COST OF LOCOMOTION: UNSTEADY MEDUSAN SWIMMING

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SUMMARY

The influence of unsteady (time varying) motion on the energetics of swimming was investigated with measurements and theoretical estimates of the specific cost of locomotion for two species of hydrozoan medusae: *Gonionemus vertens* L. Agassiz and *Stomotoca atra* L. Agassiz. These species, both about 1 g, provide a broad range of swimming speeds for which locomotor energetics can be explored. The cost of locomotion (a dimensionless ratio defined as the rate of energy consumption divided by the product of an animal's weight and speed) was estimated from the oxygen consumption rate of medusae tethered to a force platform. Swimming beat frequency, as monitored by the force platform, was correlated with velocity obtained from ciné-films of freely swimming medusae.

The specific cost of locomotion was 6·3 (dimensionless), nearly one order of magnitude greater than the extrapolated cost of locomotion for a vertebrate swimmer of equivalent body mass. The great magnitude of this cost is attributed to two aspects of the periodic pulsatile pattern of locomotion by these cnidarians: (1) the energy expenditure for periodic accelerations of the animal's mass and some mass of fluid about it and (2) the energy dissipated in bell deformations and recovery strokes. Nearly 25 % of the augmented cost is attributed to the energy required to overcome an unsteady flow force, that is the force required to accelerate fluid about the animal. Such a high cost of locomotion is apparently a general consequence of swimming with a discontinuous production of thrust.

The mechanics of discontinuous swimming are explored by measuring the hydrodynamic coefficients associated with unsteady flows (added-mass coefficients) for models of medusae. The results suggest that the effects of vortex formation and shedding may significantly increase the magnitude of the forces produced by or resisting unsteady animal locomotion.

INTRODUCTION

Studies of the energetic costs of animal locomotion have led to two generalizations: (1) the specific cost of locomotion (defined as the rate of energy consumption divided by the product of weight and speed) decreases with increasing body mass and (2) this

cost is highly dependent on the particular mode of locomotion used by an animal (see reviews by Tucker, 1975; Schmidt-Nielsen, 1977; Hargreaves, 1981). For example, for a given body mass, swimming has a lower cost than flying; flying, in turn, is less costly than running. Recent work on the high cost of transport in crustacean swimming (Hargreaves, 1981) and large energy savings in burst-and-coast swimming in fishes (Weihs, 1974) strongly suggests that these generalizations may no longer hold true.

Analyses of swimming energetics are limited to an understanding of the cost of locomotion based largely on theoretical and experimental studies of fish (mostly salmonids) that swim by continuous body undulations that yield a steady-state forward speed (Webb, 1971a,b, 1975; Wu, 1971a,b, 1977; Lighthill, 1975; Brett, 1964). Yet many animals swim using neither steady-state motion nor body undulations. Invertebrate phyla are particularly rich in examples of such non-undulatory, unsteady modes of locomotion. Rapid tail flips and rowing motions of abdominal and thoracic appendages characterize the swimming mechanisms used by numerous arthropods (Crustacea: Lockhead, 1977; Hessler, 1981; Hargreaves, 1981; aquatic insects: Nachtigal & Bilo, 1975; Nachtigal, 1980). Cephalopod molluscs, dragonfly nymphs, salps, siphonophores and medusae utilize periodic jet propulsion for both escape and routine swimming (Packard, 1969; Johnson, Soden & Trueman, 1973; Hughes, 1958; Gladfelter, 1972, 1973; Donaldson, Mackie & Roberts, 1980; Daniel, 1983, 1984; Bone & Trueman, 1982, 1983). Even some vertebrate swimmers use rowing motions in their propulsion, for example, labriform fishes swim with oar-like oscillations of their pectoral fins (Blake, 1979, 1981a,b).

All of these modes of locomotion differ considerably from undulatory swimming in two key ways: (1) energy is expended during a recovery stroke in which negative thrust is produced and (2) as a result of this discontinuous production of thrust, energy is expended in periodically accelerating the animal's mass as well as the fluid around it. Are these unsteady modes of locomotion any more costly than steady-state undulatory swimming? Recent studies of crustacean swimming suggest that the cost of transport is indeed higher than undulatory swimming but the underlying determinants of this increased cost remain unclear (Hargreaves, 1981).

This paper explores one particular mode of unsteady locomotion: discontinuous jet propulsion in hydromedusae. An existing model of this mode of locomotion (Daniel, 1983) will be tested and applied towards an analysis of the energy requirements for unsteady locomotion. The hydrodynamic coefficients associated with unsteady locomotion will also be examined. These results will, in turn, be compared to undulatory as well as burst-and-coast swimming.

