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Author(s): James R. Spotila and Edward A. Standora

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Environmental Constraints on the Thermal Energetics of Sea Turtles

JAMES R. SPOTILA AND EDWARD A. STANDORA

The thermal biology of sea turtles depends upon the heat transfer properties of their environment as well as the physical and physiological characteristics of the turtles. In water, heat loss predominates over heat gain but on land, lethal heat gain during the day is one factor that selects for nocturnal nesting activity. Small turtles, *Lepidochelys* sp. and *Eretmochelys imbricata*, can nest during the day, if exposed to wind, because they are less affected by solar radiation than larger species since they lose more heat via convection. Sea turtles employ both behavioral and physiological thermoregulation. Loggerheads, *Caretta caretta*, can raise body temperatures (T_b) 3.8 C above ocean temperatures by basking in water and green turtles, *Chelonia mydas*, can elevate T_b 5 C above ocean temperatures by basking on land. Large turtles are endothermic. Green turtles exhibit regional endothermy, with active tissues 8 C above ocean temperatures during vigorous swimming. Leatherback turtles, *Dermochelys coriacea*, have body temperatures as much as 18 C above an ambient water temperature of 7.5 C. Multichannel telemetry demonstrates that the internal temperatures of a resting leatherback are higher than carapace and ambient air temperatures indicating that heat is generated internally and not absorbed from the environment.

THE biology of sea turtles is profoundly influenced by temperature. It affects all phases of their life history. In the embryonic stages it influences incubation period and sex determination as discussed elsewhere in this symposium (Standora and Spotila, 1985; Ackerman and Seagrave, 1985), while in the juvenile and adult stages it is a controlling factor in their behavior, physiology and ecology. The thermal biology of sea turtles has been the subject of an excellent recent review by Mrosovsky (1980). In this paper we will concentrate on an analysis of the role of heat exchange in the thermal ecology of these animals.

Heat energy determines the temperature at which an animal can operate (Fig. 1). On land, heat energy exchange is by radiation, convection, evaporation and conduction (Porter and Gates, 1969). Some heat is generated internally by metabolism. In water, thermal radiation is absorbed at the surface and heat exchange is primarily by conduction and convection (Erskine and Spotila, 1977; Spotila et al., 1984). Solar radiation may add heat to a turtle if the turtle is at or just below the surface. Within the constraints imposed by the heat transfer properties of their environment and their own physical characteristics (size, shape, etc.), sea turtles can thermoregulate by changes in their physiology and behavior.

SEA TURTLES ON LAND

On land, lethal heat gain during the day is one factor that selects for nocturnal nesting activity. This is obvious from our data on body temperatures of green turtles obtained by multichannel telemetry (Standora et al., 1982). Green turtles walking on the beach at Tortuguero, Costa Rica during the day showed a rapid rise in temperatures of the plastron and carapace while body temperature rose at a slower rate (Fig. 2). Under full sun, body temperature rose 7.8 C h^{-1} for 23 min, carapace surface rose at a rate of 50.4 C h^{-1} to 53.8 C and plastron surface rose 16.7 C h^{-1} reaching 42.9 C. Operative environmental temperature, T_e, a measure of heat load on a turtle, (Crawford et al., 1983) measured with a hollow copper model turtle was 44 C. Therefore, this turtle could not complete nesting activity during the day before it would overheat and die. Under overcast sky or early in the morning, body temperatures of two turtles rose 2.6 and 2.8 C h^{-1}. Operative environmental temperature was approximately 33 C. Even under these conditions a nesting green turtle would experience severe heat stress. If a turtle came ashore at a body temperature of 31 C and took 1 to 2 h to complete nesting, it would heat up 3–6 C because of heat uptake from its environment and another 2–4 C be-

