

ENERGETICS OF SWIMMING OF A SEA TURTLE

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SUMMARY

Young (mean mass 735 g) green turtles (*Chelonia mydas*) were able to swim in a water channel at sustained speeds between 0.14 and 0.35 m.s⁻¹. Oxygen consumption at rest was 0.07 l.kg⁻¹.h⁻¹; at maximum swimming speed oxygen consumption was 3-4 times greater than at rest for a given individual. In comparison with other animals of the same body mass the cost of transport for the green turtle (0.186 l O₂.kg⁻¹.km⁻¹) is less than that for flying birds but greater than that for fish. From drag measurements it was calculated that the aerobic efficiency of swimming was between 1 and 10%; the higher efficiencies were found at the higher swimming speeds. Based upon the drag calculations for young turtles, it is estimated that adult turtles making the round-trip breeding migration between Brazil and Ascension Island (4800 km) would require the equivalent of about 21% of their body mass in fat stores to account for the energetic cost of swimming.

INTRODUCTION

Fish, while swimming, have the lowest cost of transport of all animals and forms of locomotion (Tucker, 1970; Schmidt-Nielsen, 1972); that is, they require the least energy expenditure per unit body mass to travel a given distance. However, the low availability of oxygen from water (in comparison with air) apparently limits the swimming performance in some species (Brett, 1964; Kutty, 1968*b*) and in other species may have led to the evolution of mechanisms which allow sustained anaerobic performance (Hochachka, 1961; Smit, 1965; Kutty, 1968*a*; Greer Walker & Pull, 1973). It would seem, therefore, that a swimming animal which breathes air would be less limited by oxygen availability and might have a performance superior to those which must extract oxygen from the water.

Air-breathing animals which swim upon the surface of the water are limited in their performance by the large amounts of energy which are dissipated in the production of the wake and hence have been shown to have rather high costs of transport and low efficiencies (Prange & Schmidt-Nielsen, 1970). Humans have been shown to be rather inefficient swimmers (diPrampo *et al.* 1974). This is not surprising because there is little likelihood of selective pressures for humans to develop adaptations for aquatic locomotion. The studies on humans, while useful for comparison with other forms of human activity, shed little light on the problem of swimming energetics of animals for which swimming has evolved as the primary means of locomotion.

There remain as likely subjects for study the species of mammals, birds and reptiles which breath air and swim primarily submerged. The mammals, birds and large reptiles in this group are often difficult to obtain and to keep in captivity; the large animals require rather extensive facilities for study. Some of these difficulties can be avoided with the choice of a smaller reptile as the experimental animal.

The green turtle (*Chelonia mydas*) was selected for this study because of the availability of immature animals which could easily be handled and kept in the laboratory. The choice of this species provided several other advantages for the study of the energetics of an air-breathing swimmer. First, because the green turtle undertakes long migrations on stored food reserves (Carr & Goodman, 1970) and has free access to oxygen, one can reasonably assume that it would derive the energy for swimming primarily from aerobic metabolism rather than the less efficient anaerobic pathways. This characteristic would free the investigator from the problem of the uncertain fate of anaerobic metabolic end products in the estimation of the energetic contribution of those pathways. Secondly, because the turtle has a rigid exterior shell, drag measurements can be made directly from animals or models without the hydrodynamic complexities inherent in such measurements on fish or aquatic mammals which change shape as they swim. Lastly, adult animals were available for observation and limited experimentation in the field at the breeding beaches.

This paper gives the results of measurements of oxygen consumption, drag and aerobic efficiency of immature green turtles together with field data on the performance of adults. These findings are discussed with reference to the energetic requirements of the migration of the species.

MATERIALS AND METHODS

Animals. The immature green turtles (*Chelonia mydas*) used in this study were obtained from eggs which were collected at Tortuguero, Costa Rica, and hatched in my laboratory. The hatchlings were maintained in large tanks of sea water and were fed a diet of chopped fish. Five animals were used in the swimming studies. They ranged in body mass from 250 to 900 g (mean = 735 g) and in body length (front of head to trailing edge of carapace) from 0.175 to 0.260 m (mean = 0.240).

