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Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St Croix, US Virgin Islands

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Summary

Swim speed, dive behavior and movements were recorded for seven female leatherback sea turtles (*Dermochelys coriacea* Vandelli 1761) during a single internesting interval near St Croix in the US Virgin Islands. Modal speeds ranged from 0.56 to 0.84 m s^{-1}, maximum speed range 1.9–2.8 m s^{-1}. Turtles swam continuously throughout the day and night. There were two swim-speed patterns; the most common was slightly U-shaped, with high speeds at the initiation and conclusion of the dive, and the less common was continuous high-speed swimming. The U-shaped speed patterns were coincident with vertical diving by the turtles, while the second pattern occurred most frequently during the daytime, with the turtle swimming within 2 m of the surface. This latter swim behavior appeared to be designed to maximize efficiency for long-distance travel. The hypothesis that leatherbacks rest or bask at midday during their internesting interval is refuted by this study.

Key words: Swim speed, dive, movement pattern, gravid leatherback sea turtle, *Dermochelys coriacea*.

Introduction

For any large air-breathing marine vertebrate, the ability to swim and dive efficiently is central to its survival. This is especially true for residents of the pelagic environment, who exist in a three-dimensional environment devoid of refugia and where food is frequently patchy or diffuse in distribution. The leatherback sea turtle *Dermochelys coriacea* is an example of one such large pelagic vertebrate and is one of the few reptiles to lead an open-ocean existence throughout its life. However, the activities of the leatherback at sea are only poorly defined. Studies of the submerged activities of the species are limited to vertical dive records including dive durations, dive depths and post-dive surfacing periodicity (Eckert et al., 1986, 1989, 1996; Southwood et al., 1999). While such data are quite useful for revealing some aspects of leatherback use of the ocean (e.g. preferred dive depths and dive durations), the lack of a horizontal component or some indicator of activity other than vertical movements limits our ability to understand how leatherbacks are using these three dimensional environments (Eckert et al., 1996).

The capacity to record swimming speed (distance time^{-1}) and distance traveled underwater can provide additional insight into submerged activities of the leatherback. Some studies have estimated leatherback swim speed, e.g. 0.52–2.6 m s^{-1} (Duron, 1978), 1.0–1.5 m s^{-1} (Brongersma, 1972) and 0.86 m s^{-1} (average) to 1.38 m s^{-1} (max.) (Standora et al., 1984), but such studies are rare and have usually relied on pursuing the turtles by boat and recording the time it took for the turtle to traverse between two surface observations. These data are valuable when trying to determine the range of capabilities for the species, but due to small sample sizes, lack of accounting for vertical distance traveled and the potentially adverse responses of the turtle to a pursuit boat, they are difficult to interpret when trying to understand submerged behavior.

The ability to record swim speed directly from the turtle can be used to understand other aspects of leatherback behavior. In 1986, we proposed that female leatherbacks bask or rest on the surface during the middle of the day between nesting events, because we recorded the turtles making longer surfacing bouts at midday. However, we could not confirm that they were resting because the time–depth recorders that we were using only monitored vertical excursions (i.e. dive activities) of the turtles (Eckert et al., 1986). The use of a velocity recorder in combination with a dive recorder could have confirmed whether the turtle was moving, or resting during those longer surfacing bouts.

The goal of this project was to further describe leatherback dive and movement behavior during their internesting intervals and to test the hypothesis that leatherbacks bask or rest at midday.

Materials and methods

One of the largest and best-studied nesting colonies of the leatherback sea turtle *Dermochelys coriacea* Vandelli 1761 in the northern Carribean Sea is located at Sandy Point National Wildlife Refuge, St Croix (US Virgin Islands), with

75–120 turtles nesting annually (Boulon et al., 1996). The location of this colony provides a unique opportunity for the study of deep water diving by leatherbacks because of its close proximity to deep water, the relatively short length of the nesting beach (approximately 2 km long), its relative isolation from other nesting areas, and a conservation program that maintains all-night patrols of the nesting area. The lack of other nearby nesting beaches and the continuous nocturnal patrols facilitate easy deployment and recovery of instrumented leatherbacks (Eckert et al., 1986, 1989; Keinath and Musick, 1993).

Nesting turtles were equipped with a combination of recording instruments after the methods described in previous studies (Eckert and Eckert, 1986; Eckert et al., 1986, 1989). Equipment harnesses were placed on turtles during egg laying and an instrument array, attached to a polyvinyl plate, was then mounted to the shoulder straps of the harness at the highest point of the carapace. Because the shoulder straps are thickened with vinyl tubing, the plate is elevated to bridge over the dorsal carapace ridge, which probably places the ultramarine velocity recorder above the influence of the boundary layer. In this study, I used the following instruments: ultramarine velocity recorders (UVRs) (Ultramarine Instruments Inc., Galveston, TX, USA), time–depth recorders (TDRs) (Wildlife Computers, Redmond, WA, USA) and VHF radio transmitters (Telonics, Mesa, AZ, USA).