Medusae swim by periodic accelerations of the animal and fluid around it. Thrust arises from the forceful expulsion of water from an internal cavity through a hole at the base of the animal (the velar aperture). In hydromedusae, there are no muscles that oppose those that expel water. Instead, water is drawn back into the bell by the release of elastic strain energy stored in the bell during contraction. In short, discontinuous, unsteady motion is produced by a contraction phase during which water is expelled and positive thrust is produced, followed by a relaxation phase during which negative thrust is produced. The temporal pattern of this unsteadiness is variable since medusae swim in bouts of swimming cycles interspersed with periods of

quiescence, in a pattern that depends upon the species (Leonard, 1980; Mills, 1981). The hydrozoan species studied here provide a range of such swimming patterns for which the consequences of discontinuous thrust and unsteady motions to the energy requirements for locomotion will be determined.

MATERIALS AND METHODS

Two species of hydrozoan medusae, *Gonionemus vertens* and *Stomotoca atra*, were collected from the near shore waters around San Juan Island, Washington. Individuals ranged in body size from about 0·5 to 1·5 cm (bell diameter).

Kinematics

Medusae placed in a small glass aquarium (8 × 8 cm at the base) were filmed in lateral view at 48 ± 2 frames s^{-1} using a Canon Scoopic-16 movie camera. A centimetre grid behind the aquarium served as a size reference. A shallow depth of field in the camera's lens system ensured that medusae, when in focus, were swimming parallel to the focal plane of the camera.

The instantaneous position, and bell height and diameter of swimming medusae were determined from tracings of projected images from sequential film frames to ± 0·02 cm. The instantaneous volume of a medusa was estimated by assuming radial symmetry and treating the bell as a stack of 40 to 50 cylinders; dividing the image of the medusa into a series of 40 to 50 rectangles. The volumes of these cylinders were calculated and summed. The instantaneous volume and its rate of change were used to estimate the thrust generated by bell contractions. Swimming speed was determined from the frame-to-frame difference in the position of an animal. A mean swimming speed was computed for each complete swimming cycle that was filmed.

Oxygen consumption

Individual medusae were tethered, by means of a fine wire stabbed into the apex of the bell, to a force platform. The medusa and force platform were enclosed in a Plexiglas chamber (7·5 cm on each side) filled with filtered sea water and maintained at 11 °C. The oxygen content was monitored with an oxygen electrode (YSI Inc.) placed in a small side chamber. Water was circulated between the side chamber and the chamber containing the medusa by a stir bar and a magnetic stirring motor (Fig. 1). The side chamber provided rapid circulation around the probe with little mechanical disturbance to the animal. The oxygen content of the water was monitored by passing a pre-amplified signal from the oxygen electrode through a d.c. amplifier (Gould) with offset to one channel of a strip-chart recorder (Gould 2200). This amplification technique provided an accuracy of 20 parts per billion in measurement of oxygen content.

The force platform consisted of a strain gauge mounted on a thin (0·005 cm thick) strip of precision steel shim stock. The swimming beats of medusae tethered to the force platform were monitored on one channel of a strip chart recorder for estimates of swimming beat frequency.

Oxygen consumption rates and swimming beat frequency were measured simultaneously over a period of 2–3 h for each animal. The rate of oxygen consumption by
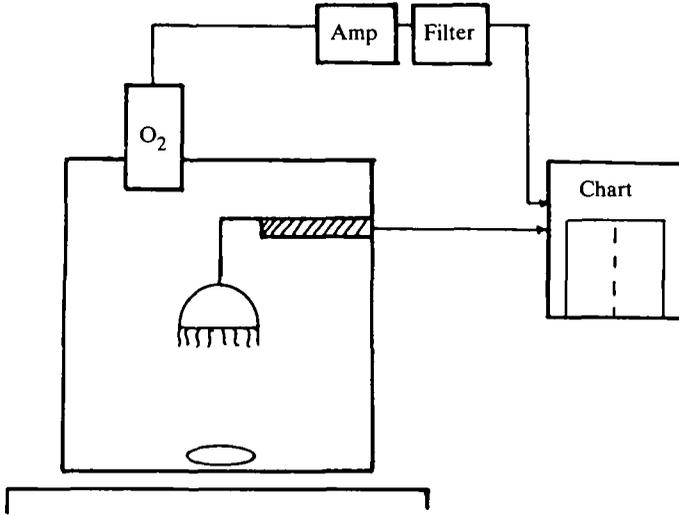
Fig. 1. Schematic diagram of the apparatus used to measure the oxygen consumption rate of medusae. Each individual was tethered to a small force platform. Signals from the force platform and the oxygen electrode (O_2) were monitored simultaneously. Amp, amplifier.

the electrode alone and any potential contaminants in the chamber was measured for 2 h between each experiment and its value was subtracted from the overall rate of oxygen consumption measured for tethered animals.

Mass measurements

To complete estimates of the specific cost of locomotion, the mass of each medusa was measured using the following protocol: (i) medusae were transferred from the oxygen measurement chamber to a holding tank containing sea water coloured with fluorescein dye; (ii) each animal was transferred from the tank of coloured sea water to a pre-weighed test tube containing $10 \, cm^3$ of clear, filtered sea water; (iii) the increase in weight of the test tube after the addition of a medusa was measured on a torsion balance to the nearest $0.01 \, g$; (iv) the change in the transmittance of the water in the test tube due to the addition of coloured water attached to an animal was measured with a spectrophotometer (Beckman, Spec-20); (v) the mass of coloured water attached to a medusa was determined by comparing the measured transmittance with that of a calibration curve constructed from the addition of known volumes of coloured sea water and this value was subtracted from the mass determined in step (iii).