Some animals seemed unable to learn to swim steadily in the apparatus and were washed to the rear screen of the working section. These animals were excluded from the study after a few trials. The individuals from which data were taken were those which swam steadily and spontaneously at the front of the working section of the water channel. Measurements were begun after approximately two weeks of daily conditioning in the apparatus.

After completion of the experiments, with the exception of one animal which was killed for drag measurements, all immature animals were returned for tagging and release. Thrust measurements in the field were obtained from adult females which had been captured after they laid their eggs on the beach at Tortuguero, Costa Rica.

Water channel. Swimming studies and drag measurements were carried out in an open, recirculating water channel (Fig. 1). The working section of the channel was 1.10 m long, 0.30 m wide and 0.25 m deep. A lattice of thin steel plates (openings approximately 33 mm square) enclosed the front of the working section while a large-mesh wire screen enclosed the rear.

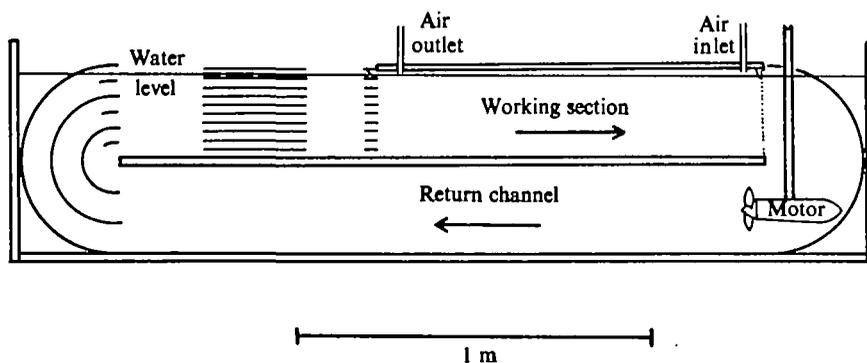


Fig. 1. Plan of water channel, side view. Direction of water flow is indicated by arrows. Dimensions and more detailed description of its operation are given in the text.

The water flowed into the working section after passing through a system of vanes and thin-walled tubes (30 mm diameter) which were adjusted to provide a uniform distribution of velocities and remove any large scale turbulence. Water speed was controlled with a variable speed electric motor mounted in the upstream end of the return channel. Power was provided to the motor from a 12 V storage battery which was continuously connected to a 15 A battery charger. Water speeds were measured in the working section by timing the transit of drops of ink which were injected upstream of the working section. Water speed was measured before and after each experiment and could be regulated to within $\pm 0.01 \text{ m.s}^{-1}$ over a range of 0.05 to 0.50 m.s^{-1} .

Metabolic measurements. The top of the working section was enclosed with a plexi-glass lid which was sealed to the sides of the channel and the water surface with flexible rubber gaskets. In operation the turtles could breathe from an air space of about 10 mm between the lid and the water surface. The inlet air for this space was passed through a CO_2 absorber and pressure regulated so that the inflow of air exactly balanced the rate at which air was drawn out of the chamber for analysis. Air was drawn from the system at a rate of from 1.5 to 3.0 l.min^{-1} . This rate was adjusted according to the rate of oxygen consumption of the animal to maintain the readings obtained within the scale of the oxygen analyser.

The air drawn from the chamber was passed through CO_2 and water absorbers. A sample of the dry, CO_2 -free air was continuously analysed for oxygen content with a Beckman G-2 paramagnetic oxygen analyser which could accurately detect changes in oxygen content of 0.001% . Air flow rates were monitored continuously with rotameters and checked at the beginning and end of each measurement with a displacement flowmeter (Vol-U-Meter, Brooks Instruments, Inc.). All flow rates were corrected to STPD. Oxygen consumption was calculated in accord with the principles given by Depocas & Hart (1957). Injection of known volumes and concentrations of nitrogen indicated no measurable leakage in the system.

Oxygen consumption was calculated from periods of not less than 10 min during which the swimming performance was continuous and the deflexion of the output of the oxygen analyser remained within a range of 0.05% . These standards were usually

attained within 30 min of the beginning of an experiment. During the experiments the air and water temperatures were $25^{\circ}\text{C} \pm 1^{\circ}\text{C}$. Oxygen consumption under 'resting' conditions was measured with the same analytical system but with the animals in a dark and dry metal container rather than the water channel.