The UVRs are custom-made electronic data loggers that determine speed and distance traveled by counting the revolutions of a small, nylon turbine over time. Each UVR measures 8 cm×5 cm×2 cm and weighs 60 g. The recorders are individually calibrated, have a stall speed of less than 0.25 m s^{-1} and are accurate to 0.005 m s^{-1}. Laboratory tests indicate that the recorders are relatively insensitive to the angle of approach (approximately ±35°), and thus remain accurate for a wide range of mounting profiles. UVRs were mounted to the leading edge of a piece of 3 mm thick polyvinyl plate that measured 21 cm×21 cm. For this study, no compensation was attempted for currents or water flow that might cause over- or underestimates of swim speed and distance. Because the sampling rates were different between the UVRs (5 s) and the TDRs (20 s), data were resampled at a common interval of 20 s when comparing diving and swim-speed data.

Turtles were also equipped with VHF transmitters (Telonics Mod 600) with a transmission distance of 25 km (although this increased significantly with increased elevation of the reception station) and battery life of 60 days. At sea, turtles were located by triangulation from a mobile, shore-based receiver (Telonics TR-4) and 5-element YAGI antenna. A Global Positioning System (Trimble Inc., Sunnyvale, CA, USA) was used to determine the receiver location and a compass mounted to the antenna mast was used to determine a bearing to the turtle. Bearings were plotted on a standard navigational chart. Since error in determining the bearing can vary between operators, and this project utilized a number of volunteers, all operators were tested for accuracy against a known radio location. Daily accuracy checks were also made by the senior investigator. Finally, the various locations were

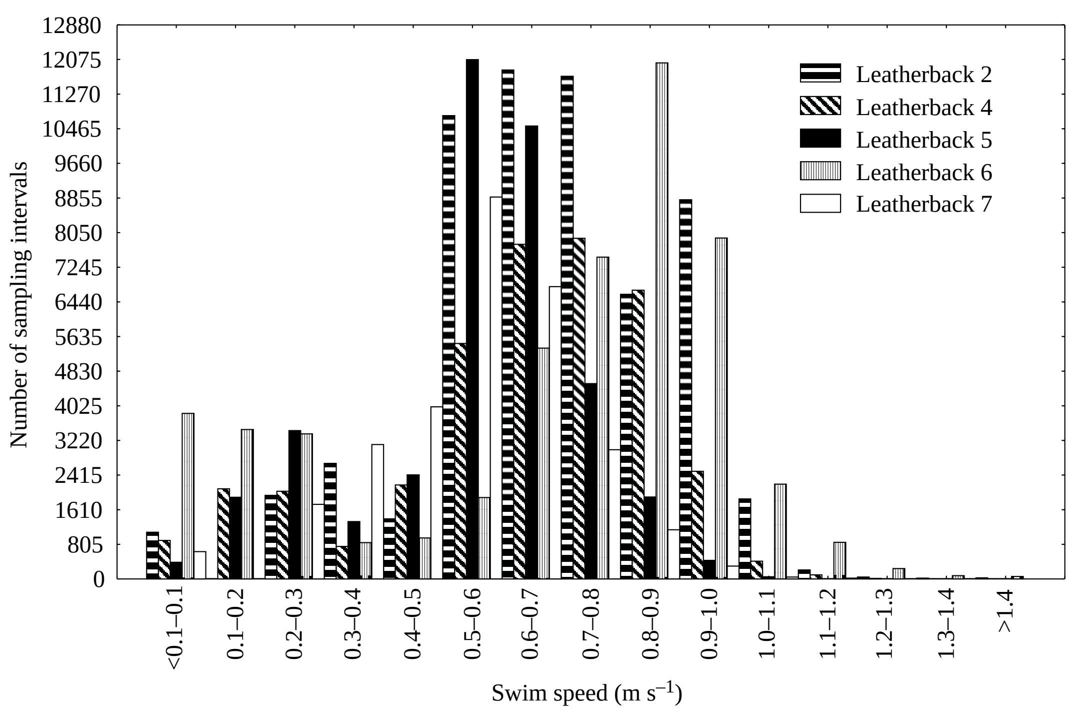


Fig. 1. Frequency distribution of swim speed for five leatherback sea turtles during one internesting interval at St Croix in the US Virgin Islands. The distribution is slightly bimodal for most turtles, with peaks at 0.2–0.4 m s^{-1} and 0.5–0.8 m s^{-1}. The duration of each sampling interval was 20 s.

