———. 1970. A radio telemetry technique for monitoring temperatures from unrestricted ungulates. Wildl. Mngt. 34:922–925.
MORGAREIDGE, K. R., AND F. N. WHITE. 1969. Cutaneous vascular changes during heating and cooling in the Galapagos marine iguana. Nature 223:587–591.
MOUNT, L. E. 1968. Climatic physiology of the pig. Arnold, London.
MROSOVSKY, N. 1968. Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature 220:1338–1339.
———, AND P. C. H. PRITCHARD. 1971. Body temperatures of *Dermochelys coriacea* and other sea turtles. Copeia 1971:624–631.
SMITH, E. N. 1976. Heating and cooling rates of the American alligator, *Alligator mississippiensis*. Physiol. Zool. 59:37–48.
SPIGARELLI, S. A., M. M. THOMMES AND T. L. BEITINGER. 1971. The influence of body weight on heating and cooling of selected Lake Michigan fishes. Comp. Biochem. Physiol. 5:51–57.
SPRAY, D. E., AND M. L. MAY. 1972. Heating and cooling rates in four species of turtles. *Ibid.* 41A:507–522.
TEMPLETON, J. R. 1970. Reptiles, p. 167–221. *In*: Comparative physiology of thermoregulation. G. C. Whittow (ed.). Academic Press, New York.

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Thermal Influences on the Swimming Speed of Loggerhead Turtle Hatchlings

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Loggerhead turtle hatchlings in laboratory tanks had a sustained swimming speed of approximately 20 cm/sec at temperatures between 25.6 and 28.9 C. Test temperatures of 30.0 and 33.0 C significantly reduced this speed. The swimming speed of hatchlings exposed to fluctuating temperatures varied with the temperature. A temperature of 33.0 C eliminated phototactic orientation.

ATLANTIC loggerhead turtles (*Caretta caretta*) nest on the barrier islands along the southeastern United States. One of the last major nesting rookeries is on Hutchinson Island, Florida, where resort motels, condominiums, restaurants and an electric generating facility are located.

Despite commercial development, large tracts of uninhabited beach still remain on the island. During summer nights, adult females crawl up the beach to deposit about 120 eggs in a 60 cm-deep nest hole. The eggs hatch 50–70 days later. The hatchling turtles dig out of the nest at night, then rapidly crawl across the beach and into the sea. Once there, the turtles must be able to swim rapidly to an area offering both food and shelter. They spend the rest of their lives in the sea, except for the mature female's beach nesting periods.

Hendrickson (1958) examined nest emergence of green turtles (*Chelonia mydas*) and suggested that temperatures over 33 C inhibit nest chamber activity and that hatchlings resume activity only with the return of lower nocturnal temperatures. Mrosovsky (1968) substantiated Hendrickson's observations, but specified 28.5 C as the temperature at which green turtles become lethargic in the nest. Both authors agree that thermal inhibition of activity is a major factor limiting the emergence of hatchling sea turtles. Nocturnal emergence can enhance hatchling sea turtle survival, therefore, by protecting them from the high surface temperatures on tropical beaches and by reducing both water loss and attacks from visually-oriented predators.

Studies on green turtles indicate the sea-finding process to be primarily visual and the brighter portion of the environment (under natural conditions, over the ocean) attracts the

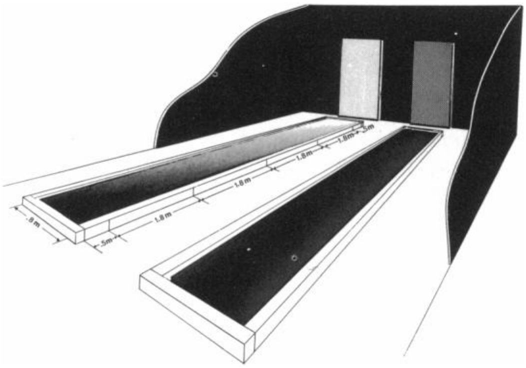

Fig. 1. Diagrammatic view of turtle swimming test tanks.

TABLE 1. LIGHT INTENSITY AT SELECTED DISTANCES ALONG EXPERIMENTAL TANKS.

