passing through the upper 5 m surface zone (Fig. 2a and 2b). The profiles suggest avoidance of the near-surface zone, with hawksbill turtles returning to the benthic environment rapidly after completion of respiration. The measured ascent and descent rates are substantially lower than rates observed in adult leatherbacks (see dive profiles in Eckert et al., 1986, 1989), the largest and most pelagic of all turtles. However, the mean rates reported by Sakamoto et al. (1990) for a female loggerhead (*Caretta caretta*) between nestings are similar to those measured by us in immature hawksbill turtles. The overall mean loggerhead rates of descent (0.23 m/sec) and ascent (0.14 m/sec) fall well within the range of mean values for hawksbill turtles (Fig. 2c and 2d). Vertical velocities in both species tend to be greater when departing from the surface than upon approach. The suggestion by Sakamoto et al. (1990) that the slower ascents may be a result of attempts by the turtles to control body temperature when experiencing strong thermal changes in the ambient water is unlikely to hold for the hawksbill turtles we studied. Temperature gradients in the water column to at least 35 m depth at Mona Island are minimal during the time periods in which our study was conducted (Van Dam and Diez, pers. obs.).

The surfacing hawksbill turtles observed by us from the clifftop were positively buoyant at all times and appeared to expend no effort in remaining afloat. Initiation of breath-hold dives therefore must require substantial effort, at least until buoyancy is reduced or overcome due to lung compression at depth. By the same scenario and without underwater exhalation, swim effort should be reduced upon breath-hold surfacing ascents. The measured vertical components of turtle swim speeds were greatest in the upper few meters of post-surfacing descent, which together with the observed descent angles indicate that turtles made vigorous submergence efforts. Surfacing ascents were slower and the turtles observed from the clifftop appeared to do little swimming during ascent near the surface suggesting that the animals relied mostly on the bouyancy provided by the lung gases. Marine turtles may benefit from a low velocity when approaching the surface because it allows them to carefully survey the surface zone for potential hazards such as floating objects or predators.

Kramer (1988) introduced the term "surfacers" to describe habitually submarine air-breathing animals. He distinguished them from "divers" which spend less than 50% of their time underwater. We believe that the hawksbill turtles studied come to the surface solely for the purpose of respiration. This behavior allows the animals to maximize submergence times to the extent that they remain underwater 96–98% of the time (Kontos and Eckert, 1988; Van Dam and Diez, 1996, 1997). We conclude that hawksbill turtles in their neritic foraging habitats should be regarded as highly accomplished "surfacers".

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