Table 1. *Summary information on seven leatherback sea turtles who were monitored for daily location, swim-speed and dive behavior, during a single internesting interval at St Croix, US Virgin Islands*

Turtle number	Curved carapace length (m)	Curved carapace width (m)	Deployment date	Recovery date	Instrument type
1	1.45	1.00	05/06/93	05/19/93	UVR, VHF
2	1.49	1.09	05/17/93	05/29/93	UVR, VHF
3	1.51	1.15	05/06/93	05/15/93	UVR ,VHF
4	1.51	1.04	05/18/93	05/29/93	UVR, VHF
5	1.59	1.16	05/07/93	05/15/93	UVR, VHF, TDR
6	1.65	1.16	05/04/93	05/13/93	UVR, VHF, TDR
7	1.69	1.22	05/04/93	05/13/93	UVR, VHF

Table 2. *Summary swim-speed statistics for five leatherback sea turtles monitored during one internesting interval at St Croix, US Virgin Island*

Turtle number	Number of 20 s sampling intervals	Speed ($m\,s^{-1}$)				
		Mean	S.D.	Median	Modal	Maximum
2	58992	0.70	0.21	0.67	0.68	2.1
4	38898	0.63	0.23	0.68	0.66	2.0
5	39029	0.55	0.18	0.58	0.56	1.9
6	50577	0.67	0.32	0.78	0.84	2.6
7	29694	0.53	0.17	0.56	0.56	2.8
All data	217199	0.63	0.24	0.66	0.67	2.8

edited by the senior investigator and obviously erroneous data were discarded (e.g. the bearing indicated that the turtle was in the center of the island). To further reduce reception error, we often used geographic features such as the central mountain ridge of the island to isolate signal direction. With transmitters as powerful as the ones used in this study, the signal strength of a close transmitter could often compromise the directionality of the signal and cause it to appear at four equal points around the receiving station – in such cases geographical features of the island could be used to screen various directions and deduce which of the bearings was the correct one. Locations of the turtles are presented as location polygons, which incorporate directional error. The goal of this tracking was to locate each turtle at least once in every 24 h period.

Two of the seven turtles were also equipped with Wildlife Computers (Redmond, WA) Mk3 TDRs to monitor dive patterns. The cylindrical TDRs measured 15 cm×2.5 cm and weighed 100 g in air. Each TDR consists of a microprocessor-controlled data logger sampling depth (pressure) at user-programmed time intervals. These Mk3 data loggers contained 124 K of RAM and were programmed to sample depth at 20 s intervals, which allowed the TDR to record dive behavior for a 10-day internesting interval. Maximum depth range of these recorders was 475 m with a resolution of 2 m. Programs supplied by the manufacturer allow the determination of dive depth, dive duration, surface duration, ascent rate, descent rate and bottom time.

Results

Seven turtles were equipped with VHF radios and velocity recorders, two of these turtles also carried TDRs (Table 1). Of the seven deployed, five velocity/distance records (leatherbacks

Table 3. *Percentage of total time registered by the velocity recorder as speed zero for five leatherback sea turtles during one internesting interval at St Croix, US Virgin Islands*

Turtle number	Speed=0 $m\,s^{-1}$ (% of total time recorded)
2	1.85
4	2.30
5	0.99
6	7.44
7	2.13

Table 4. *Percentage of time spent in type 1 or type 2 swim behavior for five leatherback sea turtles during one internesting interval at St Croix, US Virgin Islands*

Turtle number	Time (%)	
	Type 1	Type 2
2	75.16	24.57
4	97.80	1.98
5	92.70	3.50
6	59.50	34.10
7	78.40	20.90
All	88.79	9.98