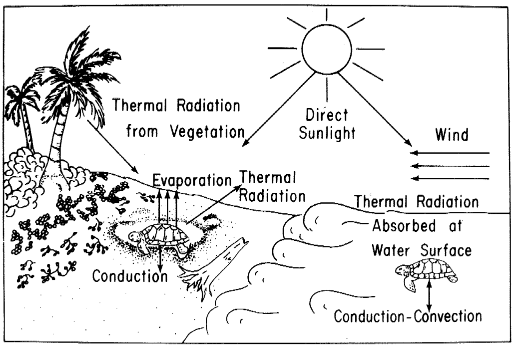

Fig. 1. Heat exchange between sea turtles and their environment. On land heat transfer occurs via radiation, convection (wind), evaporation and conduction. In water heat transfer occurs by conduction-convection.

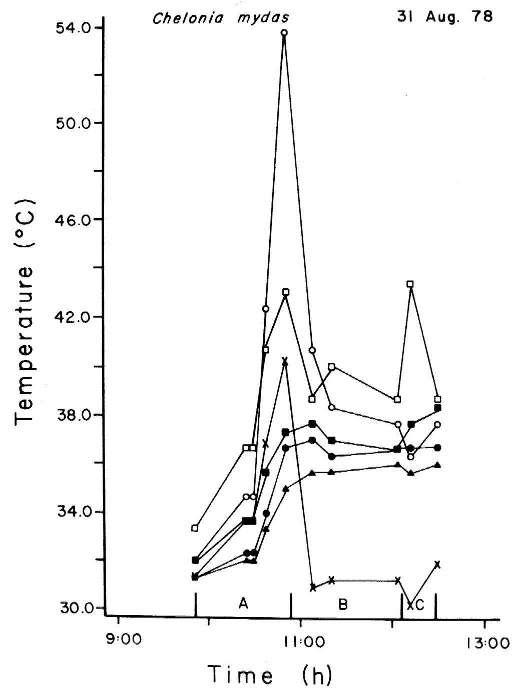

Fig. 2. Telemetered temperatures of a 117 kg adult, female green turtle exercising on land at Tortuguero, Costa Rica. Triangles represent deep body, solid squares are inside plastron, solid circles are inside carapace, open squares are plastron surface, open circles are carapace surface and crosses are unshaded air temperatures. At the beginning of the period indicated as A, the turtle was on its back in the shade. The second data points indicate when this female began to walk on the beach while exposed to full sunlight and a clear sky. When carapace surface temperature reached 53.8 C, the turtle entered the surf (period indicated by B). Deep body temperature continued to rise slowly due to the turtle's internal heat lag. The turtle was placed on its back on the beach (C) and the plastron surface heated. Its temperature dropped quickly when the turtle was placed in the shade (last data point) (Standora et al., 1982).

cause of its elevated metabolism (Mrosovsky, 1980; Standora et al., 1982), reaching 36–41 C when it finished nesting. Thus, it would probably have to return to the water due to heat stress before completing its nest. Eight reports of *Caretta caretta* and *Chelonia mydas* nesting during the day on Florida beaches (Fritts and Hoffman, 1982) include three turtles that emerged in the dark or just before dawn, one that emerged in the evening, and one in midmorning. Of the remaining three turtles, one had been injured by a shark, and two emerged between 1115 and 1450. There are few other instances of diurnal nesting reported for large sea turtles. This is not surprising given the danger of overheating, in addition to the obvious problem of predation.

In light of these data it is surprising that some sea turtles regularly nest during the day (*Lepidochelys kempi* and *L. olivacea*). These species emerge in mass nestings during which thousands of females come ashore in "arribadas." In *L. olivacea* an arribada extends over several days and turtles nest throughout the day and night. In *L. kempi* the arribada occurs during the day and is associated with a strong onshore or offshore wind. This raises an obvious question "Why do ridleys nest during the day when larger sea turtles do not?" The answer to this question is found in the heat exchange properties of these animals and those of their environment.