Drag measurements. A one-component balance which responded only to forces parallel to the water flow direction was constructed to measure drag. One of the turtles used in the study was anaesthetized and then frozen. A bolt was threaded through the dorso-ventral axis of the body and attached to one arm of the balance. The other arm of the balance was connected to a force transducer (Hewlett Packard model FTA-100-1). The output of the transducer was demodulated with a carrier amplifier and recorded with a potentiometric recorder. The transducer was calibrated with known weights over the range of measured drag forces. The attitude of the turtle in the water flow and position of the appendages were adjusted to produce the minimum drag over the range of speeds studied. Drag was calculated from the force indicated by the transducer which was corrected for drag on the partially immersed arm and the slight difference in length of the arms of the balance. The drag measurements were derived from the mean value of the output of the transducer recorded from experiments at a given speed of approximately 2 min duration. The overall accuracy of the system was within 12%.

Overall aerobic efficiency was calculated by dividing the power output (the product of the drag and velocity) by the metabolic power input. This was calculated from the steady rate of oxygen consumption when the rate of one litre of oxygen per hour was assumed to be equivalent to 5.59 W (R.Q. = 0.8).

Thrust measurements. Thrust developed by adult animals in the field was measured with a 200 lb (900 N) spring scale. A nylon line, 50 m in length, was attached to the trailing edge of the shell of the captured turtle on the beach. The turtle was released and the speed at which the line was paid out was measured when the animal had entered the water and had begun swimming steadily away. When the end of the line was reached it was halted. The steady force then sustained by the turtle was recorded. Periodic bursts of higher forces were noted and correlated with observations of increased swimming activity. After the data were obtained, the turtle was pulled back to the shore and freed from the line.

RESULTS AND DISCUSSION

Swimming speed and oxygen consumption. The turtles were studied at sustained swimming speeds within the range of $0.14\text{--}0.35\text{ m}\cdot\text{s}^{-1}$ (not all could sustain the upper limit of this range). Individuals were clearly capable of short bursts of much faster swimming (estimated at $1\text{--}2\text{ m}\cdot\text{s}^{-1}$). However, these high speeds were never maintained for more than a few seconds. The short duration of the episodes of very fast swimming may have been a function of the confinement imposed by the size of the working section. At water speeds in excess of $0.35\text{ m}\cdot\text{s}^{-1}$, the turtles appeared to become exhausted and were swept to the rear of the working section. At speeds below $0.14\text{ m}\cdot\text{s}^{-1}$, the turtles seemed to ignore the water flow and consequently would not swim steadily.