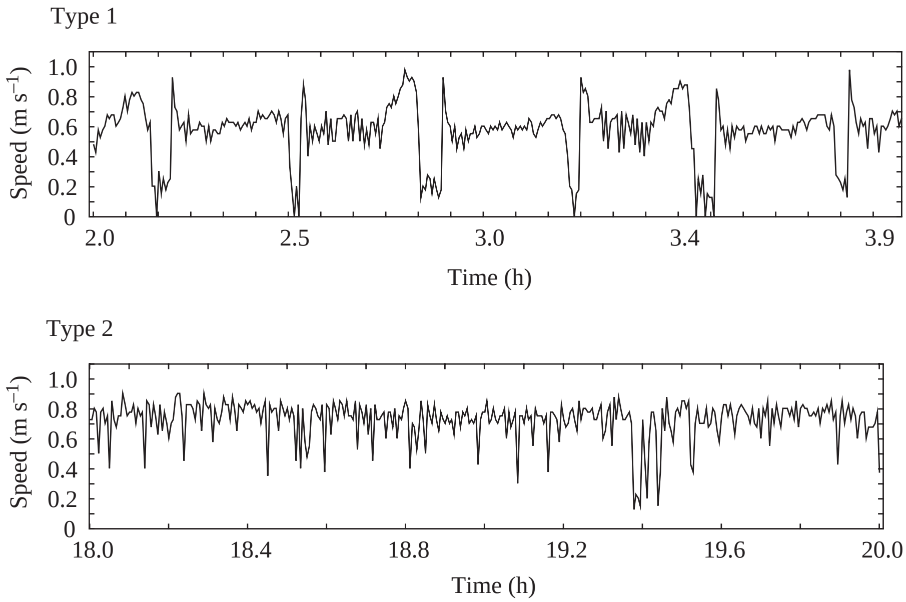


Fig. 2. Two sections of the swim-speed record from leatherback 2, illustrating type-1 and type-2 swim behavior. Type-1 is characterized by speed slowing then increasing over a 5–15 min period, bordered by intervals of very low or zero speed. Type-2 speed behavior is characterized by periods of continued high speed swimming without abrupt speed drops. Type-1 behavior is most common for all turtles, but the proportion of type-2 swimming increased during the last few days of each internesting interval.

2, 4, 5, 6, 7) and two TDR records (leatherbacks 5, 6) were obtained. Swim-speed data are not normally distributed (Kolmogorov–Smirnov one-sample test of normality with Lilliefors probabilities; $P<0.01$ for all data sets) and are somewhat bimodal, which created a problem in trying to describe 'typical' swim speeds of the species (Fig. 1). Also because this is the first such report on swim speed of the species, I report more descriptors than might normally be presented, including mean, median, mode and maximum (Table 2). The mean swim speed for all turtles was $0.62\pm0.24\,\mathrm{m\,s^{-1}}$ (±S.D., N=217199), with individual means ranging from $0.53\,\mathrm{m\,s^{-1}}$ to $0.70\,\mathrm{m\,s^{-1}}$. Swim speeds were significantly different among turtles (Friedman analysis of variance, ANOVA; $P<0.000$). Overall, median swim speed was $0.66\,\mathrm{m\,s^{-1}}$ (range 0.56–0.78 $\mathrm{m\,s^{-1}}$). Finally, modal speeds ranged from 0.56 to $0.84\,\mathrm{m\,s^{-1}}$ with a mean modal speed of $0.67\pm0.10\,\mathrm{m\,s^{-1}}$ (± S.D.). Maximum swim speeds were 1.9–2.8 $\mathrm{m\,s^{-1}}$, although it should be cautioned that this maximum speed does not represent a sustained speed, but rather the highest speed during a single sampling interval of 20 s. There was no correlation between swim speed and curved carapace length of the turtle (Pearson–Product moment test, P=–0.59).

There was very little time when turtles were not moving forward. The percentage of time in which speeds were recorded

Table 5. *Summary of distance (km) swum by five leatherback turtles during each day of a single internesting interval at St Croix, US Virgin Islands*

Inter-nesting day	Distance swum (km) Leatherback 2	Leatherback 4	Leatherback 5	Leatherback 6	Leatherback 7
Day 1	4.63	48.13	47.04	55.85	45.08
Day 2	58.63	45.13	47.52	56.04	49.75
Day 3	52.75	50.41	43.84	57.98	47.54
Day 4	52.59	46.26	40.71	54.86	44.79
Day 5	53.08	38.68	43.48	51.35	43.24
Day 6	55.80	41.23	46.75	59.42	41.78
Day 7	61.94	52.14	46.37	64.90	42.55
Day 8	57.87	57.00	51.90	63.70	
Day 9	54.80	58.07	53.79	53.01	
Day 10	68.41	2.19	5.33	64.16	
Day 11	71.04			29.43	
Day 12	69.16				
Mean	58.69	48.36	46.79	58.38	45.42
S.D.	6.55	7.46	4.34	5.02	3.22
Total	660.70	439.24	426.73	610.70	314.73

Means and S.D. values are calculated for only those days in which a full 24 h record was available.