Added-mass coefficients

A crucial component of an analysis of the cost of unsteady swimming is the work done in periodically accelerating fluid around an animal. This work is proportional to the added-mass coefficient of a swimming animal (see Discussion).

Added-mass coefficients were measured for 10 balsa wood models: five ellipsoids and five hemiellipsoids (medusa models). Each model was prepared on a lathe and water-proofed. The mass of each model was measured on an electrical balance to $\pm 0.001 \, g$. The mass of displaced water, m_d, was determined from the weight of

submerged models using the following relationship:

$$m_d = (W_d - W)/g,$$

where W_d is the weight of a submerged model; W is its weight in air, and g is gravitational acceleration. A fineness ratio for ellipsoidal models was defined as the ratio of the length of the axis of revolution to the diameter of the model. For hemiellipsoidal models it is the ratio of the length of the axis of revolution to the radius. Thus I define both spheres and hemispheres to have fineness ratios of 1·0.

Models were attached to the tip of an aluminium sting that was bolted to a force platform similar to those of Koehl (1977) and Denny (1982). The force platform was calibrated with a 1-g dynamometer (Scherr Tumico). Force measurements were reliable to ± 0·5 mN.

Models were accelerated in a long trough of water with their axes of revolution parallel to the direction of motion. Suspending the force platform and attached model from the ceiling with wires approximately 3 m long and allowing the apparatus to swing like a pendulum from various initial deflections provided a range of accelerations. Acceleration of the models was measured with an accelerometer (Entran Devices, model EGA-125) mounted at the tip of the sting behind the model. Outputs of the accelerometer and force platform were monitored on a dual channel strip-chart recorder. The force required to accelerate the sting alone was subtracted from the total force required to accelerate attached models. Each model was accelerated 8 to 10 times.

For the first few diameters of travel, the total force required to accelerate each model was dominated by their inertia and added-mass. Thus their added-mass coefficient was expressed as:

$$\alpha = (F - ma)/(m_d a),$$

where F is the total force, m is the mass of the model and a is its acceleration (for details of the equation refer to Discussion and Batchelor, 1967).

ABBREVIATIONS

a	acceleration	t_c	duration of contraction phase
A	area of velar aperture	t_r	duration of relaxation phase
C_d	drag coefficient	u	instantaneous velocity
f	overall beat frequency	$\hat{U}$	overall mean swimming speed
F	force	$\bar{U}$	mean speed within a single swimming
g	gravitational acceleration		cycle
m	mass of medusa or model	V	volume of medusa
m_d	mass of displaced fluid	W	weight of medusa or model
P	total power output	w_d	weight of displaced fluid
P_j	power to produce a jet	α	added-mass coefficient
P_f	power to fill bell	ϱ	density of water
S	projected area of medusa	η_m	muscle efficiency
t	time	η_e	elastic energy storage efficiency

RESULTS

Kinematics

Large volume changes and unsteady body motions are key characteristics of swimming medusae (Fig. 2). During one complete swimming cycle the volume of the subumbrellar cavity changes by about 50 % (Fig. 2A). This volume change results in a velocity that is highly unsteady, varying by about a factor of 3 in the 0·1 s during a contraction phase (Fig. 2C). For four individuals from each species, the mean swimming speed within one cycle was about 5·0 cm s^{-1} and the mean cycle duration was about 0·3 s (Table 1). A general time-averaged mean was defined by the following equation: $\hat{U} = \bar{U}tf$, where $\bar{U}$ is the mean swimming speed within one complete cycle, t is the duration of one complete swimming cycle and f is the overall swimming beat frequency (t<1/f since medusae swim in bouts of pulses). This value was used to correlate the swimming beat frequency obtained during oxygen consumption measurements with overall mean speed.

Patterns of locomotion

Gonionemus vertens swam in bouts of 5 to 10 bell contractions, each bout lasting 1 to 3 s followed by periods of quiescence lasting around 10 to 90 s. *Stomotoca atra*, like *G. vertens*, swam in bouts of 5 to 10 bell contractions, but the periods of quiescence were considerably shorter – about 10 s. Thus, on average, *S. atra* swam with a greater swimming beat frequency that *G. vertens*.

Oxygen consumption

The two species provided a range of swimming beat frequencies over which metabolic rate was measured. Because of their higher swimming beat frequency, the size-specific oxygen consumption rate was higher for *S. atra* than for *G. vertens* (Fig. 3). Combining the data for both species shows that, for all practical purposes, the size-specific rate of oxygen consumption increases linearly with swimming beat frequency. Two linear regression equations show that the individual with a particularly high swimming beat frequency does not create an artificial increase (broken line includes the individual with a high beat frequency, $r^2 = 0·94$; the solid line neglects that individual, $r^2 = 0·85$).