The primary heat source for a turtle on the beach during the day is solar radiation. Experiments with alligators (*Alligator mississippiensis*) indicate that the body temperatures of large reptiles are more coupled to the absorption of solar and thermal radiation than are the body temperatures of small reptiles because large individuals are less affected by the cooling effect of wind than smaller ones (Terpin et al., 1978). All animals on land are surrounded by a boundary layer of air that adheres to their surface and retards heat exchange with the air (Fig. 3). Moving air strips away the boundary layer and increases heat transfer by convection (Foley and Spotila, 1978). Large size results in a thicker boundary layer and reduces the effect of con-

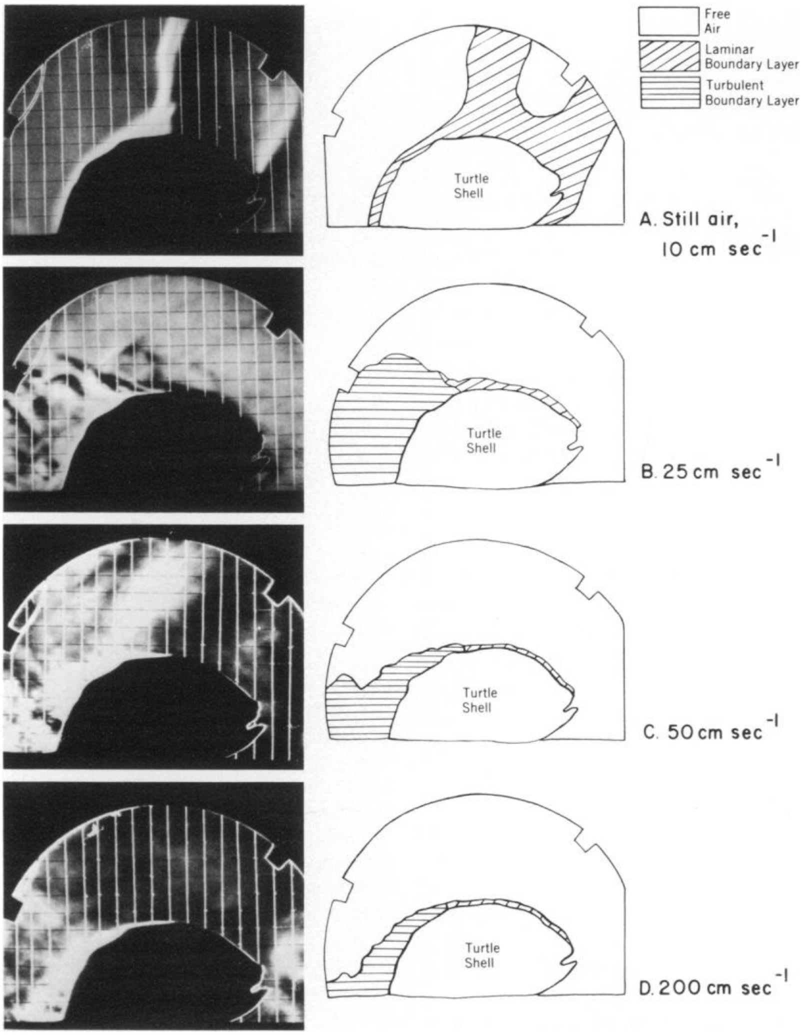

Fig. 3. Schlieren pictures of a heated box turtle shell, with regions of laminar and turbulent flow shown in the accompanying diagrams. Wind (flow from right to left) strips away the boundary layer and brings surface temperature closer to air temperature (Foley and Spotila, 1978).

vection (Spotila et al., 1981). Convection theory as related to animals is discussed at length by Gates (1980:268–305). Mitchell (1976) provides a general predictive relation for convection heat transfer from animal forms based on an equation for convection from a sphere. Using his equations we can evaluate the effect of wind on the heat exchange of sea turtles and explain why small species can nest during the day while large ones cannot.

