

THE EFFECTS OF CURRENT VELOCITY AND TEMPERATURE UPON SWIMMING IN JUVENILE GREEN TURTLES *CHELONIA MYDAS* L.

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Young green turtles, *Chelonia mydas* responded to increasing current velocities by swimming upstream for a greater proportion of the time. At temperatures of 21-25°C currents equivalent to 1-2 body lengths s⁻¹ induced continuous upstream swimming. At low current velocity the turtles usually employed 'dog-paddle' (ipsilateral synchronized) swimming. At swimming speeds of 0.8-1.4 body lengths s⁻¹ they switched to synchronized forelimb flapping, with stationary rear limbs. Maximum dog-paddle speed was about 40% of maximum speed using synchronized foreflippers: the latter mechanism is clearly capable of generating far more propulsive power. Maximum sustained swimming speeds at 25°C, 21°C and 15°C were 3.31, 2.96 and 2.09 body lengths s⁻¹ respectively; the speed at 15°C was significantly lower than at the other two temperatures, and could not be sustained for more than 2-4 min before instability in pitch, roll and yaw prevented the animal from swimming upstream. A detailed analysis of the swimming mechanism at different temperatures is presented. This demonstrated a significant degradation of co-ordination of swimming at 15°C, even though the lethal temperature of green turtles is well below 10°C. The significance of this finding is discussed in terms of vulnerability of the species to cold.

INTRODUCTION

The swimming of green turtles (*Chelonia mydas* L.) has attracted much study (Carr, 1952; Walker, 1971; Blake, 1981; Davenport, Munks & Oxford, 1984; Wyneken, 1988; Wyneken & Salmon, 1992). Most attention has been paid to swimming by simultaneous beating of the forelimbs, though green turtles, like other cheloniid sea turtles, use other swimming modes at low speed (Davenport *et al.*, 1984; Davenport & Pearson, 1994).

Hatchling and juvenile sea turtles live in the open ocean, mostly drifting with currents (Caldwell, 1968; Carr & Meylan, 1980; Stoneburner, Richardson & Williamson, 1982), though persuasive recent evidence indicates that they are capable of directional swimming (Lohman & Lohman, 1996) using various cues (magnetic, wave direction). Because they move over great distances, they are likely to encounter changing thermal conditions young turtles may also be swept into cold waters and suffer cold-stunning (e.g. Meylan & Sadove, 1986; Witherington & Ehrhart, 1989; Morreale *et al.*, 1992).

The study reported here was designed to investigate how the swimming mechanism of young green turtles was affected by current speed and by temperature.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE

Twelve green turtles were sent as recent hatchlings from the Lara Reserve, Cyprus, to the School of Ocean Sciences, University of Wales, Bangor, where they were held in large tanks of sea-water (34‰; 25°C) and fed upon commercially-available floating trout pellets.

They were studied about one month after arrival in the UK; at this time their body lengths (snout to tail) ranged from 105-122 mm and their weights from 33.5-70.5 g. After study the animals were returned to the Mediterranean.

FILMING

The turtles were filmed in a flume giving laminar flow over all of the current velocities employed in the study (Fig. 1). This had a long (3 m) square-section (400x400 mm) perspex trough supplied with sea water by a powerful pump and guarded by a gate that could be used to control water depth. The velocity of water flow was controllable by a valve, though this provided only very coarse control and could not be preset to a given current speed. Water flow rate was estimated by determining the rate of movement of weighted polystyrene floats over known distances within the flume (using video-recording and triplicate measurement). For the present study the flume was used to produce laminar flow without wave action. The flume was housed in a building at ambient temperature (*ca* 12°C), but the flume contents were heated during the present study to one of four nominal experimental temperatures (15°, 21°, 22.5° or 25°C). Temperature control was accurate to ±1°C. A section of the flume 600 mm in length was cordoned off by two very coarse mesh (50 x 50 mm) screens, and a grid of vertical lines set 100 mm apart was marked on it. This section was used in all quantitative studies of turtle swimming.