The specific cost of transport, C (a dimensionless ratio defined as $P/W\hat{U}$, where P is the rate of energy consumption, W is the weight of the animal and $\hat{U}$ is its velocity)

Table 1. *Measured and assumed values for the kinematics of swimming medusae*

	Cycle duration, t (s)	Mean Speed, $\hat{U}$ (cm s^{-1})
Gonionemus vertens	0·30 ± 0·06	5·4 ± 0·3
Stomotoca atra	0·33 ± 0·07	4·7 ± 0·4
Assumed	0·3	5·0

Values correspond to means over one complete swimming cycle ($N = 4$, both species).
The overall mean swimming speed is defined as $\hat{U} = \bar{U}tf$, where $\bar{U}$ is the mean swimming speed within one cycle.
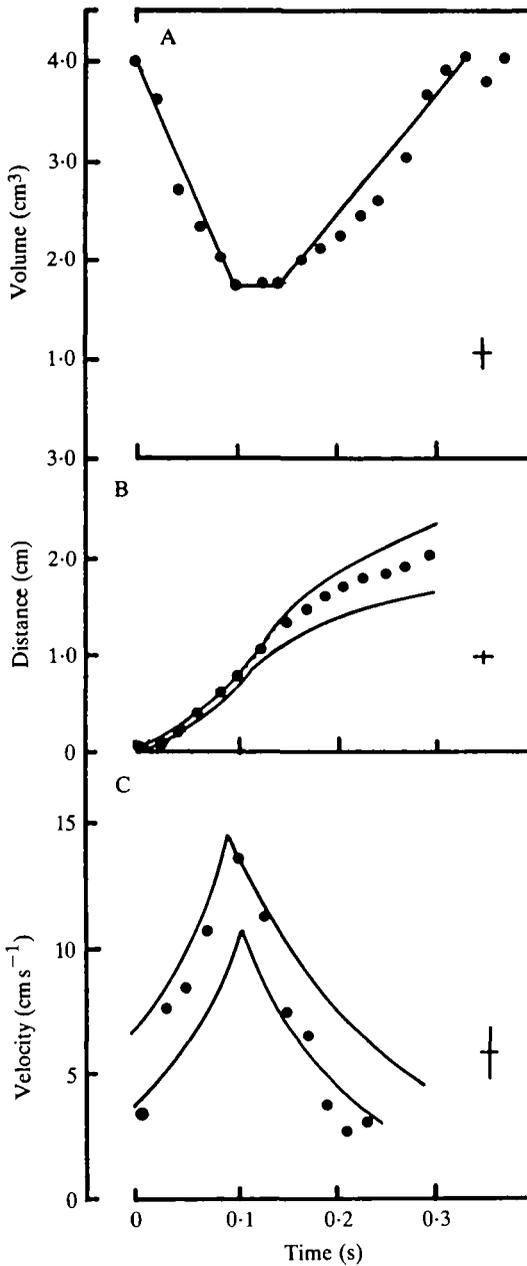
Fig. 2. The instantaneous volume, distance travelled and velocity of *Gonionemus vertens* are plotted as functions of time. The solid line in the top panel shows the function for the volume change that was used in conjunction with theoretical estimates of thrust and swimming speed (refer to Discussion). The small oscillation in volume of the bell at the end of the relaxation phase has an amplitude of oscillation that is about 10 % of the initial deformation – the value used as an estimate of elastic energy storage efficiency. Measured and predicted kinematics are shown in the bottom two panels. The two solid lines for each panel correspond to the upper and lower bounds to the theory, based on error associated with the input parameters. Crosses at the lower right corner of each panel indicate the error, based on the accuracy of time and displacement measurements.
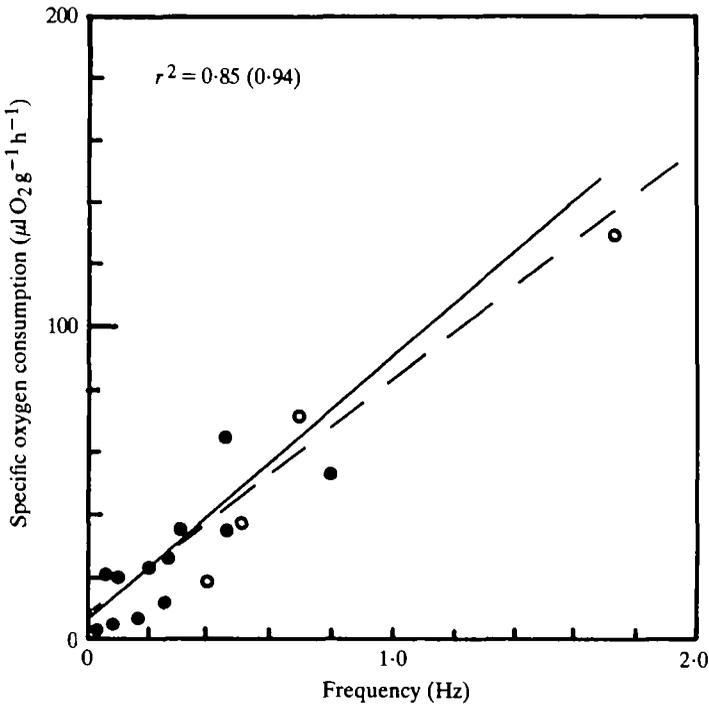
Fig. 3. The specific oxygen consumption rate is plotted against swimming beat frequency for *Gonionemus vertens* (solid circles) and *Stomotoca atra* (open circles). The solid line corresponds to a linear regression of these data (both species) without including the individual with a particularly high swimming beat frequency ($r^2 = 0.85$, $N = 15$); the broken line includes that individual ($r^2 = 0.94$, $N = 16$).