The oxygen consumption varied considerably at a given speed but generally

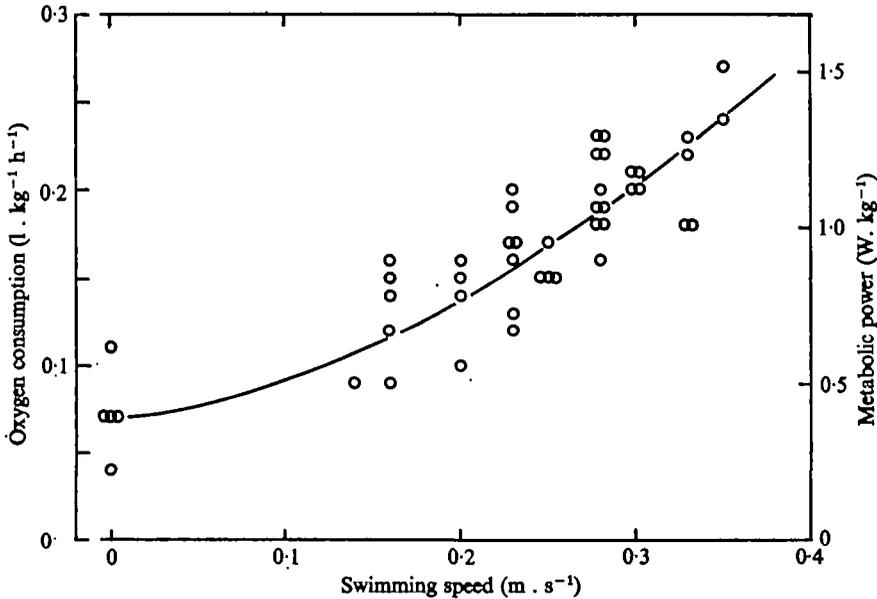


Fig. 2. Measurements of oxygen consumption and metabolic power of green turtles at rest and at various swimming speeds. The regression line has the equation: oxygen consumption ($\text{l.kg}^{-1}.\text{h}^{-1}$) = $0.07 + 0.978$ (swimming speed, m.s^{-1})^{1.662}. The correlation coefficient, r , for the line is 0.78.

showed an upward trend with increasing speed (Fig. 2). The rate of energy dissipation necessary to move an object through the water under the conditions described is generally represented as a function of the water speed raised to some power. Accordingly, a least squares power regression analysis was performed on the data shown in Fig. 2. The equation for the regression line, oxygen consumption ($\text{l.kg}^{-1}.\text{h}^{-1}$) = $0.07 + 0.978$ (swimming speed, m.s^{-1})^{1.662}, has a rather low correlation coefficient ($r = 0.78$) but can serve to describe the general trend in the relationship. Considering the fact that the collection of these data was dependent upon the voluntary cooperation of a reptile, the scatter is somewhat less than one might expect.

The mean resting oxygen consumption was $0.071 \text{ O}_2.\text{kg}^{-1}.\text{h}^{-1}$. This value is essentially identical to that estimated for adults of the species ($0.069 \text{ l O}_2.\text{kg}^{-1}.\text{h}^{-1}$) by Mrosovsky & Pritchard (1971) and is slightly lower than similar measurements on newly hatched green turtles ($0.099 \text{ l O}_2.\text{kg}^{-1}.\text{h}^{-1}$; Prange & Ackerman, 1974). Hughes *et al.* (1971) and Hutton *et al.* (1960) report values for other species of turtle in the range of $0.03\text{--}0.15 \text{ l.kg}^{-1}.\text{h}^{-1}$ at similar temperatures. At a maximum swimming speed, oxygen consumption is between 3 and 4 times greater than resting levels. This ratio is similar to that reported by Hughes *et al.* (1971) for their specimens of the Aldabra giant tortoise [*Geochelone (Testudo) gigantea*] of the same body masses.

In studies of fish swimming, the speed of different-sized individuals is standardized by representation in terms of body lengths per unit time (L.s^{-1}). This form of presentation (Fig. 3) does little to reduce the scatter in the measured levels of oxygen consumption. It does, however, suggest that the green turtles studied may encounter a limit to their sustained swimming speed at about 1.5 L.s^{-1} . Carr, Ross & Carr (1974) tracked adult green turtles at Ascension Island and found the maximum

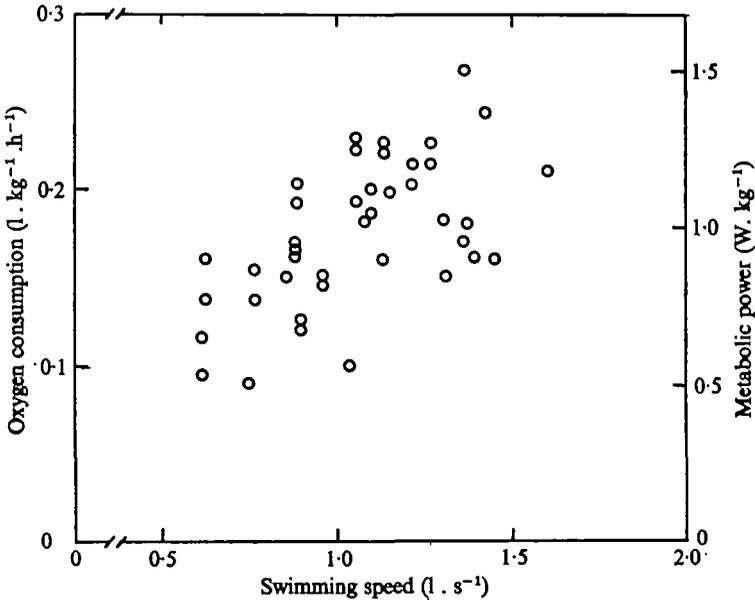


Fig. 3. Oxygen consumption and metabolic power of green turtles compared at various swimming speeds calculated as body lengths per second ($L \cdot s^{-1}$).