Turtles were filmed with a Panasonic F10 video-camera directed normally to the side surface of the cordoned-off section of the flume from a distance of 5 m (to minimize parallax problems). The camera was fit-

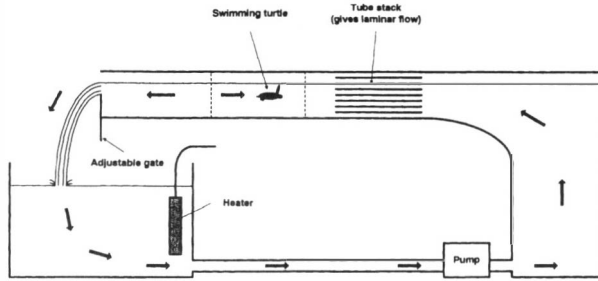


FIG. 1. Flume arrangement.

ted with a high speed (0.001 s) shutter. Film was analysed by freeze-frame and play-back through a Panasonic AG6200 video-recorder and monitor, coupled with drawings made by placing acetate sheets over the monitoring screen. Calculation of foreflipper angles of attack followed the procedure of Davenport *et al.* (1984).

EXPERIMENTAL PROTOCOL

The first objective was to determine the effect of current speed on direction of swimming in the turtles. The flume was first adjusted to temperature and then the pump switched off. A turtle was introduced to the work section of the flume and allowed to acclimate to conditions for 15 min (by this time the initial rapid movement had subsided). The animal was filmed for 5 min, and the proportion of time that the animal swam in the 'up-stream' direction was established. The flume pump was switched on, and a gentle flow along the flume produced. Again the animal was filmed for 5 min. Flow was increased in stepwise fashion, 5 min of filming taking place at each new flow velocity. The experiment was repeated at 15°C, 21°C, 22.5°C and 25°C, using a different turtle in each case.

Davenport *et al.* (1984) established that young green turtles normally used ipsilaterally-synchronized swimming ('dog-paddle') when swimming slowly at 25°C. In the second experiment, at each experimental temperature (15°C, 21°C and 25°C), three turtles, in turn, were each placed in the flume with the flow switched off and allowed to settle down. Water flow was gradually increased until the animals started to use synchronized action of the forelimbs for swimming; the flow rate corresponding to this transition was then measured (in triplicate).

The third experiment consisted of an investigation of the maximum sustained swimming speed at 15°C, 21°C and 25°C. Each turtle was introduced to the flume, and the water velocity gradually increased until the animal just started to lose ground within the working area of the flume, despite swimming continuously. Eleven reliable measurements were made at 25°C, 12 at 21°C and 8 at 15°C; other measurements had to be discarded because animals touched the screens at either end of the working area, or (in the case of animals held at 15°C) yawed sideways and touched the sides of the flume. At 25°C and 21°C the animals swam continuously for at

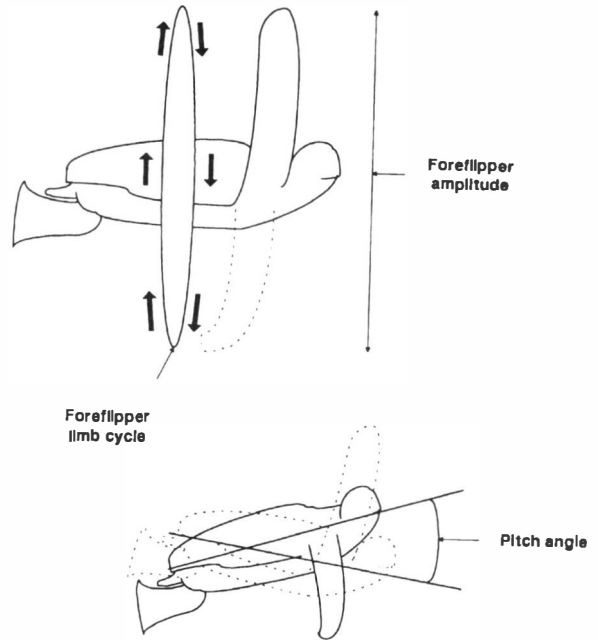


FIG. 2. Diagram illustrating measured features of turtle swimming.