was determined by assuming 1 litre of oxygen corresponds to an expenditure of 20 kJ of energy. Using the specific oxygen consumption rate for both species along with the time-averaged estimate of swimming speed as a function of swimming beat frequency the cost of locomotion was estimated to be 6.3 ± 1.5 (dimensionless) (Fig. 5). The cost of transport is nearly one order of magnitude greater for medusae than it is for a fish (projection of existing data) of equivalent body mass swimming at a steady speed by continuous undulations.

Added-mass coefficients

As can be expected from theory, the added-mass coefficient increases with decreasing fineness ratios (Fig. 4). Agreement between theory and measurement is excellent, especially for ellipsoids whose fineness ratio exceeds 0·8. For these ellipsoids, the mean measured added-mass coefficient deviates no more than 10% from theory. The most oblate ellipsoid, however, has an added-mass coefficient that is considerably higher than theory predicts. This deviation is most probably a result of the effects of vortex formation and shedding that are not incorporated in the ideal flow theory used to predict added-mass coefficients. Because of their blunt trailing edges, medusa models are also likely to produce vortex motions in the fluid about them and, thus, experience high added-mass coefficients.
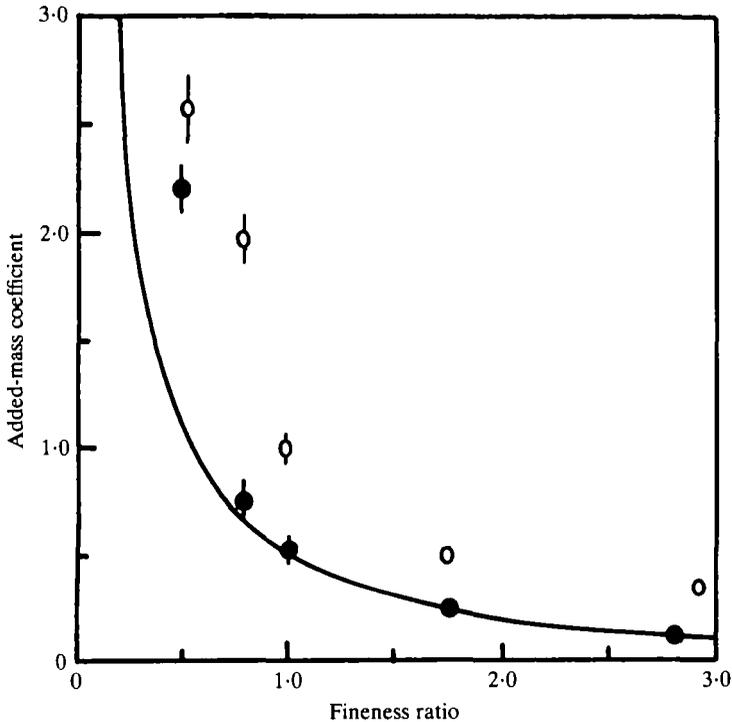
Fig. 4. Measured (circles) and theoretical (solid line after Lamb, 1932; Kochin, Kibel & Roze, 1964; Brennan, 1982) added-mass coefficients are plotted against fineness ratio for ellipsoids (solid circles) and hemiellipsoids (open circles: medusa models). The standard deviation of each measured value is indicated with a vertical line. Each point represents the mean of 8 to 10 measurements.

DISCUSSION

The cost of locomotion for unsteady, discontinuous medusan swimming is nearly one order of magnitude greater than its value for undulatory vertebrate swimmers of equivalent mass. To understand the reasons for this higher cost we must first explore the underlying mechanics and examine the validity of a model of medusan swimming. From this approach we may then explore the consequences of added-mass forces and discontinuous motion to the energy requirements of medusae and other swimmers.