Distances in meters to end of tank	Lux
8.2	7.2
7.7	7.7
5.9	10.7
4.1	20.0
2.3	42.9
0.5	96.8

hatchling turtles (Ehrenfeld and Carr, 1967). Additional studies show that, for a variety of reasons, they will move toward the brightest available light (Ehrenfeld, 1968; Mrosovsky and Shettleworth, 1968; Mrosovsky, 1970, 1972). It has also been documented that artificial lighting at developments near hatching sites will disorient loggerhead hatchlings (McFarlane, 1963).

Once in the sea, hatchlings swim far offshore and seek refuge in drifting sargassum weed (Caldwell, 1969; Fletemeyer, 1978). Either decreased swimming speed from thermal inhibition of activity or disorientation could lengthen the time they spend in reaching the protective sargassum mats and thus reduce the turtles' survival potential.

In this study, I examined the influence of water temperature on the sustained swimming speeds of loggerhead turtle hatchlings; I also monitored the effects of abrupt thermal changes, such as might be encountered in a discharge from an electric generating station, on these swimming rates.

MATERIALS AND METHODS

Hatching and maintenance.—Loggerhead turtle nests were excavated from the sand on Hutchinson Island, Florida, 26 May–5 Aug. 1977, immediately after the adult female left the nest site. Twenty-five or more eggs from each of 13 nests were transported by commercial aircraft to Atlanta, Georgia, where they were incubated in damp-sand-filled 12-l plastic pails until they hatched. During the period of study, the incubation room temperature averaged 28.2 C (range 27–30 C) which was consistent with subsurface beach temperatures on Hutchinson Island during the same period. To minimize egg disturbance, internal nest temperatures were not taken. These would be slightly higher than ambient temperature, because of metabolic heat produced by the eggs (Carr and Hirth, 1961).

Hatching occurred 4 Aug.–22 Oct. 1977. Turtles were allowed to emerge naturally from the nests. In order to eliminate pre-test conditioning to a light stimulus, no light was present in the room during incubation, hatching or the holding period before testing.

Genetic variability, incubation temperature and age at testing could influence the swimming speed of hatchlings. Potential variation due to these factors was reduced by distributing turtles from different nests into tests at various thermal regimes. Turtles were tested 4–48 hours after emergence to reduce the potential of different levels of activity from turtles of different ages (Mrosovsky, 1968). Each turtle was used for one experiment only. Following these experiments, all live turtles were returned to Hutchinson Island and released.

Test tanks.—Swimming tests were conducted in two shallow tanks containing artificial seawater (Fig. 1). Each was 8.2 × 0.8 m, was constructed of cement blocks, and lined with black plastic. Each tank was marked into four 1.8-m compartments, with a 0.5-m turning area at each end.

Temperature control.—Water temperatures at the start of each test were regulated to ±0.3 C. This was done with immersion heaters controlled by high-precision mercury thermoregulators coupled to an electronic temperature control relay (Versatherm Models 2151 and 2149). To eliminate physical obstructions to swimming turtles, heaters were removed from the tanks imme-