least 10 min during the experiments; at 15°C no more than 2-5 min elapsed before yawing terminated trials. Swimming speed was calculated from the measured water flow and the relative movement of the turtle in that flow. Swimming was periodically interrupted by the turtle taking breaths at the surface, during which they often employed brief dog-paddle; the recorded maximum swimming speeds (transformed to body lengths s^{-1} for comparability) were those observed during immersed swimming, so in most cases were faster than the water velocity, even though the turtle was losing ground overall because of the need to take breaths. During the periods of sustained fast swimming, sufficient videotape was collected to allow detailed analysis of use of the forelimbs, and to measure the degree to which the body of the animal pitched on each swimming stroke (Fig. 2).

RESULTS

EFFECT OF CURRENT SPEED ON DIRECTION OF SWIMMING

From Table 1 it can be seen that, whatever the temperature, the turtles responded to increasing current speed by swimming upstream for more and more of the time. For each animal, the relationship between current speed and proportion of time spent swimming upstream was roughly linear (regression analysis yielded r^2 values between 72% and 89% in each case). By the time that current speed had risen to the equivalent of some 1-2 body lengths s^{-1} , the turtles were swimming directly into the current for almost all of the time at 21°C, 22.5°C and 25°C. At 15°C the situation was rather different; because the animal's swimming was discernibly less efficient, due to pitching and yawing, it was unable to sustain a heading, and was often swept downstream before regaining its position.

TABLE 1. Effect of current speed on direction of swimming in juvenile *Chelonia mydas*. Animals were held in a flume and subjected to gradually-increasing current speed. The proportion of time that they spent swimming in the 'upstream' direction (as opposed to downstream or laterally) was assessed.

Turtle no.	Temperature (°C)							
1	15.2	Current speed (m s ⁻¹)	0	0.023	0.070	0.085	0.125	0.190
		% time swimming upstream	7	20	29	57	55	67
2	21.0	Current speed (m s ⁻¹)	0	0.030	0.125	0.174	0.260	-
		% time swimming upstream	8	41	50	66	91	-
3	22.5	Current speed (m s ⁻¹)	0	0.026	0.060	0.088	0.200	0.225
		% time swimming upstream	20	27	50	83	95	96
4	25.0	Current speed (m s ⁻¹)	0	0.020	0.138	0.167	0.190	-
		% time swimming upstream	19	26	35	66	86	-

TEMPERATURE, SPEED AND SWIMMING MODE

From Table 2 it may be seen that the turtles continued to use dog-paddle until a swimming speed of around 0.8-1.4 body lengths s⁻¹ was reached. Dog-paddle swimming was at the surface, and permitted easy breathing as the head was always emersed. Once the turtles had switched to synchronized foreflipper-flapping, all swimming took place with the animal totally immersed, and breathing became an intermittent, rhythmic activity. There was no statistically significant effect of temperature on transition speed.

EFFECT OF TEMPERATURE ON SUSTAINED SWIMMING SPEED

Temperature had a significant effect on swimming speed (Table 3). Although there was no statistically significant difference between swimming speeds recorded at 25°C and 21°C, the turtles held at 15°C were much slower and could only sustain a maximum swimming speed (mean 2.09 body lengths s⁻¹) 63% of that recorded at 25°C (mean 3.31 body lengths s⁻¹). Q₁₀ for swimming speed over this temperature range was 1.58. It was also evident that swimming at 15°C was less efficient; the animals showed instability in roll, pitch and yaw, and they often broke the surface with their foreflippers at the top of the limbstroke, unlike the animals studied at the higher temperatures, which were always completely immersed.