Table 6. *Summary of diving data as recorded by a time-depth recorder on two female leatherback sea turtles during a single internesting interval at St Croix, US Virgin Islands*

	Depth (m)	Dive time (min)	Surface interval (min)	Bottom duration (min)	Descent rate ($m\,s^{-1}$)	Ascent rate ($m\,s^{-1}$)
Leatherback 5						
All data						
Mean	93.0	10.3	3.4	2.6	0.54	0.32
S.D.	72.8	6.8	7.9	1.9	1.5	1.9
N	971	971	971	971	971	971
Maximum	490	23.3	166.6	8.7	24.8	9.4
Day						
Mean	111.6	11.2	4.2	2.9	0.71	0.28
S.D.	79.7	6.8	8.0	2.0	2.0	2.6
N	503	503	503	503	503	503
Maximum	490	22.7	166.6	7.3	24.8	9.4
Night						
Mean	73.0	9.4	2.5	2.3	0.36	0.35
S.D.	58.3	6.7	7.7	1.8	0.12	0.16
N	468	468	468	468	468	468
Maximum	294	23.3	166.6	8.7	0.8	1.4
Leatherback 6						
All data						
Mean	64.0	10.2	8.9	3.2	0.28	0.30
S.D.	57.0	7.2	19.3	2.6	0.11	0.14
N	978	978	978	978	978	978
Maximum	480	29.3	294	11.7	1.2	1.0
Day						
Mean	93.7	12.4	16.1	3.8	0.31	0.35
S.D.	67.8	6.3	29.1	2.4	0.12	0.16
N	382	382	382	382	382	382
Maximum	480	29.3	294	11.7	1.0	1.0
Night						
Mean	44.9	8.9	4.3	2.8	0.26	0.27
S.D.	38.3	7.3	3.6	2.6	0.10	0.12
N	596	596	596	596	596	596
Maximum	184	28.7	39.7	11.0	1.2	0.7

as zero ranged from 0.99% to 7.42% (Table 3). There was no relationship between time of day and length of time that the turtles were not moving (Pearson–Product moment, $r=-0.0261$). In other words, turtles did not appear to stop swimming at any particular time of day, as might be assumed if they were basking or resting.

Two distinct swim-speed patterns are found in the records (Fig. 2). Type 1 is defined by swim speed decreasing slowly and then increasing again over a 5–15 min period, usually bordered by a rapid drop to intervals of very low or zero speed. Most swimming (mean range 59.5–97.8%) could be placed in the type-1 category (Table 4). Type-2 speed behavior is defined as a period of continued high-speed swimming with limited variation and without the speed drops that characterized the type-1 speed pattern. Type-2 swimming occurred for 1.98–34.1% of the swim-speed record for each turtle. The proportion of type-1 and type-2 swimming varied by day of the internesting interval, with a higher proportion of type-2 swimming seen during the last few days of the interval.

The UVRs are capable of accurately measuring distance traveled by the turtle. The total distance swum for each turtle was 314.7–660.7 km (Table 5) over their respective internesting intervals. The weighted mean distance swum per day for all turtles was 52.58±8.05 km (± S.D.). Daily swimming distances were significantly different among turtles (ANOVA; $P=0.00006$, calculated only from days in which distance data were available for a full 24 h) and ranged from 38.68 to 71.04 km (Table 5). However, the difference does not appear to be a function of turtle size. The distance swum per day by each turtle varied over the course of the internesting interval. All turtles exhibited a pattern of decreasing distance traveled until mid-internesting period (day 5), and then an increasing distance per day until the turtle nested again.

Dive patterns were monitored for two of the turtles

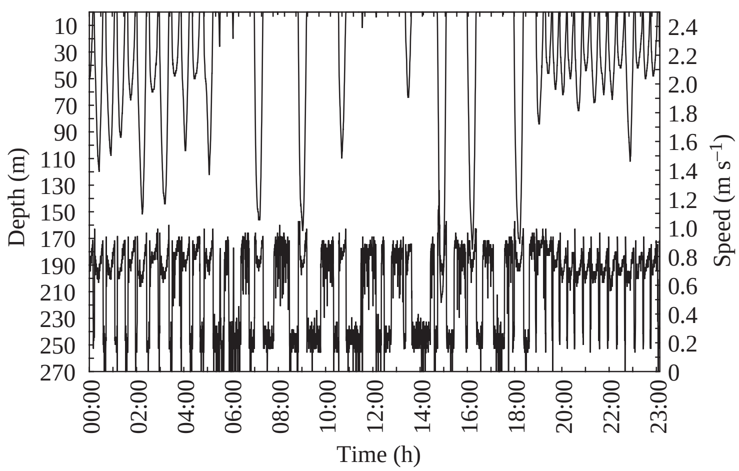


Fig. 3. A 24 h section of the simultaneous swim-speed and dive record for leatherback 5, illustrating the relationship between dive profile and swim speed. Dive behavior is similar to that recorded in previous dive studies at St Croix, with shallower and more frequent diving at night (19:00 h–05:29 h) than during the day (05:30 h–18:59 h).