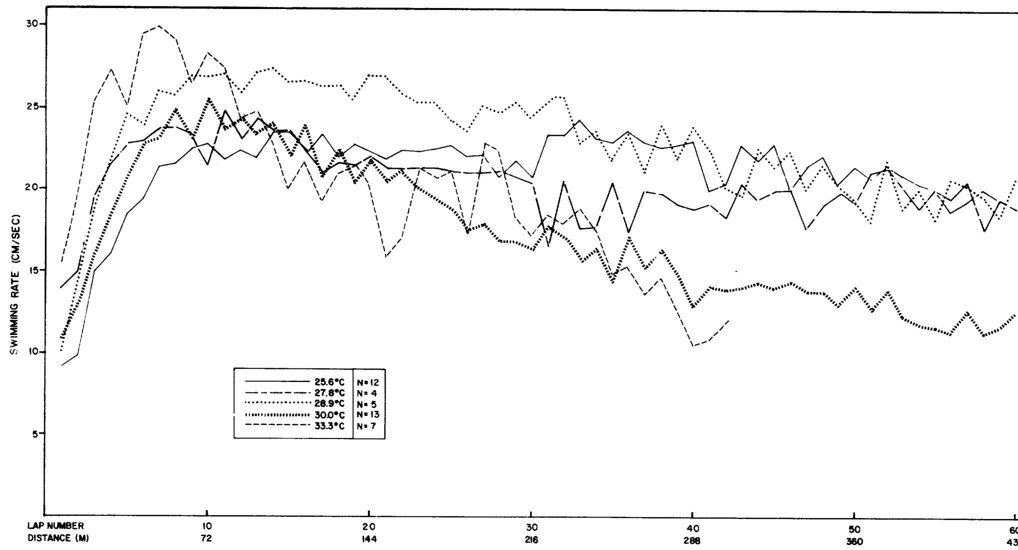

Fig. 2. Swimming speeds of hatchling loggerhead turtles at various temperatures.

diately before the tests. Even with heater removal, water heat loss averaged less than 0.5 C during these tests.

Light control.—Tests were conducted in a light-tight laboratory room. The only illumination was from two 15-watt incandescent lightbulbs reflecting onto a white sheet at each end of the tank. This light constituted the photic stimulus and was the lowest illumination that let the experimenters observe the turtles. Tank illumination ranged from 7.2 lux at the distal end to 96.8 lux near the proximal end (Table 1).

Experimental procedures.—A single turtle was placed at one end of the tank and allowed to swim toward the light at the far end. When the turtle completed the length of the tank, the light stimulus was switched to the other end. The turtle would rapidly orient and swim toward the new light location. In this fashion, turtles were tested for 30 or more tank lengths (laps). The times required to swim each 1.8-m distance were measured with a digital stopwatch with cumulative interval timing. Swimming speeds (cm/sec) for the four quarter-laps were averaged.

Thermal regimes.—Individual turtles were transferred directly from the sand in the nest pail to the swimming tank without thermal acclimation, to simulate natural thermal exposure. Temperatures of 25.6, 27.8, 28.9, 30.0 and 33.3 C were selected for constant temperature exposure tests, since these reflect summer ocean temperatures at Hutchinson Island and the 3.0 C temperature elevation potentially encountered near the electric generating station's offshore discharge.

Since hatchling turtles may encounter the heated discharge after being in water at ambient temperatures, additional tests were conducted in a fluctuating thermal regime to simulate conditions encountered by turtles swimming in and out of a thermal plume. After swimming speed was established over 10 or 20 laps at one temperature, the turtles were gently transferred to the second test tank containing water 2.2, 3.3 or 4.4 C warmer. Swimming speeds at the increased temperatures were determined over the same number of laps as the first part of the test; the turtles were then returned to the lower temperature to complete the last third of the test. Control animals were similarly handled after 10 or 20 laps and returned to water of the same temperature.

Results

General observations.—Some light scattering and reflection from the plastic sheeting was apparent, but the turtles oriented and swam toward the brightest light. Naive turtles placed in the test tanks had less than a one-min delay in ori-