swimming speed was up to $7.2 \text{ km} \cdot \text{h}^{-1}$ ($= 2.0 \text{ m} \cdot \text{s}^{-1}$). The body length of these turtles is between 1.2 and 1.5 m; their maximum swimming speed is thus also about $1.5 L \cdot s^{-1}$. This finding suggests that there may be a general limit for the swimming speed of green turtles which is related to the body length.

For an animal which must rely on stored energy reserves the total energy requirement for a migration may be more important than the time involved. Thus the animal may preferably travel at a speed which minimizes the overall use of energy and which may not necessarily be the maximum speed of which the animal is capable. Division of the oxygen consumption at a given speed by that speed gives the energy cost for an animal to travel a unit distance (cost of transport). Comparison of this value with the speed of swimming (Fig. 4) shows that the green turtles studied had a minimum cost of transport at about $0.26 \text{ m} \cdot \text{s}^{-1}$, which is about 75 % of the maximum swimming speed. In comparison with other animals of the same body mass, the minimum cost of transport of the green turtle ($0.186 \text{ l O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) is slightly less than that for flying birds ($0.224 \text{ l O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$, calculated from the equation given by Tucker, 1970) but twice as great as that for fish swimming ($0.09 \text{ l O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$, estimated from Schmidt-Nielsen, 1972, p. 56). The green turtle's presumed advantage of more readily available oxygen supply apparently has not allowed it to swim at a lower cost than fish.

Conceivably, at least three other factors may contribute to the difference in cost of transport between fish and the green turtle. The values for cost of transport for some fish may be an artifact of the calculation. Because the cost of transport is derived solely from oxygen consumption, the exclusion of a sustained anaerobic component from the calculation of the metabolic power input would give values which are too low. For fish in which there is reason to suspect a sizeable sustained anaerobic

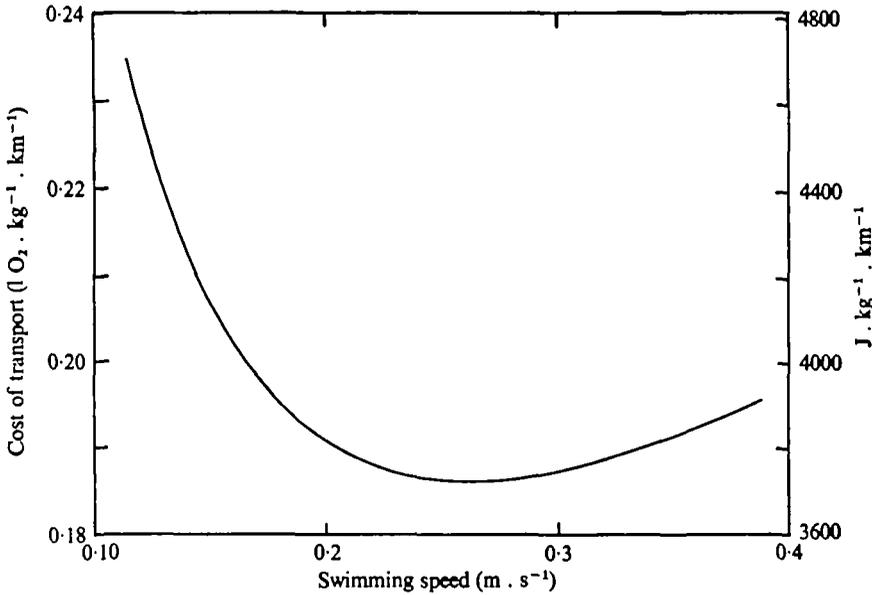


Fig. 4. Cost of transport for swimming green turtles, mean body mass 0.735 kg. Curve calculated from regression line given in Fig. 2.

component, e.g. goldfish (Kutty, 1968a), the energetics of locomotion might well be re-examined.