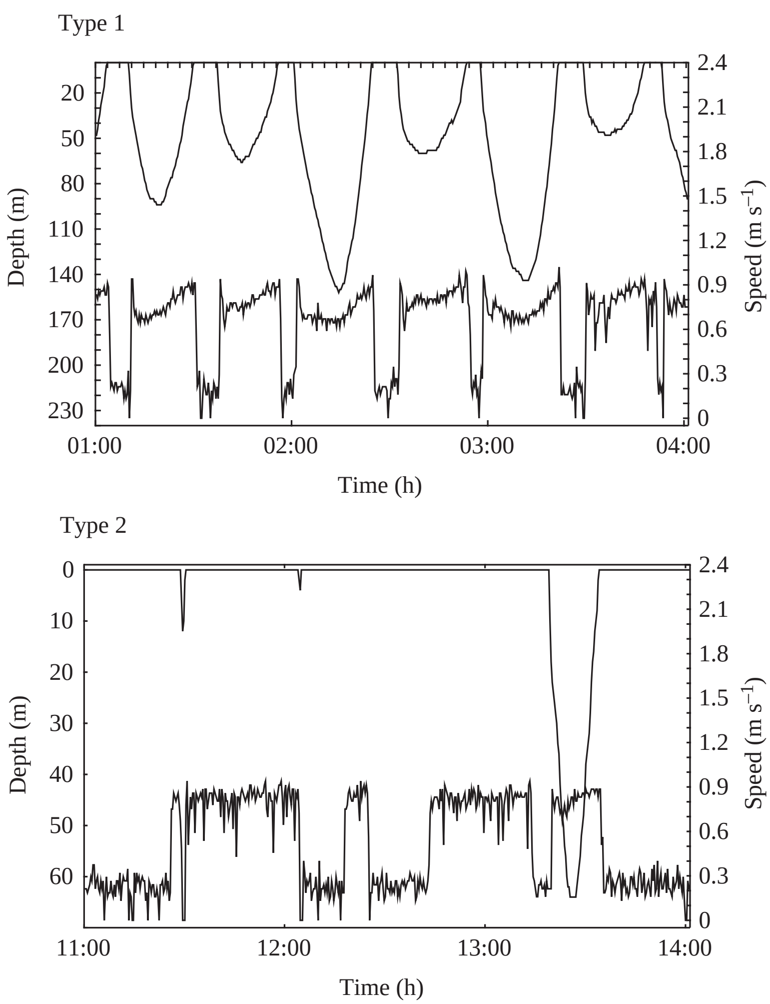


Fig. 4. Two sections of the swim-speed and dive records of leatherback 6, illustrating how type-1 speed records follow the profile of dive depth, while type-2 speed records occur during shallow swimming by the turtle when the TDR may be registering a depth of 0 m.

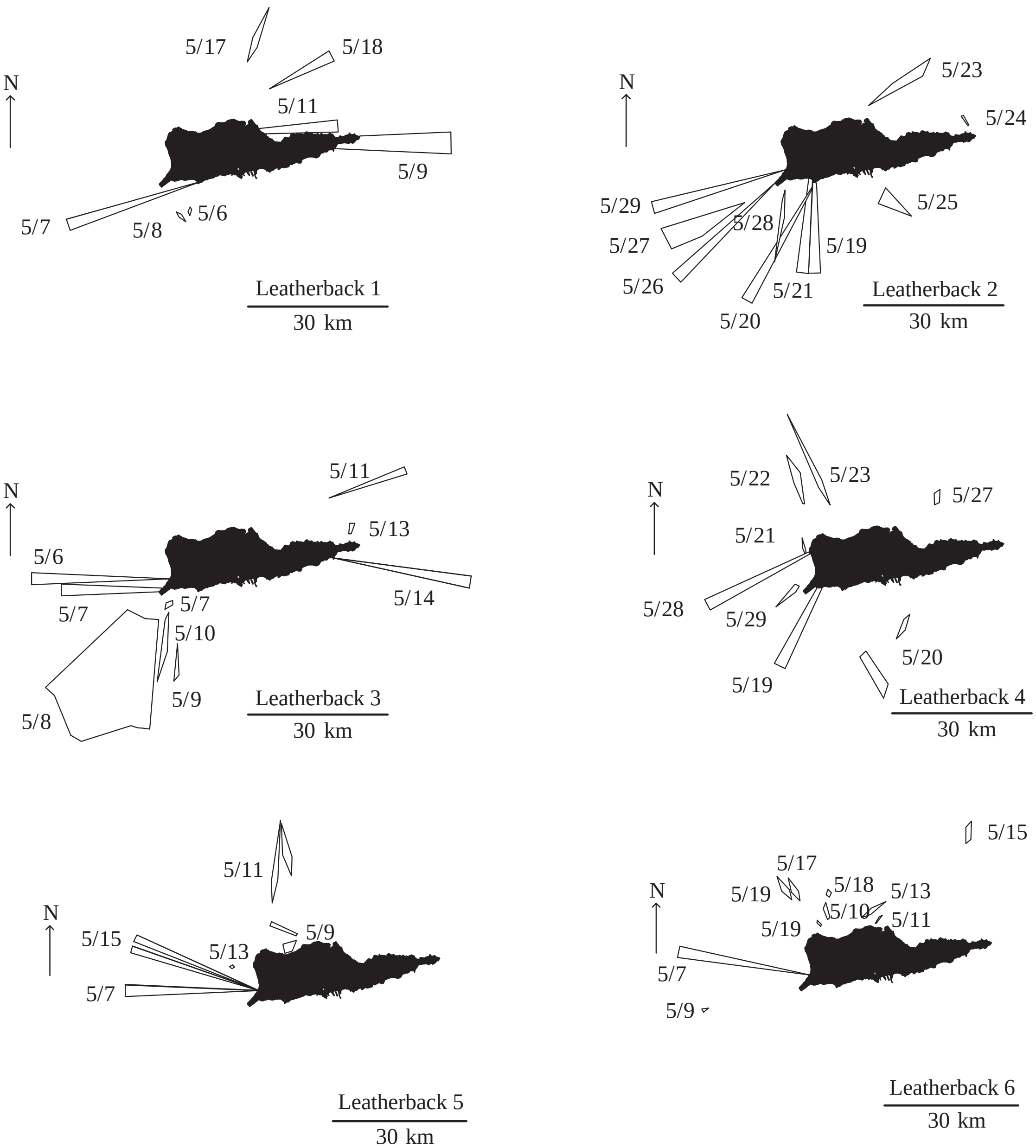
simultaneously with their swim speeds. Overall, dive patterns were similar to those observed in our earlier studies (see Eckert et al., 1986, 1989). Turtles dived directly to depth and returned directly to the surface (Fig. 3). There were significant statistical differences in dive behavior between the turtles for all but the bottom time (time spent at maximum depth) (Mann–Whitney *U*-test, $P<0.05$). Day dives were deeper and longer, with longer surface and bottom durations and faster ascent and descent rates than those at night (Table 6).