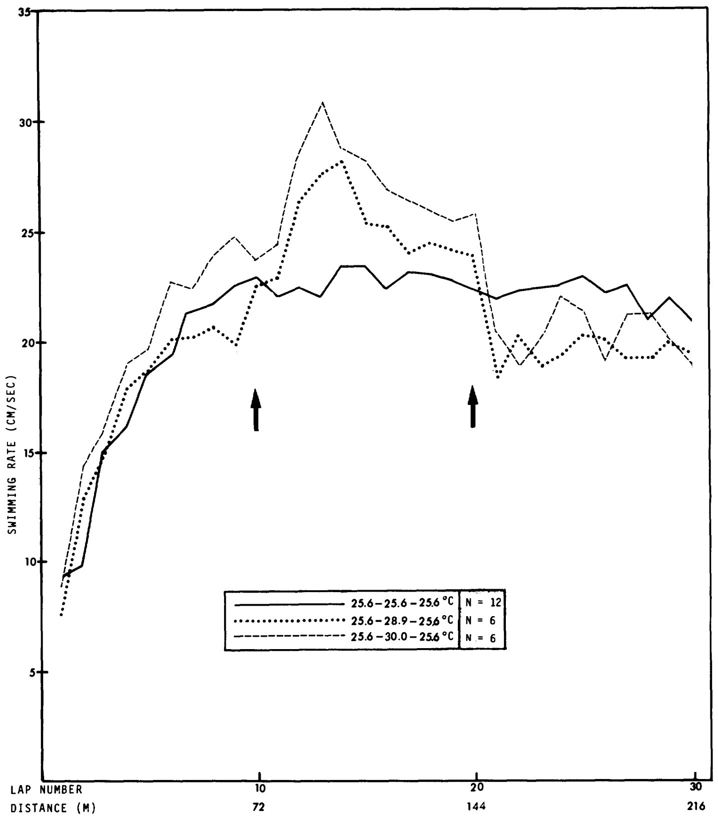

Fig. 3. Mean swimming speeds over 30 laps of hatchling loggerhead turtles exposed to three temperature regimes. Thermal change marked by arrow.

entation to light. During this time, the turtles remained in the first 0.5 m of the tank before slowly starting to swim toward the light stimulus. Swimming speeds increased rapidly over the first five laps, as the turtles acclimated to their environment and exhibited a stronger response to light stimulus. Most turtles reached a maximum swimming speed of 23 to 30 cm/sec between laps 7 and 10.

Swimming speeds in constant temperatures.—After attaining their maximum rates, turtles exposed to constant temperatures of 25.6 and 27.8 C showed a slight decrease in speed which stabi-

TABLE 2. RESULTS OF REGRESSION ANALYSES OF SPEED AND DISTANCE (LAP) FROM MAXIMUM TURTLE SPEED TO END OF TEST.

Temperature	Slope (b)	Intercept (a)	Error sum of squares	N*
25.6	−0.052	23.610	0.01421	270
27.8	−0.079	23.170	0.02919	200
28.9	−0.178	29.502	0.01845	190
30.0	−0.264	26.024	0.01486	450
33.3	−0.308	28.125	0.04031	169

* N equals the total number of swimming speed determinations made at each test temperature.

TABLE 3. RESULTS OF *t*-TEST FOR SIGNIFICANT DIFFERENCES BETWEEN PAIRS OF REGRESSION SLOPES AT VARIOUS TEMPERATURES.

Temperature	33.3	30.0	28.9	27.8	25.6
25.6	9.37*	14.53*	7.81*	1.26	—
27.8	6.59*	10.33*	4.00*	—	
28.9	4.26*	5.43*	—		
30.0	1.79	—			
33.3	—				

* Significant at 0.05.

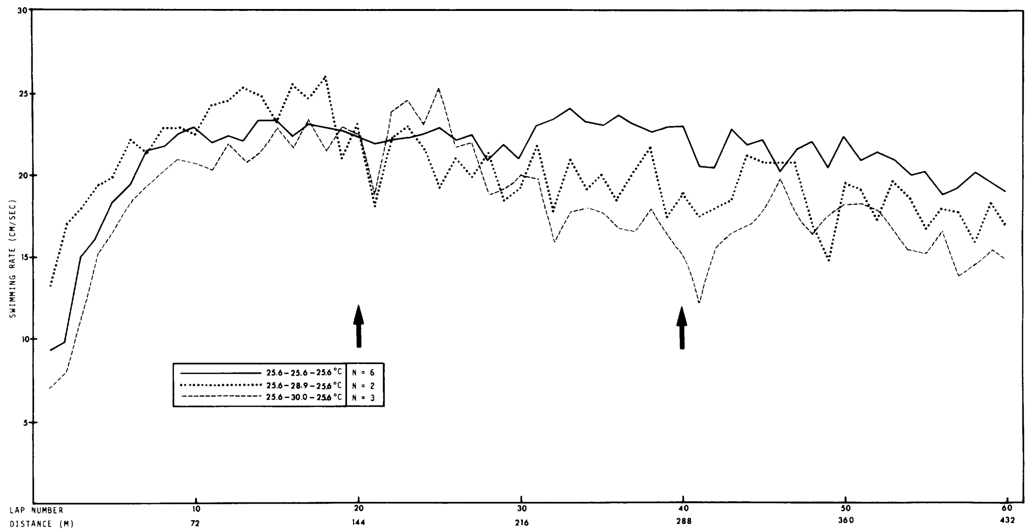

Fig. 4. Mean swimming speeds over 60 laps of hatchling loggerhead turtles exposed to three temperature regimes. Thermal change marked by arrow.