TABLE 2. Effect of temperature on speed at which young green turtles switch from 'dogpaddle' swimming to synchronized foreflipper flapping. ANOVA showed that temperature did not have a significant effect on transition speed ($P=0.294$). Means±SD based on $n=3$.

Temperature (°C)	Mean transition swimming speed (body lengths s ⁻¹)	SD
25	1.32	0.29
21	1.44	0.50
15	0.83	0.52

EFFECT OF TEMPERATURE ON SWIMMING MECHANISM

From Tables 4 and 5 it is evident that temperature affects several features of the swimming mechanism. At 25°C the turtles showed little body pitch (Table 4) and employed high frequency limbstrokes of lower amplitude than at 21° or 15°C. At 21°C the amplitude of limb beat was significantly greater ($P<0.05$), but the frequency of beat was not significantly reduced; the mean angle of body pitch was greater, but not to a statistically significant extent. At 15°C the amplitude of limb beat was similar to that employed at 21°C, but the frequency of limb beat was much lower ($P<0.05$) and the pitch angle much greater ($P<0.05$). Study of the calculated angles of attack of the foreflippers (Table 5) at the midpoints of the up and down strokes showed no significant differences between 21°C and 25°C (downstroke $P=0.261$; upstroke $P=0.685$), but the mean downstroke angle of attack at 15°C was greater to a highly significant extent ($P=0.000$) than at the other study temperatures. The mean angle of attack at 15°C on the upstroke was also quite different (and much less) than at the other temperatures ($P<0.01$).

DISCUSSION

The finding that young green turtles swim into currents is neither unexpected or novel - many aquatic animals automatically swim into currents provided that cues (visual or non-visual) are available to inform them

TABLE 3. Effect of temperature on sustained swimming speed in juvenile *Chelonia mydas*. ANOVA showed that temperature had a significant effect on swimming speed ($P=0.002$).

Temperature (°C)	Mean maximum swimming speed (body lengths s ⁻¹)	SD
25	3.31	0.66 ($n=11$)
21	2.96	0.78 ($n=12$)
15	2.09	0.53 ($n=8$)

TABLE 4. Effect of temperature on foreflipper flap frequency, vertical amplitude of foreflipper movement and angle of body pitch in juvenile *Chelonia mydas* swimming at maximum sustained speed in a flume. ANOVA revealed significant temperature effects on foreflipper flap frequency ($P=0.012$), pitch angle ($P=0.000$) and vertical amplitude of foreflipper movement ($P=0.000$). Means \pm SD based on $n=4$.

Temperature (°C)	Mean foreflipper flap frequency (limb cycles s ⁻¹)	SD
25	1.47	0.33
21	1.32	0.21
15	1.05	0.20
	Mean foreflipper amplitude (mm)	SD
25	64.3	11.9
21	72.3	6.9
15	73.5	6.5
	Pitch angle (°)	SD
25	2.6	3.4
21	6.4	5.5
15	11.9	6.9

that they are moving in relation to the earth's surface (e.g. fish; Bainbridge, 1975). In the flume situation many visual cues were available to the turtles from all directions (screens in front and behind, flume walls with markings on either side, the ceiling above and floor below); in the open ocean this would not be true, but there will be circumstances when visual cues are available (shoreline, clouds, starfields etc). For young green turtles of the size studied here, they swim constantly upstream when current velocities reach about 0.5 km h⁻¹. Maximum sustained swimming speeds corresponded to about 1.4 km h⁻¹, so it is clear that ability to fight currents is limited - off Florida, Gulf Stream velocities are as high as 14 km h⁻¹ (Raymont, 1963).