Combining dive depths with swim speed showed a close linkage between swim-speed type and dive profile (Fig. 3). For type-1 dives (as defined by swim speeds), turtles slowed their rates of travel as they descended until they reached the bottom of the dive, then gradually increased speed as they ascended (Fig. 4). For type-2 dives, characterized as continuous swimming at a steady rate without the mid-dive decrease in speed, dives were very shallow (Fig. 4). In fact, for a high proportion (69.38% for leatherback 6 and 61.24% for leatherback 5) of the type-2 speed profiles, depth was recorded as 0 m. Such results were likely to have been caused by the turtle swimming below the surface, so that its UVR was submerged, but at depths of less than 2 m, which is the minimum resolution of the TDR.

It was impossible to locate each turtle daily, but locations were determined an average of 76% (range 89–54%) of the days between nesting events (Fig. 5). Turtles were located primarily on the west end of St Croix, but also ranged around the island, particularly to the north side. A common post-nesting movement pattern was for turtles to move directly off Sandy Point and remain for up to 3 days, then move around the island (either clockwise or counterclockwise) to the north coast, where they resided for a few days before returning to Sandy Point. From the maps it appears that distance swum per day was variable. However, the UVRs showed that actual variation in distance traveled per day was small (Table 5). Turtles would often remain in a general area for a few days, then move almost all the way around the island to another area where they might remain for another few days.

Discussion

One of the most startling results of this study is that leatherbacks swim continuously, with little or no resting. In our earlier work (Eckert et al., 1986, 1989), we proposed that the turtles were basking or resting at the surface during midday when our time depth records indicated that the turtles were at the surface. However that hypothesis now appears to be unsupported by this new data. Since these turtles rarely stopped moving,



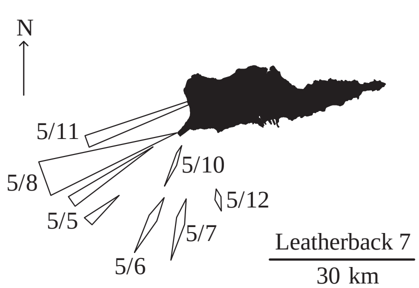


Fig. 5. Daily locations of seven leatherbacks during a single internesting interval around the island of St Croix, US Virgin Islands (in black). Locations were established using directional VHF radio telemetry, in which turtle location was determined relative to the location of a shore-based VHF radio receiver and recorded as a compass bearing. Since each bearing has an inherent error, the probable location was expressed as a triangular shaped polygon. Where triangulation occurred, because a turtle was located from a number of shore-based locations, only the area where the polygons overlapped is shown. The primary nesting area on St Croix is Sandy Point National Wildlife Refuge on the southwest tip of the island. Dates are expressed as month/day.

surface resting or basking must not occur. Our combined TDR and UVR records indicate that while the turtles are near the surface, they are still moving forward. If the turtles were truly surfaced with their carapace exposed, as might be expected during basking, the impeller in the velocity recorders would have stopped spinning, dropping the speed to zero. Such speed drops are clear in type-1 swim-speed patterns, when the turtle surfaces to breathe.