lized at approximately 20 cm/sec (Fig. 2). Turtles tested at 28.9 C showed a more marked decline in speed, but also stabilized their speed at approximately 20 cm/sec. Turtles tested at 30.0 C slowed considerably, and their speed had not stabilized by lap 60. These turtles showed a greater reduction in speed than those tested at lower temperatures, but they continued to orient to the light and swim for the duration of the experiment. Turtles tested at 33.3 C attained the highest maximum speed of almost 30 cm/sec at lap 7, then slowed in an erratic but precipitous fashion. The decline in speed was continuous over the remaining laps that these turtles swam. Of the seven turtles tested at 33.3 C, six stopped by lap 42. These turtles remained at the surface of the water and swam aimlessly. They appeared active and alert but would not orient to the light. Substitution of a brighter light had no effect. When nonresponsive turtles were then placed in water at 30.0 C, they showed no resumption of the phototropotaxis within 5 min. The single turtle that finished the test maintained an average rate of 15.5 cm/sec (individual turtles are not plotted in Fig. 2).

Linear regression analysis was applied to the data from the time of maximum speed to the end of the test (Table 2). Differences between pairs of regression slopes at the various test temperatures were determined by t-tests (Table 3). The results showed that swimming speeds were significantly different at the various test temperatures except for the 25.6–27.8 C and 30.0–33.3 C comparisons.

Swimming speeds in fluctuating temperatures.—Experiments to determine turtle responses to fluctuating thermal regimes were conducted with a base temperature, an elevated temperature and a return to base temperature. Tests with 25.6 and 30.0 C as the base and elevated values of 28.9, 30.0, 32.2 or 33.3 C were conducted over both 30 and 60 laps. The swimming speeds of turtles subjected to a fluctuating thermal regime were compared with the swimming speeds of turtles tested at a constant temperature that was equal to the base temperature.

In the 30-lap tests, the turtles were exposed to each temperature for 10 laps (Fig. 3). Exposure time for each 10-lap segment was five to seven min depending on speed. When the base temperature was 25.6 C, temperature elevations to either 28.9 or 30.0 C produced an increase in turtle swimming speed. During the 10 laps at this elevated temperature, the turtles showed a decline in swimming speed but maintained speeds above those of the 25.6 C base. At lap 21 the turtles were transferred back to the base temperature, and their swimming speeds showed an immediate and pronounced decline. This cold shock response was reduced

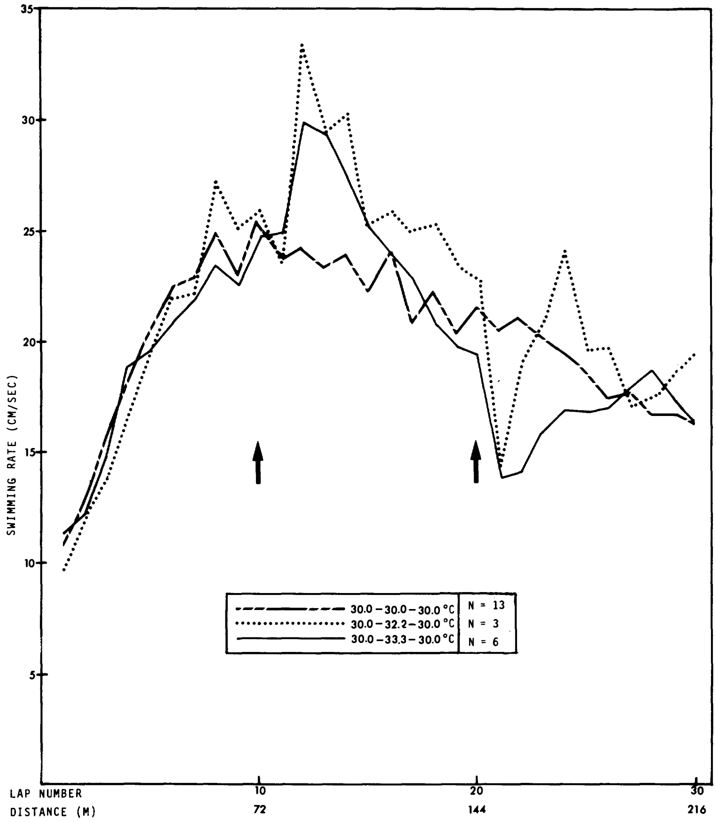

Fig. 5. Mean swimming speeds of hatchling loggerhead turtles exposed to three temperature regimes for 30 laps. Thermal change marked by arrows.

within one or two laps, and the swimming speed returned to a stable although slightly lower rate than the base speed. Alteration of swimming speed was attributed to a thermal influence rather than handling since turtles treated in a similar fashion but returned to the same temperature showed no significant change in swimming speed.