Mechanics and model predictions

Unsteady motion occurs whenever the velocity of an animal changes with time. For an animal that swims unsteadily, its instantaneous thrust must be balanced by the force to overcome its inertia as well as two hydrodynamic forces: drag and the acceleration reaction (the reaction in the fluid to changes in the animal's velocity). An approximation of this force balance for a jet-propelled animal is given by the following differential equation (Daniel, 1983) (see above for symbol definitions):

$$(\varrho/A)(dV/dt) = SC_d u^2/2 + \alpha \varrho V(du/dt) + \varrho V(du/dt), \qquad (1)$$

where ϱ is the density of water, A is the area of the velar aperture, V is the instantaneous volume of the animal, C_d is the animal's drag coefficient, u is its velocity,

and α is its added-mass coefficient. The term on the left-hand side of this equation corresponds to the instantaneous thrust produced by the animal as fluid is ejected at a rate (dV/dt). The first term on the right hand side is the animal's instantaneous drag; the second term, the reaction in the fluid to the animal's acceleration; and the third term, the force required to overcome the animal's inertia.

Since all the factors in equation 1 are time-dependent functions, an analytical solution cannot be obtained. A fourth order Runge-Kutta method provides a numerical solution to this equation (Golomb & Shanks, 1965). The numerical predictions of the animal's instantaneous position and velocity are given by two lines to indicate extremes in the predicted kinematics based on error in measurement of the input parameters: the dimensions of the animal and the duration of the contraction and relaxation phases (Fig. 2B,C).

The predictions underestimate the actual deceleration of medusae between the end of the contraction phase and the onset of the relaxation phase (Fig. 2C). This discrepancy reveals a strong limitation to the application of equation 1 in medusan swimming: thrust produced by bell contractions is treated as a steady jet directed away from the animal during contraction and into the animal during relaxation. In reality, the jet produced by bell contractions is unsteady, resulting in periodic vortex rings travelling away from the animal during propulsion and into the animal during relaxation. Ellington (1984a,b), Weihs (1977) and Seikman (1963) showed that pulsed jets of this nature can generate greater thrust than a steady jet of equivalent volume flow rate. These vortex theories predict that when consecutive propulsive vortex rings are separated by less than three ring radii, thrust augmentation over an equivalent steady jet will occur.

While the instantaneous momentum balance given by equation 1 does not account for any such vortical flows produced by an unsteady jet, it does provide a model for which experimental verification is more direct. It predicts instantaneous kinematic parameters such as displacement and velocity which are easily measured. The vortex theories, in contrast, only yield estimates of the average thrust produced by a propulsive stroke. Given the agreement between the measured values and those predicted by equation 1 (Fig. 2A,B), neglect of the effects of periodic vortex rings appears justified for estimates of the energy requirements for locomotion.

Added-mass

The acceleration reaction dominates the hydrodynamic force resisting the motion of medusae and thus represents a major energy expense in unsteady locomotion. This force is also an important component in analyses of thrust and resistance in many forms of fish swimming (Lighthill, 1975; Wu, 1977; Blake, 1981a,b; Webb, 1978, 1979, 1982; Webb & Skadsen, 1980; Weihs, 1972, 1973, 1981). Given the overwhelming importance of the acceleration reaction in aquatic locomotion, a closer examination of added-mass coefficients in light of the present results is warranted.

For the most part, analyses of aquatic propulsion have relied on added-mass coefficients derived from ideal flow theory (for an exception see Webb, 1979). But, as the results in Fig. 5 suggest, real flow effects may play an important role in determining the magnitude of the added-mass coefficient. For the most oblate ellipsoid, the measured added-mass coefficient is nearly twice the theoretical value. This difference
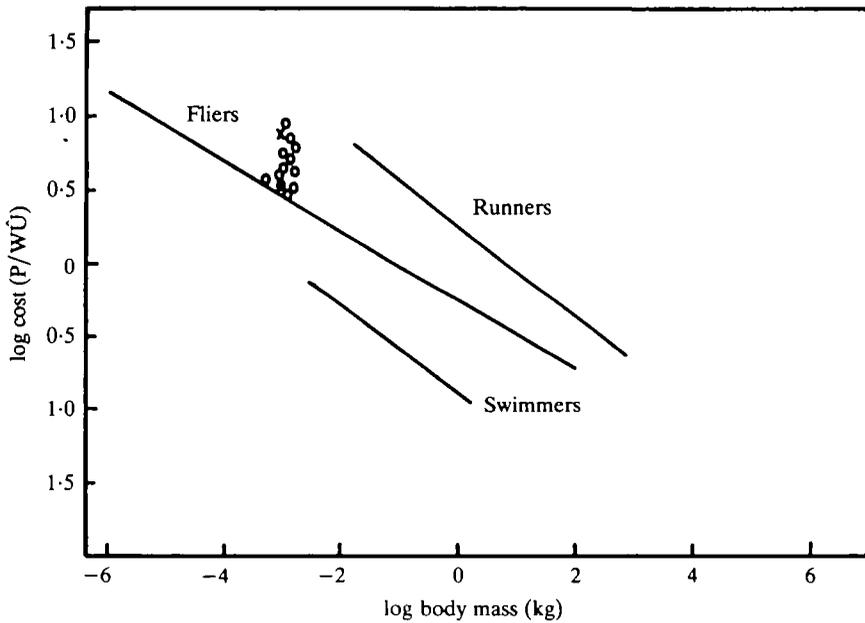
Fig. 5. The log of the specific cost of transport is plotted against the log of body mass for medusae (open circles). The solid circle corresponds to a predicted cost based on an assumed muscle efficiency of 20 % and an assumed efficiency of elastic energy storage of 10 %.The cross corresponds to a prediction based on the assumption that both efficiencies are 10 %. The solid lines, from Tucker (1975), are shown for reference.