For fish such as the salmonids, e.g. trout (Webb, 1971), there is little likelihood of a sustained anaerobic component in the power input. However, correction for the effect of temperature on oxygen consumption, which would also lessen the difference in cost of transport between the fish and the turtle, must be considered. The data on which the cost of transport for fish is largely based were obtained from Brett's study (1965) of salmon at 15 °C. The cost of transport of salmon is substantially increased at the temperature used for the turtle study (25 °C). Brett (1964) provides data which can be used to illustrate this point. At a speed where the availability of oxygen is apparently not limiting ($3 \text{ L} \cdot \text{s}^{-1} = 0.54 \text{ m} \cdot \text{s}^{-1}$), 50 g salmon acclimated to 25 °C have a cost of transport of $0.223 \text{ l O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$. For a ten degree increase in temperature the oxygen consumption increased by a factor (Q_{10}) of 1.41. If this value is applied to fish of the same body mass as the turtles, their cost of transport increases from 0.09 to $0.13 \text{ l O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$. This value approaches that ($0.186 \text{ l O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) for the turtles.

A third explanation for the higher cost of transport for the turtles comes from observations of their behaviour while swimming. At each breath the turtles ceased swimming and used their flippers to help lift their heads above the water surface. This interruption of swimming for respiration must reduce the overall efficacy of their swimming. Fish need not interrupt their forward progress for ventilation. Perhaps an air-breathing swimmer such as a porpoise which does not pause in its locomotion to breathe would have a lower cost of transport than the turtles.

Drag and aerobic efficiency. The total drag on the preserved green turtle (overall length, 0.270 m) over the range of speeds studied is shown in Fig. 5. The equation

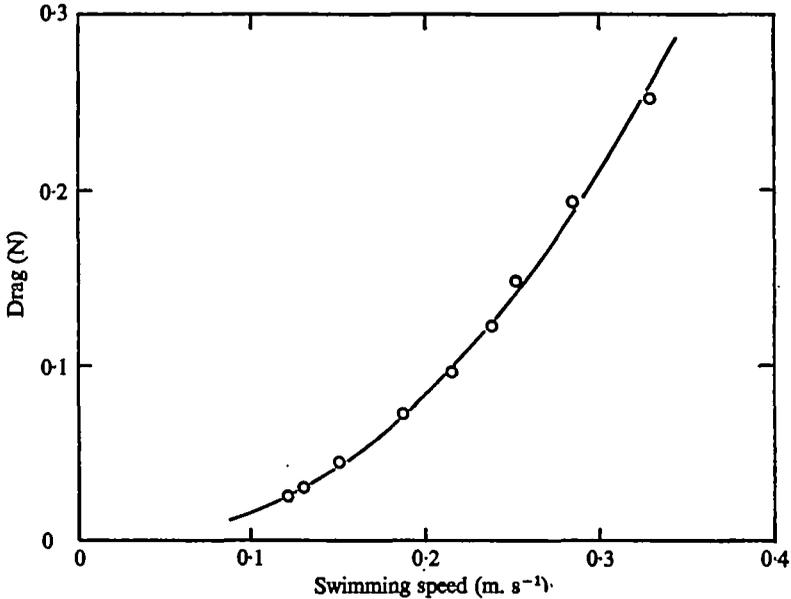


Fig. 5. Drag on preserved (model) green turtle at various water speeds. The line has the equation: $D = C_d \frac{1}{2} \rho U^2 L^2$ where D is drag (N); C_d is drag coefficient ($91.29 U^{0.281}$); ρ is density; U is swimming speed (m. s^{-1}); and L is the body length (m). The correlation coefficient, r , is 0.99.

given with Fig. 5 was used to estimate the drag on each turtle for which oxygen consumption had been measured. The turtles studied were assumed to be geometrically similar. Therefore the square of the body length was used in place of the projected area in the derivation of the equation for drag (Prandtl & Tietjens, 1934). Within the range of Reynold's numbers encountered in these measurements (10^4 – 10^5), drag coefficients for most objects do not undergo abrupt transitions. This was assumed to be the case in the application of the equation to the turtles studied. The regularity of the drag data further supports this assumption.