Convective heat transfer for a turtle or any object immersed in a fluid (air, water, etc.) is a function of many different variables, including size, shape, and orientation of the object; density, viscosity, specific heat and thermal conductivity of the fluid; velocity of flow; and occurrence of laminar or turbulent flow (Gates, 1980). Many of these variables can be combined in dimensionless groups which allow us to compute the convective heat transfer coefficient and from it the amount of heat transfer between an object and the fluid in which it is immersed. Two important dimensionless variables are the Reynolds number (Re) which is an indication of whether flow over a surface is laminar or turbulent and the Nusselt number (Nu) which is

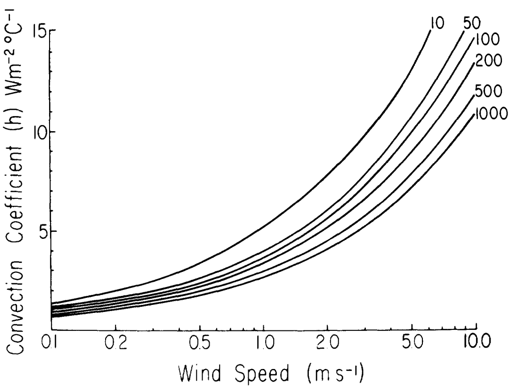

Fig. 4. Effect of body size and wind speed on the convection coefficients (h) of sea turtles in air. Numbers adjacent to curved lines indicate mass in kg. Calculations are based on equations from Mitchell (1976) as discussed in the text.

TABLE 1. THEORETICAL OPERATIVE ENVIRONMENTAL TEMPERATURES (T_e) FOR TWO DIFFERENT SIZED SEA TURTLES RESTING ON THE BEACH AT TORTUGUERO, COSTA RICA ON A SUNNY DAY IN AUGUST.

Body mass (kg)	Wind speed ($m\ s^{-1}$)	T_e (°C)
50	0.1	58.3
50	2	44.2
50	5	30.0
200	0.1	58.7
200	2	47.2
200	5	36.0

related to boundary layer thickness and can be used to compute the convective heat transfer coefficient (h). Mitchell (1976) computed h by first deriving equations to define Re and Nu and then computing h as a function of Nu.

In Mitchell's terminology, organism mass is replaced by volume

$$V = m/\rho \qquad (1)$$

where V is volume in m^3, m is mass in kg and ρ is bulk body density. The characteristic dimension (e.g., trunk diameter or length) is defined as

$$L = V^{1/3} \qquad (2)$$

where L is volume-related characteristic dimension in m. The Reynolds number is given as

$$Re_L = vL/\nu \qquad (3)$$

where v is velocity in ms^{-1}, and ν is fluid kinematic viscosity in m^2s^{-1} (relationship of dynamic viscosity to density of the fluid). From a graph of Re vs Nu numbers for a wide variety of organisms Mitchell determined

$$Nu_L = 0.34\ Re_L^{0.6} \qquad (4)$$

and computed h for spherical objects as

$$h = \frac{Nu_L k}{L} \qquad (5)$$

where k is thermal conductivity in $Wm^{-1}\ C^{-1}$. This relationship between body size, wind speed and convection coefficient is seen in Fig. 4. As wind speed increases for a given sized turtle the convection coefficient gets larger and as body size increases for a given wind speed h gets smaller. Thus, small turtles are more affected by wind speed than large ones.