As in previous studies, turtles spent more time near the surface during the middle of the day. This was also the time at which type-2 swim patterns were more common. Why would leatherbacks swim for extended periods at shallow depths, in contrast to the vertical diving which makes up the majority of their activities? It is likely that such behavior is to enhance swim efficiency. The most efficient depth (as measured to the middle of the body's diameter) for swimming animals is three times the maximum diameter of the body (Blake, 1983). This is deep enough to remove the effects of wave drag generated by a swimming turtle, yet shallow enough to allow for rapid surfacing (to breathe). The average curved carapace width (CCW) of the seven turtles in this study was 112.3 cm, which is one-half of the circumference of this very cylindrical turtle. To confirm the relationship between CCL and circumference, I measured the width and circumference for five other female leatherbacks. The mean ratio between CCL and circumference is 1.95. The average diameter of the instrumented turtles is calculated at 71.5 cm. Maximum swimming efficiency should therefore be at a depth of 2.1 m (as measured to the center of the turtle's body) or 1.8 m from the dorsal surface of the carapace (where the recording instruments are located). Days in which turtles exhibit the highest proportion of type-2 activity correspond closely to days in which they travel the greatest distances. It appears that when leatherbacks desire to move long distances they utilize an extremely efficient subsurface swimming mode, which is exhibited as type-2 swimming. Shallow subsurface swimming also explains why daily movement records and swim distance records are in disagreement. Leatherbacks swim continuously at constant rates of travel, and travel about the same distance each day. However, the horizontal distance traveled varies by how much vertical diving they do. If such vertical diving is to forage, as we proposed earlier, then a useful indication that a turtle has reached a foraging habitat can be determined from the extent of its horizontal distance traveled. With the increasing use of satellite telemetry to study habitat use of leatherbacks (Eckert, 1998; Eckert and Sarti, 1997; Hughes et al., 1998; Morreale et al., 1996), such a method for identifying foraging areas could be very useful.

That turtles seemed to make most of their long horizontal movements during the middle of the day is also an interesting observation. One possible reason for this behavior is that shallow swimming during the day provides the opportunity to use a sun compass for navigating back to their nesting beach, as used by many bird species (Berthold, 2001). It is also possible that mid-day periods are not useful for foraging, as most of the prey is located within the deep scattering layer and beyond typical foraging depths of the species (Eckert et al., 1989). Thus, the turtles choose to move long distances at a time when foraging opportunities are limited.

Swim speeds were quite regular, with little variation in speed. Irrespective of the statistic used (mean, median, mode), leatherbacks swim at a rate of approximately 0.65 m s^{-1} (range 0.62–0.67 m s^{-1}). Each turtle had a distinct speed preference that was unrelated to its size; however, this lack of relationship between size and speed may reflect the limited size range of the turtles used in this study. It is interesting to note that leatherback 2 was missing approximately 50% of its right front flipper, yet its modal and maximum swim speeds are indistinguishable from the other turtles.

Type-1 speed patterns usually occurred during vertical dives in which the turtle initiates each dive with a bout of high-speed swimming that gradually slows as it descends to maximum depth and then gradually accelerates during ascent. The high-speed swimming at the beginning of the dive is probably an effort to overcome the effects of positive buoyancy, but as the lungs compress it is able to glide to the maximum depth of the dive with reduced energy expenditure. Green turtles exhibit complete lung collapse at 90 m (Berkson, 1966). For leatherbacks with their flexible plastron and smaller lungs (Eckert, 1989), lung collapse probably occurs at even shallower depths. As the turtle ascends, the opposite occurs, allowing the turtle to accelerate near the completion of the dive by utilizing positive buoyancy. Similar behavior to improve diving efficiency has been demonstrated for marine mammals (Davis et al., 2001; Williams et al., 2000).

To conclude, leatherback turtles do not bask during the middle of the day as we previously proposed. Rather, they use this time to travel from one area to another with best efficiency. Leatherback sea turtles also rarely stop swimming during their internesting intervals, and they travel at relatively constant rates of speed. Further, the distance traveled per day by these turtles is relatively uniform. When foraging, most of that travel is spent moving between the surface and depth, but if moving long distances or migrating, the turtles swim just below the surface.

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