between theory and measurement is probably a result of vortex formation and subsequent vortex shedding as fluid passes around the edges of the model: the sharper the edge, the greater the deceleration of flow around that edge and the greater the tendency for vortex formation. Ideal flow theory cannot account for such motions and is thus limited to accelerations of small amplitude (less than about 3 object diameters, Birkhoff, 1960). Animals that propel themselves by large amplitude undulations of bodies with strongly elliptical cross section or by means of an oar-like appendage (pectoral fins and beetle hindlimbs) may produce greater thrust because of real flow effects on the magnitude of the added-mass coefficient. Measured added-mass coefficients that include the effects of vortex formation will provide more reasonable estimates of the forces associated with such unsteady motions.

Rates of energy expenditure

The total rate at which a swimming medusa expends energy must, at the very least, equal the power required to produce a jet plus the power required to refill the bell between consecutive jets. The former can be estimated from the product of the thrust and the velocity of ejected fluid. By assuming the derivative on the left-hand side of equation 1 is constant (see Fig. 2A), the power requirement for a steady jet becomes:

$$P_j = \varrho \Delta V^3 / (At_c)^2, \tag{2}$$

where ΔV is the animal's volume change during the contraction phase (the volume of ejected fluid) and t_c is the duration of the contraction phase. The power requirement scales approximately as mass to the power 5/3 (details in Daniel, 1983).

During repeated contractions, subumbrellar swimming muscles expend energy not only in producing a jet but also in deforming the bell. Of the energy imparted to the bell, some is returned by elastic recoil and some is dissipated by the action of viscosity both within the fluid surrounding the animal and within the bell. The ratio of the energy returned by elastic recoil to the total energy imparted to the bell is the efficiency of elastic energy storage. Thus, the total energy expended in refilling the bell is:

$$P_f = (\varrho \Delta V^3)/[(At_r)^2 \eta_e], \tag{3}$$

where t_r is now the duration of the relaxation phase and η_e is the efficiency with which the bell stores elastic strain energy. Given some muscle efficiency (the efficiency of converting chemical to mechanical energy), the total power output becomes:

$$P = (P_j + P_f)/\eta_m, \tag{4}$$

where η_m is the muscle efficiency.

Since medusae swim in bouts of pulses, an appropriate time average of the total power output should reflect measurements of oxygen consumption rates over a broad range of swimming beat frequencies. Each term in equation (4), therefore, must be weighted for its duration and the overall swimming beat frequency. The total average power output for an animal swimming with a beat frequency, f, becomes:

$$P = (P_j t_c + P_t t_r)f/\eta_m. \tag{5}$$

The average power requirement for swimming is thus linearly related to two efficiency terms: muscle efficiency and the efficiency of elastic energy storage. There are at present no independent estimates of the efficiency of coelenterate muscle. One can assume, however, that muscle efficiency will not be much greater than 0·2, the maximum efficiency commonly expected for vertebrate striated muscle. Recent studies of insect flight power requirements suggest that muscle efficiency may be much lower – around 0·1 (Ellington, 1984b). For present purposes, these values – 0·1 and 0·2 – will be used as extremes in estimates of the cost of transport.

The efficiency of elastic energy storage may be estimated from any free oscillations the bell undergoes following a swimming cycle. For a perfectly elastic structure in a vacuum, release of a load will result in oscillations which proceed undamped in time. With any viscous dissipation, the oscillations will decay in time and the ratio of successive oscillations is a measure of the efficiency of elastic energy storage (Nielsen, 1962). Since medusae swim in a viscous medium and their bell is viscoelastic, oscillations following the release of subumbrellar swimming muscles will be damped. Such an event is shown in Fig. 2A where, following the relaxation phase, the volume of the bell decreases slightly and then returns to its resting shape. The ratio of the amplitude of the free oscillation to the amplitude of the maximum volume change is of the order of 0·08.