By combining the data in Fig. 4 with microclimatological data for a sunny day on Tortuguero beach, we can analyze the heat load for different sized sea turtles and compute their operative environmental temperatures using standard energy budget equations (Porter and Gates, 1969; Spotila et al., 1972). On a sunny afternoon in Aug. heat radiation absorbed by a turtle (assuming an absorptivity to solar radiation of 0.7 and that one half the body surface is exposed to the sun) would be 864 Wm^{-2} on the upper surface or 432 Wm^{-2} when averaged over the entire surface. Heat gain from the sand at a temperature of 40 C would be 272 Wm^{-2} when averaged over the entire surface. Operative environmental temperatures for 50 and 200 kg sea turtles for these conditions depend upon wind speed (Table 1). In still air, small and large sea turtles would both suffer severe heat stress. At a wind speed of 2 $m\ s^{-1}$ this stress would be reduced and at higher wind speeds (5 $m\ s^{-1}$) these turtles would experience T_e of 30 and 36 C. Thus, a 50 kg ridley turtle could come ashore when wind speed at ground level was at least 3.3 $m\ s^{-1}$ while a large green turtle (200 kg) could not avoid overheating until wind speed was at least 4.5 $m\ s^{-1}$. If we take into account the addition of metabolic heat due to nesting, these values would increase to at least 4.5 $m\ s^{-1}$ and 6.5 $m\ s^{-1}$. Thus, it is not surprising that ridley turtles only come ashore to nest on windy days. This may also explain reports of daylight nesting by *Chelonia depressa* in the Gulf of Carpentaria in Australia (Bustard, 1973) and *Eretmochelys imbricata* in the Camore Island Group in the Indian Ocean (Fritts and Hoffman, 1982).

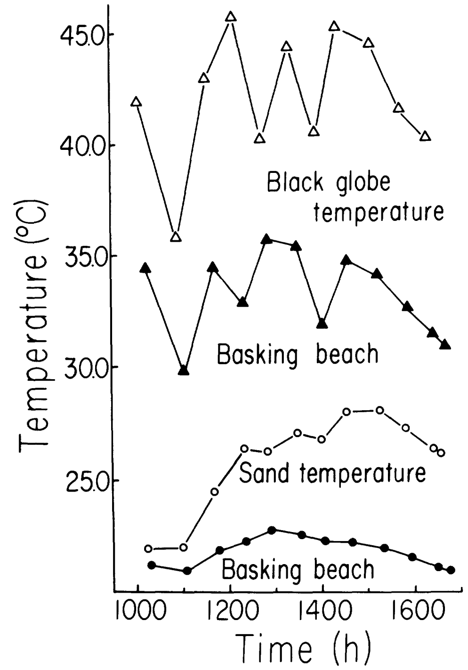

Fig. 5. Sand temperatures (lower two curves) and black globe temperatures (upper two curves) of a beach used for basking (closed circles and triangles) and one not used for basking (open circles and triangles) by green turtles at French Frigate Shoals in the Pacific Ocean (166°13′W, 23°52′N). Redrawn from Whittow and Balazs (1982).

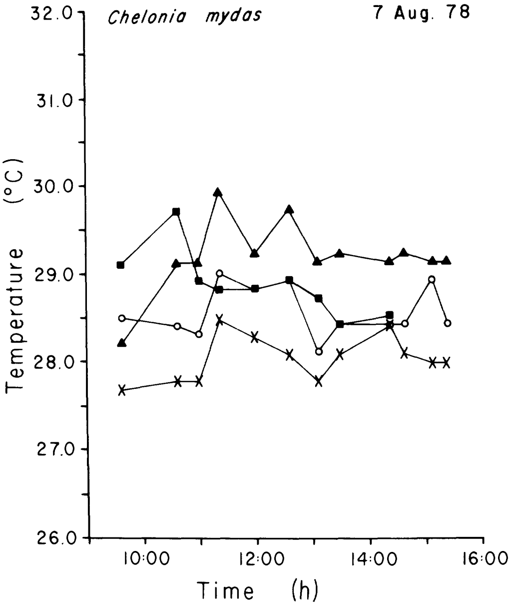

Fig. 6. Temperatures of a 110 kg free-swimming, adult female, green turtle obtained using sonic telemetry at Tortuguero, Costa Rica. Triangles represent deep body, solid squares are inside plastron, open circles are carapace surface, and crosses represent water temperatures. This female was released at 1100 h, remained a few hundred meters off shore and was relatively inactive (Standora et al., 1982).