This study is the first to give some indication of the relative efficiency of different swimming modes in *Chelonia mydas*. If it is assumed that young green turtles switch from dog-paddle to synchronized foreflipper flapping when they are travelling as fast as possible using the former mode, then the maximum dog-paddle speed is about 40% of the maximum speed using synchronized foreflippers. Superficially, since drag increases roughly with the square of the swimming speed, this would suggest that turtles develop around six times as much power when swimming with synchronized foreflippers as when dog-paddling. However, the increase in maximum speed will not simply result from the greater propulsive efficiency of synchronized foreflipper flapping, but will involve a component of avoidance of the high-drag zone at and near the air-water interface. Hertel (1966) studied the drag of a spindle-shaped object of thickness t' , and

TABLE 5. Effect of temperature on angle of attack (°) of the foreflipper blade at the midpoint of the down or upstroke when swimming continuously using synchronized foreflipper flapping. Angles were calculated as described by Davenport *et al.* (1984). ANOVA revealed significant temperature effects on both downstroke angles ($P=0.000$) and upstroke angles ($P=0.004$).

Temperature (°C)	Downstroke		Upstroke	
	Mean	SD	Mean	SD
25	40.2	9.1	-17.0	6.2
21	46.7	5.1	-18.5	2.9
15	73.7	6.8	-3.2	5.2

found that drag started to increase from the normal deeply submerged value at a depth of 3 t' and rose to a maximum at 0.5 t' below the water surface (when the upper surface was in contact with the underside of the surface film). When moving from a deeply submerged position to the maximum-drag zone, the drag on a moving object will rise by a factor of about 5. Obviously turtles are not spindle-shaped, but by switching from surface dog-paddle to submerged synchronized foreflipper flapping, young turtles will encounter less drag.

At 15°C the turtles were not only substantially slower in their swimming than at 21°C or 25°C, (the Q_{10} of 1.56 is in the range that would be expected from an ectothermic species), but were also less efficient, implying a thermal effect on co-ordination. As well as rolling and yawing (not investigated quantitatively here), they showed greatly increased body pitch (Table 4), and calculations indicate that the foreflipper beat was less effective; at 21°C and 25°C the mean distance travelled per forelimb cycle was 2.25 body lengths, while at 15°C it was only 2 body lengths. Particularly interesting were the angles of attack of the foreflipper blades. At 21°C and 25°C the mean angles of attack on the downstroke were 46.7° and 40.2° respectively; corresponding mean angles on the upstroke were -18.5° and -17° respectively. These angles of attack are slightly greater than those reported by Davenport *et al.* (1984) for rather larger young green turtles (200-300 g; experimental temperature 25°C), but imply that forward propulsion was being generated on both up and downstrokes. At 15°C the picture was very different: on the downstroke the calculated mean angle of attack was high (73.7°), implying a flipper at, or close to, a stalled condition (see Davenport *et al.*, 1984 for discussion) generating much drag and little lift; a strong upward pitch component would be predicted. On the other hand the very low mean angle of attack on the upstroke (-3.2°) indicates that little or no propulsion was being produced on the upstroke. This analysis only applies to the midpoints of the strokes, and it should be remembered that the calculated angles of attack do not take into account induced water velocity (Weis-Fogh, 1973)

which reduces the effective angle of attack (whether positive or negative). However, it is clear that the young turtles use their flippers in a very different fashion at 15°C than at the two higher temperatures.

The finding that young green turtles exhibit substantially degraded swimming at 15°C is of interest in the context of vulnerability to cold. Green turtles have a lower lethal temperature well below 10°C (Schwartz, 1978), and temperatures below 10°C have been implicated in cold-stunning (Morreale *et al.*, 1992). However, there is evidence that feeding is impaired at temperatures below 20°C (e.g. Bjorndal, 1979) and will cease at 15-16°C (Davenport *et al.*, 1989). Felger *et al.* (1976) reported onset of torpidity at this temperature (though they worked on the 'black' variant, sometimes classified as a separate species, *Chelonia agazzizi*), so it seems likely that *Chelonia mydas* loses effective control over its ability to respond to currents in its environment at around 15°C, and will soon passively float downstream. However, the data presented in this study are for very small animals. Larger turtles may be capable of generating metabolic heat and sustaining effective swimming until rather lower temperatures are reached. It is also the case that the turtles were given relatively little time to acclimate to 15°C; their response was an acute one. Ideally, a longer acclimatory period would have been desirable, but it was feared that such long-term exposure to low temperatures might compromise the animals' subsequent growth and survival.