The temperature regime of 25.6/30.0/25.6 C was used in a 60-lap test, with thermal changes over 20 laps (Fig. 4). Although the thermal responses were not as pronounced as in the 30-lap tests, the turtles did show a general decrease in swimming speed during the higher temperature period and a sharp cold shock response when returned to water at 25.6 C. Only two turtles were tested at a 25.6/28.9/25.6 C, 60-lap regime (Fig. 4), and they showed extremely erratic responses.

Turtles exposed to thermal regimes of 30.0/32.2/30.0 C and 30.0/33.3/30.0 C over 30 laps (Fig. 5) showed a response pattern similar to that described for the 30-lap studies with the 25.6 C base. Following the cold shock, turtles that had been exposed to 32.2 C quickly recovered to the control animal rate. Those that had been subjected to 33.3 C made a comparatively slow return to the control rate. Sixty-lap tests were done at 30.0/33.3/30.0 C (Fig. 6). Basically similar response patterns were observed in both 30-lap and 60-lap tests.

Discussion

Within a moderate range of thermal tolerance, activity or speed in ectothermic animals generally increases with temperature rise and then falls when a species-specific critical temperature level is exceeded (Precht et al., 1973). Although little has been published on hatchling turtle swimming speed, the activity reactions of the hatchlings tested in various temperature

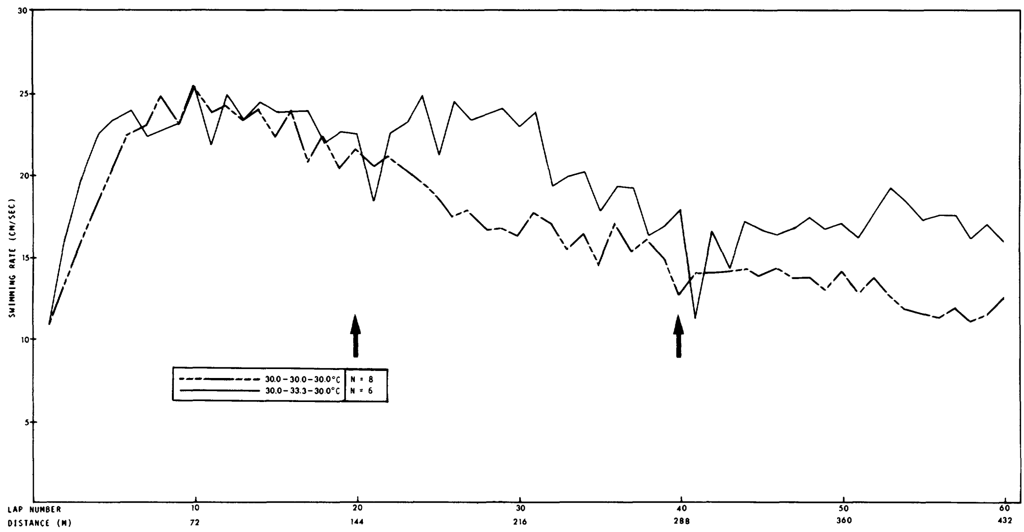

Fig. 6. Mean swimming speeds of hatchling loggerhead turtles exposed to two temperature regimes for 60 laps. Thermal change marked by arrows.

regimes typify the activity responses of other organisms.

Hatchlings exposed to temperatures between 25.6 and 28.9 C had swimming speeds which stabilized at approximately 20 cm/sec after a 45 to 60 min exposure. The speed of juvenile green turtles forced to swim against a current has been found to range between 14 and 35 cm/sec (Prange, 1976). That result is consistent with the sustained speeds observed in this study for loggerhead hatchlings, considering their smaller size and the different stimuli applied. Frick (1976) reported an average swimming speed of 43 cm/sec for hatchling green turtles, and Ireland et al. (1978) found an average of 25 cm/sec. Since both studies were done in the natural environment, oceanic currents may have had a significant influence.