BASKING ON LAND

Terrestrial basking has been reported for green turtles in the northwestern Hawaiian Islands (Balazs and Ross, 1974; Balazs, 1976, 1980; Whittow and Balazs, 1982), in Australia (Bustard, 1973), and historically in the Galapagos Islands and Mexico (Fritts, 1981). The most complete study of this phenomenon is for *C. mydas* at French Frigate Shoals in the northwestern Hawaiian Islands (Whittow and Balazs, 1982).

Here turtles came ashore and basked on the side of islands facing the outer reef and the prevailing northeast trade winds. Sand temperatures and black globe temperatures (an approximation of T_e) were lower on the basking beach than on a beach on the opposite side of the island that was not used by basking turtles (Fig. 5). In light of the above discussion of convection and T_e for sea turtles, it is apparent that the T_e on the basking beach was moderate and would allow turtles to maintain a stable, elevated body temperature for an extended period of time without danger of overheating. The duration of basking was inversely related to black globe temperature suggesting that high heat loads placed these turtles under heat stress. Carapace temperatures were as high as 40.0–42.8 C. By flipping sand on their carapaces and rear flippers, turtles could reduce surface temperature by as much as 10 C, apparently reducing heat load on peripheral tissues as well as to the deep body. It is of interest to note that green turtles did not orient towards the sun or wind. The same was true for freshwater turtles, *Pseudemys scripta* (Spotila et al., 1984). In this latter species a change in orientation had no effect on T_e (Crawford et al., 1983). Terrestrial basking in Hawaiian green turtles appeared to be fostered by cool ocean temperatures (26.3 C) and a combination of white sand beaches with steady wind and moderate solar intensity that allowed these turtles to reach an elevated body temperature (31.3 C maximum) without being heat stressed. Most of these turtles were females and most of this activity took place during the nesting season. This thermoregulatory behav-

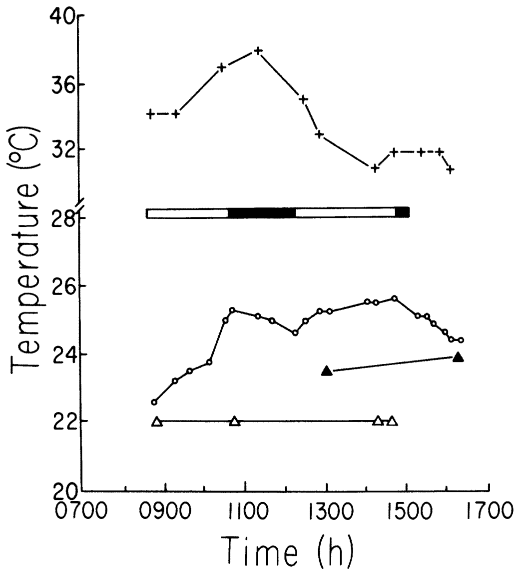

Fig. 7. Body temperature (open circles) of a 42 kg loggerhead during voluntary surface basking in sunlight. Open bar: basking in elevated posture. Closed bar: submerged. Closed triangles: air temperature. Open triangles: water temperature. Crosses: black bulb temperature (Sapsford and van der Riet, 1979).

ior, by keeping females warmer than water temperature, may cause an accelerated rate of development of eggs, with a corresponding reduction in inter-nesting interval.