The product of drag and velocity gives the power output at a particular swimming speed. This product divided by the aerobic power input (determined from oxygen consumption) gives the aerobic efficiency of swimming (Fig. 6). The increase in efficiency with increased swimming speed is to be expected from the relationships given above for oxygen consumption and drag to swimming speed. Since the power output has the greater proportional increase, the aerobic efficiency should be higher at higher speeds.

If one assumes that the resting power input is constant and independent of speed, its value may be subtracted from the total power input at a given speed in an effort to find the efficiency of the locomotion alone. There is little change in the efficiency values after this correction. Swimming in the lower speed ranges becomes 1.5–2.5% efficient instead of 1–2%; at the higher speeds efficiency becomes 11–14% instead of 8–10%. While efficiency calculated in this manner may be relevant in terms of the comparison of the mechanics of locomotion, the total energy necessary for the living animal is the more biologically important value. In either case efficiency is a rather nebulous term since its components, in the case of an animal, can be only grossly

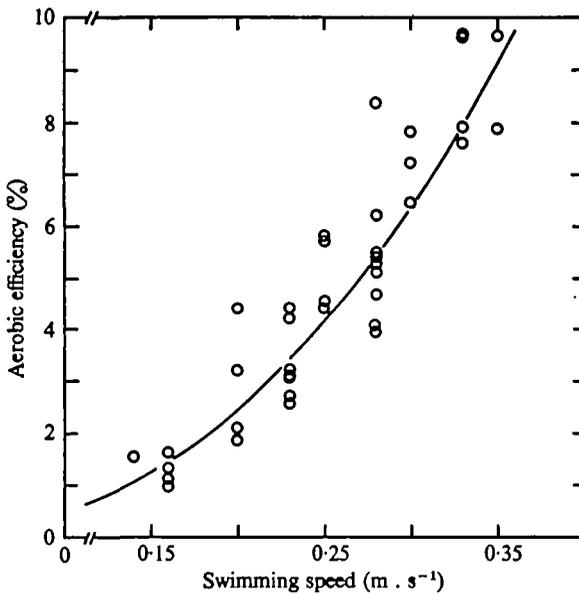


Fig. 6. Aerobic efficiency of swimming green turtles. The regression line has the equation: aerobic efficiency (%) = 106.17 (swimming speed, $m \cdot s^{-1}$)^{1.44}. The correlation coefficient, r , is 0.87 .

defined. The cost of transport is probably a more appropriate parameter by which to compare the energetics of locomotion. In the case of the green turtle, it can be seen that its most efficient swimming speed is not the most economical speed at which to swim.

The overall efficiency is useful, however, in support of the assumption that the long-term anaerobic contribution to the energetics of sea turtle swimming is relatively insignificant. If there were a substantial anaerobic component, its exclusion from the calculations would give an artificially low power input and, hence, a rather high apparent efficiency. For example, Smit *et al.* (1971) found aerobic efficiencies in goldfish which approached 40% as oxygen levels were lowered in the water. The values found for the green turtle are well within the value expected for aerobic work (23%, Asmussen, 1953).

Under conditions of forced diving the green turtle is clearly tolerant of long periods of anoxia (Berkson, 1966). Tolerance of anoxia under quiescent conditions need not necessarily imply that an animal uses sustained anaerobic metabolism during periods of activity. That is, the lack of oxygen *per se* is probably less important than the rate of accumulation and the means available for disposal of metabolic end products. When active, the green turtle has ready access to oxygen and presumably has been under no evolutionary pressure to evolve alternate pathways to dispose anaerobically of the end products of glycolysis. When inactive, the low rate of metabolism gives a low rate of lactate accumulation in these animals (Berkson, 1966). While submerged and inactive, the green turtle is apparently tolerant of anoxia and exists on a low rate of anaerobic metabolism until it returns to the surface and free access to oxygen.