The sustained swimming speed of loggerhead turtle hatchlings can be heat-limited. In the present study, I found reduced swimming speeds at temperatures of 30 C and above and a loss of phototactic orientation at a temperature of 33.3 C. These results are reflective of the heat-limited activity of hatchlings within the nest at 33 C reported by Hendrickson (1958). Mrosovsky and Shettleworth (1968) examined temperature effects on crawling response in green turtle hatchlings and reported that, in one-minute tests, turtles acclimated to temperatures of 19–29 C had a reduced crawling activity at higher temperatures, with a marked lethargy at 26 C. One-minute tests and tests on land are not directly comparable to the present study but support the concept of lower activity at higher temperatures. Reported differences in the temperature levels that produce heat-limited responses may be due to factors such as thermal history differences of the individual turtles, species variation, or test duration.

Turtles respond to an abrupt increase in temperature by an initial increase in swimming speed followed by a decline in activity as the body temperature increases.

The mean ocean temperature at the Hutchinson Island rookery during the July, August and September period of maximum emergence seldom exceeds 30 C. The present study indicates that brief encounters with slightly higher temperatures than this may reduce swimming speed and also indicates that exposed turtles rapidly return to a near normal rate when the temperature returns to ambient. The effect of prolonged exposure to slightly elevated temperatures was not measured although tests of 60 laps (about 50 min exposure) at 30 C indicate that swimming and therefore survival may be considerably reduced if the exposure were longer. Encounters with temperatures of 33 C could reduce the hatchlings' survival potential by possibly affecting their orientation mechanism.

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Literature Cited

Caldwell, D. 1969. Baby loggerhead turtles associated with sargassum weed. Quart. J. Fla. Acad. Sci. 31:271–272.

Carr, A., and H. Hirth. 1961. Social facilitation in green turtle siblings. Anim. Behav. 9:68–70.

Ehrenfeld, D. W. 1968. The role of vision in the sea-finding orientation of the green turtle (*Chelonia mydas*). 2. Orientation mechanism and range of spectral sensitivity. Anim. Behav. 16:281–287.

———, and A. Carr. 1967. The role of vision in the seafinding orientation of the green turtle (*Chelonia mydas*). *Ibid.* 15:25–36.

Fletemeyer, J. R. 1978. Underwater tracking evidence of neonate loggerhead sea turtles seeking shelter in drifting sargassum. Copeia 1978:148–149.

Frick, J. 1976. Orientation and behaviour of hatchling green turtles (*Chelonia mydas*) in the sea. Anim. Behav. 24:849–857.

Hendrickson, J. R. 1958. The green sea turtle, *Chelonia mydas* (Linn.), in Malaya and Sarawak. Proc. Zool. Soc. Lond. 130:455–535.

Ireland, L. C., J. A. Frick and D. B. Wingate. 1978. Nighttime orientation of hatchling green turtles (*Chelona mydas*) in open ocean. *In*: Animal migration, navigation and homing. K. Schmidt-Koenig and W. T. Keeton (eds.). Springer-Verlag, New York.

McFarlane, R. W. 1963. Disorientation of loggerhead hatchlings by artificial road lighting. Copeia 1963:153.

Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature 220:1338–1339.

———. 1970. The influence of the sun's position and elevated cues on the orientation of hatchling sea turtles. Anim. Behav. 18:648–651.

———. 1972. The water-finding ability of sea turtles. Brain, Behav. Evol. 5:202–225.

———, and S. J. Shettleworth. 1968. Wavelength preferences and brightness cues in the water finding behaviour of sea turtles. Behaviour 32:211–257.

Prange, H. D. 1976. Energetics of swimming of a sea turtle. J. Exp. Biol. 64:1–12.

Precht, J., J. Christophersen, H. Hensel and W. Larcher. 1973. Temperature and life. Springer-Verlag, New York.

Applied Biology, Inc., 641 DeKalb Industrial Way, Atlanta, Georgia 30033. Accepted 9 July 1979.