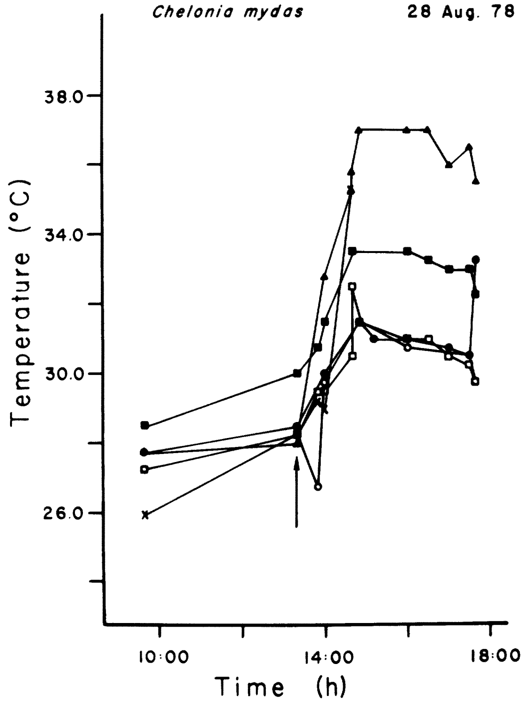

Fig. 8. Temperatures of a 121 kg adult, female green turtle free swimming vigorously in the Caribbean Sea near Tortuguero, Costa Rica. Symbols are as in Fig. 2 except that crosses represent water temperature. Arrow indicates when turtle entered the surf (29 C). This turtle was continuously active and pulled a large polyurethane float and long length (30 m) of manilla rope (diameter 1 cm).

SEA TURTLES IN THE WATER

Convection coefficients in water are approximately 100 times greater than in air (Gates, 1980). Therefore, heat transfer is very rapid between the surface of a turtle and the water and heat loss predominates over heat gain by metabolism. In general, the body temperatures of inactive adult green, loggerhead and ridley turtles are within 1–2 C of sea temperature (Mrosovsky and Pritchard, 1971; Hirth, 1962; McGinnis, 1968; Sapsford and van der Riet, 1979; Heath and McGinnis, 1980; Standora et al., 1982). In these animals most heat loss is across the soft skin of the neck and proximal area of the flippers, followed by the plastron, carapace and scaled epidermis on the distal areas of the flippers (Heath and McGinnis, 1980). Multichannel telemetry data (Fig. 6) demonstrates that the body temperature of a resting adult green turtle is above carapace and plastron temperatures which in turn are above water temperature. This suggests that this turtle has some endothermic capability when minimally active (Standora et al., 1982).

In addition to metabolic heat production, sea turtles can also raise their body temperatures above ambient by basking. Aquatic basking has been observed in captive *Caretta caretta, Chelonia mydas* and *L. olivacea* (Sapsford and van der Riet, 1979). A 42 kg *Caretta caretta* raised its body temperature 3.8 C above water temperature by basking in sunlight while keeping a substantial portion of its carapace exposed above the water surface (Fig. 7). Basking during overcast conditions did not cause a rise in body temperature.

In general, sea turtles have body temperatures of 25–33 C. Mean selected temperatures of hatchling loggerhead *C. caretta* are reported as 28–30 C (Owens and Ralph, 1978). Nesting females have temperatures which range from 25.8 C–30.5 C (Mrosovsky, 1980). The temperatures of water occupied by loggerheads during the summer along the Atlantic Coast of the United States can be estimated from data from airborne radiation thermometer charts presented by Bell and Richardson (1978) and range from 25–30 C. These data, plus data on temperatures for maximum sustained swimming speeds of hatchlings (25.6–28.9 C) (O'-Hara, 1980) indicate that the mean selected temperature range for this species is 25–30.5 C. Data reported by Mrosovsky (1980, Fig. 5) indicate that the mean selected body temperature of leatherback turtles ranges from 25.5–33 C. Data are not available to estimate the mean selected body temperature of other sea turtle species.

Lethal temperatures are known for some sea turtle species (Mrosovsky, 1980). Upper lethal temperatures appear to range from 33–40 C (Bustard, 1970; Faulkner and Binger, 1927). Lower lethal temperatures for loggerhead, Kemp's ridley and green turtles range from 5.0–6.5 C (Schwartz, 1978). These temperatures are reflected in the lowest surface water temperatures (7 C) reported in association with sea turtles off the Atlantic coast of the United States by Bell and Richardson (1978) and in the temperatures at which cold stunning of loggerhead and green turtles occurs in Mosquito Lagoon, Florida (Erhart, 1983).