Energetics of migration. The values for oxygen consumption, drag and efficiency

are directly applicable to the swimming energetics of immature green turtles. They may also be used to predict the energetic requirements for the migration of the adults. The immature turtles have been observed to feed while they swim (Frick, 1975) but the adults apparently undertake migration of up to 3000 miles (4800 km) solely on stored energy supplies (Carr & Goodman, 1970). The minimization of energetic cost of swimming therefore becomes of much greater importance to the adults.

Because of the uncertainty of the relationship of metabolism to body mass in turtles (Hutton *et al.* 1960) and the scatter in the values obtained for oxygen consumption, the drag data are probably the more reliable starting point from which to estimate the cost of migration. The mean swimming speed observed by Carr *et al.* (1974) for green turtles was 0.57 m.s^{-1} . The mean carapace length of six turtles of the same population at Ascension Island was 1.08 m; a mean body mass of 175 kg can be estimated for these turtles from the equation given by Hirth & Carr (1970). Assuming that the equation for drag used for the small turtles obtains for the adult turtles (Reynold's number = 7×10^5), the drag on the adult turtle should be about 29.4 N. The power output will be 16.7 W. Comparison of measured thrust from tethered turtles gives a further check on the validity of the estimated drag values. For the range of speeds ($0.9\text{--}7.2 \text{ km.h}^{-1}$) observed by Carr *et al.* (1974), the estimated drag is between 4.4 and 521.1 N. The average sustained force (thrust) measured from ten adult green turtles at Tortuguero, Costa Rica was 91 N; the range of thrust measured was 66.7 to 364.8 N. The average swimming speed for the Tortuguero turtles ranged from 1.4 to 3.6 km.h^{-1} . Within the limitations of the field technique, and given that at steady swimming speeds thrust should equal drag, the field data confirm the validity of the estimated drag values.

If it is further assumed that the adult turtles may be as much as 10% efficient, then the rate of metabolism necessary for swimming will be 167 W. The round trip migration of 4800 km would require approximately 2300 h spent swimming during which time a total of $1.41 \times 10^9 \text{ J}$ would be required from energy stores. If this energy store is fat from which $3.77 \times 10^4 \text{ J.g}^{-1}$ can be utilized then the fat store required would be about 37 kg. This would amount to about 21% of the body mass of an adult turtle. If the energetic requirements for the migration are based upon the green turtles' maximum and presumably most efficient observed speed, 7.2 km.h^{-1} , it can be calculated that the distance could be covered in only 667 h but would require 663 kg of fat, more than three times the body mass of the turtle. This calculation gives further support to the greater relevance of cost of transport compared to overall efficiency in the description of the energetics of locomotion.

The amount of fat in a green turtle has been reported to vary from less than one percent to more than 4% (Atwater & Woods, 1896; Carr & Main, 1973; Hirth & Hollingworth, 1973). These values were obtained from such measurements as refined oil content and exclude muscle fat (7.6% of muscle mass, Rao & Dutt, 1965); fat content so calculated may be less than that which is really available in the whole animal. More importantly, these values were not obtained from animals about to embark upon a migration but from ones which may have had depleted fat stores.

Examination of data on the fat content of migratory birds (Odum, Connell & Stoddard, 1961; King & Farner, 1965; Johnston, 1966; Johnston & Downer, 1968) shows that several species may have up to 50% of their body mass in fat prior to

long migrations. Birds which are non-migratory or post-migratory have fat stores of about 5%. If even a part of this range of fat storage can be assumed for sea turtles then it can be concluded that the round trip migration between Brazil and Ascension Island could be accomplished totally on the energy from fat stores.

CONCLUSIONS

The green turtle, like other submerged swimming animals, has a low energetic cost to travel a given distance. Depending upon the treatment of the data, this cost may be as low as that of fish. The greater availability of oxygen confers no apparent advantage upon the turtle; it may be, in the case of the turtle, that other constraints are more important than oxygen availability.

The calculations from which the energy requirements of migration are estimated could be improved by the addition of more data on the drag and oxygen consumption measured directly from the adult animals. Nevertheless they provide a reasonable set of values from which to account for the component of the green turtle's overall energy budget which comprises locomotion.

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