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REFERENCES

- Bainbridge, R. (1975). The response of fish to shearing surfaces in the water. pp.529-540 In *Swimming and Flying in Nature Volume 2* (ed. Wu, Y-T. T., Brokaw, C. J. & Brennan, C.). New York: Plenum Press.
- Bjorndal, K. A. (1979). Cellulose digestion and fatty acid production in the green turtle *Chelonia mydas* L. *Comparative Biochemistry & Physiology* **63A**, 127-133.
- Blake, R. J. (1981). Mechanics of drag based mechanisms of propulsion in aquatic vertebrates. *Symposia of the Zoological Society of London* **48**, 29-52.
- Caldwell, D. K. (1968). Baby loggerhead turtles associated with sargassum weed. *Quarterly Journal of the Florida Academy of Science* **31**, 271-272.
- Carr, A. (1952). *Handbook of Turtles*. New York: Comstock.
- Carr, A. & Meylan, A. (1980). Evidence of passive migration of green turtle hatchlings in sargassum. *Copeia* **1980**, 366-368.
- Davenport, J., Antpas, A. & Blake, E. (1989). Observations of gut function in young green turtles *Chelonia mydas* L. *Herpetological Journal* **1**, 336-342.
- Davenport, J., Munks, S. & Oxford, P. J. (1984). A comparison of swimming in marine and freshwater turtles. *Proceedings of the Royal Society of London* **B220**, 447-475.
- Davenport, J. & Pearson, G. A. (1994). Observations on the swimming of the Pacific ridley, *Lepidochelys olivacea* (Eschscholtz, 1829): comparisons with other sea turtles. *Herpetological Journal* **4**, 60-63.
- Felger, R. S., Clifton, K. & Regal, P. J. (1976). Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. *Science* **191**, 283-285.
- Hertel, H. (1966). *Structure-form-movement*. New York: Reinhold.
- Meylan, A. B. & Sadove, S.S. (1986). Cold-stunning in Long Island Sound, New York. *Marine Turtle Newsletter* No. **37**, 7-8.
- Lohmann, K. L. & Lohmann, C. M. F. (1996). Orientation and open-sea navigation in sea turtles. *Journal of Experimental Biology* **199**, 73-81.
- Morreale, S. J., Meylan, A. B., Sadove, S. S. (1992). Annual occurrence and winter mortality of marine turtles in New York waters. *Journal of Herpetology* **26**, 301-308.
- Raymont, J. E. G. (1963). *Plankton and Productivity in the Oceans*. Oxford: Pergamon Press.
- Schwartz, F.J. (1978). Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. *Florida Marine Research Publication* No. **33**, Florida Department of Natural Resources.
- Stoneburner, D. L., Richardson, J. I. & Williamson, G. K. (1982). Observations on the movement of hatchling sea turtles. *Copeia* **1982**, 963-965.
- Walker, W. F., Jr. (1971). Swimming in the sea turtles of the family Cheloniidae. *Copeia* **1971**, 229-233.
- Weis-Fogh, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *Journal of Experimental Biology* **59**, 169-230.
- Witherington, B. E. & Ehrhart, L. (1989). Hypothermic stunning and mortality of marine turtles in the Indian River lagoon system, Florida. *Copeia* **1989**, 696-703.
- Wyneken, J. (1988). Functional innovations in swimming: analyses of sea turtle locomotor patterns. *American Zoologist* **28**, 13A [Abstract].
- Wyneken, J. & Salmon, M. (1992). Frenzy and postfrenzy swimming activity in loggerhead, green and leatherback hatchling sea turtles. *Copeia* **1992**, 478-484.