By substituting the above estimates of muscle and elastic energy storage efficiencies into equation 5, one can estimate the total power requirements as a function of
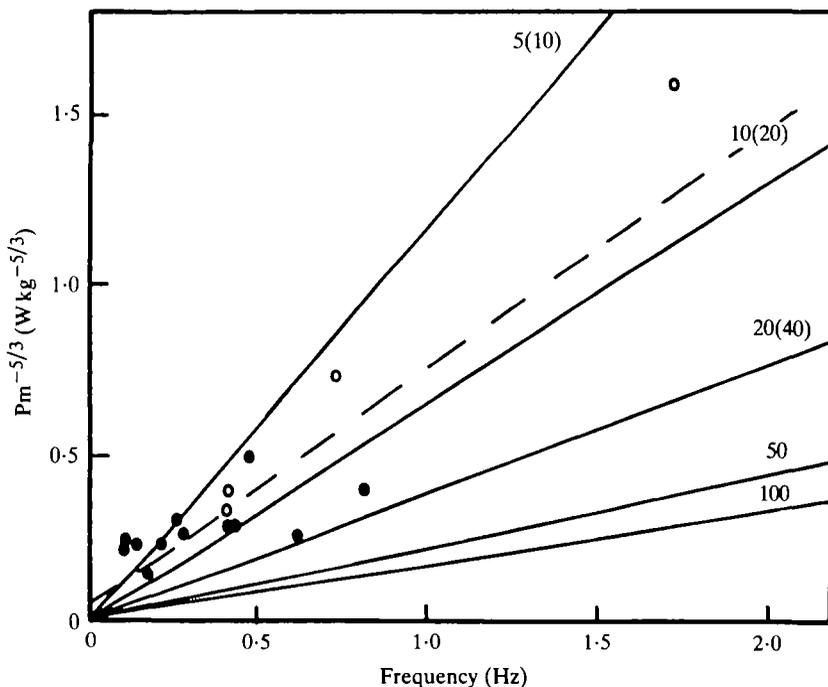
Fig. 6. Predicted and measured power requirements are plotted against swimming beat frequency for a variety of elastic energy storage efficiencies (indicated above each line). Power is divided by mass to the power 5/3 to correct for size differences (see equation 2). The values of energy storage efficiency outside parentheses correspond to predictions with an assumed muscle efficiency of 20%. Those inside parentheses correspond to an assumed muscle efficiency of 10%. Halving the efficiency of muscle implies a doubling in the efficiency of elastic energy storage. Measured power requirements for swimming are also plotted against swimming beat frequency for *Gonionemus vertens* (solid circles) and *Stomotoca atra* (open circles). The broken line represents the linear regression of the measured values ($r^2 = 0.92$, $N = 16$).

swimming beat frequency and compare these values with measurements (Fig. 6). Two points emerge from such a comparison: (1) within a reasonable range of efficiencies, values for the power requirements as predicted from the force balance (equation 1) adequately describe measured values and (2) nearly 50% of the total power requirement for swimming is dissipated during recovery.

Cost of locomotion

Dividing the predicted power requirements (Fig. 6) by the predicted mean swimming speed given by equation 1 yields the total cost of transport. For a 1-g medusa which swims unsteadily at a beat frequency of 0·5 Hz, equation 1 predicts a mean swimming speed of about 8 cm s^{-1}. If unsteady flow forces are ignored, the speed would be about 15 cm s^{-1} (see Daniel, 1983 for method of computation). Measured mean swimming speeds are about 5 cm s^{-1} for medusae of approximately 1 g swimming, on average, at a value of 0·5 Hz. Thus, including unsteady forces provides a more reasonable estimate of swimming performance. With (i) power requirements predicted by equation 5, (ii) a swimming speed of 8 cm s^{-1}, (iii) an efficiency of elastic energy storage of 0·08 (Figs 2A,6), and (iv) a muscle efficiency of either 0·1 or 0·2, the predicted cost of locomotion nicely brackets the measured values.

Neglecting unsteady forces results in an overestimate of swimming speed and thus a large underestimate of the total cost of transport. Just as energy is expended in producing a jet and deforming the bell, so too must it be expended in periodically accelerating the animal's mass and some mass of fluid around it – the added-mass. Nearly 50 % of the cost of transport may be attributed to the work done on the hydrodynamic force related to the added mass (the acceleration reaction). Since the added-mass coefficient is about $1 \cdot 0$ for medusae which are approximately hemispherical, nearly 25 % of the cost is devoted to overcoming the acceleration reaction alone. The cost required to periodically accelerate the mass of the animal plus the added-mass is greater than the total cost of locomotion for a steady swimmer of equivalent body mass.

As mentioned above, unsteady motion occurs whenever the velocity of an object varies in time. For medusae, variation in velocity occurs in at least two relevant time scales: one in which swimming bouts are interspersed with periods of quiescence and another in which, within a swimming bout, thrust is produced discontinuously. The former, called 'burst-and-coast' has been studied both theoretically (Weihs, 1974) and experimentally (Videler & Weihs, 1982) in fishes. Contrary to the present results, which show a high cost of transport for discontinuous thrust production, burst-and-coast locomotion can yield significant energy savings. These savings are a result of reduced drag associated with a glide phase.

Even though medusae swim in bouts, in a manner similar to burst-and-coast swimming, their cost of locomotion is considerably higher than one might predict on the basis of previously studied swimmers or on the basis of the Weihs' analysis. Their higher cost of locomotion arises from a situation peculiar to discontinuous, unsteady swimming: energy is expended in both accelerating and decelerating the animal's mass and its added mass. This increased energy requirement may surpass any potential energy savings gained by swimming with discrete bouts of bell contractions.

A discontinuous production of thrust will, in general, lead to a higher cost of locomotion than for swimming with continuous body undulations or in a burst-and-coast mode.

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