Warm Blooded Turtles?

Leatherback turtles occur often along the coast of Canada and New England (Bleakney, 1965; Shoop et al., 1981). They have been reported from as far north as Sedgwick Bay (52°36'N, 131°82'W) in British Columbia, swimming actively at a temperature of 11.6 C, and in the North Sea (61°18'N, 4°E) off western Norway (Willgohs, 1957). Mrosovsky and Pritchard (1971) reported that leatherback turtles nesting in Surinam and French Guiana had body temperatures of 30.5–31.3 C when sea temperature was 28.3 C. Frair et al. (1972) reported that a leatherback caught off Nova Scotia had a body temperature of 25.5 C when held in water at 7.5 C. This information, in addition to anatomical evidence for a counter current heat exchanger in the front and rear flippers of this turtle (Greer et al., 1973) suggests that the leatherback turtle has considerable endothermic capability and can maintain its body temperature well above the temperature of its environment. Neill and Stevens (1974) caution that while these data indicate that leatherbacks do enjoy great thermal inertia and have some endothermic capabilities, they do not conclusively demonstrate that these turtles can regulate body temperature by physiological means.

Two recent studies on green turtles and one on a leatherback lend support to the hypothesis that large turtles have considerable endothermic capability. Jackson and Prange (1979) found that oxygen consumption of exercising adult green turtles was 10 times the standard resting value. Standora et al. (1982) reported that an adult green turtle swimming vigorously had a body temperature of 37.1 C in water of 29.1 C (Fig. 8). They concluded that *C. mydas* was endothermic. It had a highly aerobic metabolism, (Prange, 1976; Prange and Jackson, 1976) increased its metabolism when active, displayed considerable thermal inertia because of its large size and the excellent insulatory properties of its shell, and exhibited both heterothermy and regional endothermy (Standora et al., 1982).

Standora et al. (1984) recently acquired new data using a multichannel temperature transmitter that clearly indicates that an adult leatherback turtle is endothermic. A 172 kg turtle heated internally from 29.6–30.1 C while inactive on land for 2½ h, with air temperature dropping from 26.2–21.8 C and carapace surface temperature dropping from 26.4–25.3 C.

Given the large size attained by adult leatherback turtles and their anatomical adaptations that conserve heat (counter current heat exchangers and insulating layer of subepidermal fat) we expect that these turtles should be capable of maintaining large temperature differentials between their body core and surrounding water. More data are needed to test this hypothesis for free swimming leatherbacks in cold water.

Conclusions

The thermal biology of sea turtles is a compromise between the constraints imposed by the physical environment and the physical, physiological and behavioral characteristics of the turtles. Heat energy exchange analysis helps us to clarify the thermal energetics of these animals. On land heat gain can rapidly lead to heat stress and this prevents large species from daytime terrestrial activity. In water, heat loss predominates over heat gain and the body temperatures of most sea turtles remain close to water temperatures. However, large sea turtles can be endothermic. Recent experimental studies have quantified the role of heat exchange in the basking behavior of sea turtles and in their ability to employ endothermy to control body temperature in warm and cold oceans.

Finally, we believe that the studies reviewed in this paper indicate that more can be learned about the thermal biology of sea turtles from a few well planned quantitative experiments than from years of random temperature measurements and anecdotal observations. A quantitative approach will provide more insight into the ecology of sea turtles with less adverse impact on these species than will other less quantitative techniques.

ACKNOWLEDGMENTS

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DEPARTMENT OF BIOLOGY, STATE UNIVERSITY COLLEGE, BUFFALO, NEW YORK 14222. Accepted 6 Nov. 1984.