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Costs of transport for the scyphomedusa *Stomolophus meleagris* L. Agassiz

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The rhizostome scyphomedusa *Stomolophus meleagris* swims continuously at speeds up to $15 \text{ cm}\cdot\text{s}^{-1}$. Mean velocities increased as a power function of wet weight up to 70 g but were mostly constant thereafter. Bell pulsations ranged from 1.7 to 3.6 Hz. Reynolds numbers equalled 900 – 13 000. During activity, medusae consumed $0.05 \text{ mL O}_2\cdot\text{h}^{-1}\cdot\text{g WW}^{-1}$ ($1.2 \text{ mL O}_2\cdot\text{h}^{-1}\cdot\text{g DW}^{-1}$), at 30°C . Rates for inactive medusae were 50% less. The estimated cost of transport ranged from $2 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ at 5 g to $1 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ at 1 kg. These rates are comparable to those of fishes and about 1/50th that of planktonic crustaceans. These results were unexpected in light of the typical inefficiency (power output/power input) of jet swimming. However, *S. meleagris* has a very low respiration rate relative to crustaceans and fish, which probably compensated for low swimming efficiency.

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La Scyphoméduse Rhizostome *Stomolophus meleagris* nage continuellement à des vitesses atteignant $15 \text{ cm}\cdot\text{s}^{-1}$. Les vitesses moyennes augmentent selon une fonction exponentielle avec la masse fraîche jusqu'à 70 g, puis restent à peu près constantes aux masses supérieures. Les pulsations de la cloche varient de 1,7 à 3,6 Hz. Le nombre de Reynolds se situe entre 900 et 13 000. Durant ses phases d'activité, la méduse consomme $0,05 \text{ mL O}_2\cdot\text{h}^{-1}\cdot\text{g MF}^{-1}$ ($1,2 \text{ mL O}_2\cdot\text{h}^{-1}\cdot\text{g MS}^{-1}$) à 30°C . Les taux diminuent de moitié chez les méduses inactives. Le coût du transport est estimé à $2 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ à une masse de 5 g et de $1 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ à 1 kg. Ces taux se comparent à ceux des poissons et représentent 1/50 de ceux des crustacés planctoniques. Ces résultats sont inattendus, compte tenu de l'inefficacité habituelle (entrée/sortie de puissance) de la nage par propulsion. Cependant, *S. meleagris* possède un taux respiratoire très faible par comparaison aux crustacés et aux poissons, et cela compense sans doute sa faible efficacité de nage.

[Traduit par la revue]

Introduction

Natural selection may maximize locomotory efficiency and thereby improve an animal's fitness by diverting more energy to reproduction. One measure of locomotory efficiency is the cost of transport (amount of energy used by an animal to move a unit distance). Among small aquatic animals, the cost of transport is relatively high for crustacean zooplankton compared with fishes (Torres 1984; Morris *et al.* 1985). This is because crustaceans are small, have high specific metabolic rates, and are poor swimmers (Torres 1984; Morris *et al.* 1985).

In contrast to crustaceans and even some fishes, swimming costs are lower in some gelatinous zooplankton (Trueman *et al.* 1984). This may seem counterintuitive, since medusae, siphonophores, and salps are thought to be relatively inefficient swimmers owing to their intermittent, accelerating and decelerating, jet locomotion (Bone and Trueman 1982, 1983; Daniel 1983, 1984, 1985).

In medusae, swimming propulsion results from contraction of the myoepithelium lining the subumbrellar cavity wherein water is jetted rearwards. As a result, kinetic energy is stored in the elastic mesoglea of the exumbrella until used to refill the bell cavity with water (Gladfelter 1972a; Trueman 1980; Daniel 1983, 1985).

Regarding swimming efficiencies of gelatinous zooplankton, Bone and Trueman (1982, 1983) predict that salps may be the most efficient swimmers because they refill their jet chambers with water brought in from ahead of the animal (rather than behind as in medusae and siphonophores), thus suffering less "refill" drag.

Daniel (1985) has shown that the cost of locomotion for two species of small hydromedusae is high. However, recent studies by M. E. DeMont (manuscript in preparation) have shown that medusan locomotion may be more efficient than was previously thought. He found that the hydromedusa *Polyorchis penicillatus* could force the bell to oscillate near its resonant frequency and could thereby reduce the amount of energy needed for locomotion.

Although the mechanics of the locomotory system of one scyphomedusa has been studied (Gladfelter 1972b), nothing is known about its costs of transport. Because some scyphomedusae, the semaeostomes, have long oral arms and numerous tentacles, they probably have high drag coefficients and thus have a high cost of transport. Another order, the rhizostomes, filter zooplankton prey from the water using massive sieve-like oral arms (Larson 1978) and therefore probably have increased locomotory costs owing to the drag induced by their oral-arm filters. However, *Stomolophus meleagris* may be an exception because it is apparently more dependent on turbulence to bring prey into contact with the arms than it is on direct filtration (Larson 1978). Consequently, it could have a low cost of transport. Additionally the large size of these medusae may further reduce transport costs, as is evident for other animals (Schmidt-Nielsen 1972).

The objective of this study was to estimate the costs of transport for various size classes of *Stomolophus meleagris* medusae (with mass ranging over more than two orders of magnitude), by measuring their swimming speeds and respiration rates.

Stomolophus meleagris is seasonally abundant in inshore waters of the Gulf of Mexico (Mayer 1910). It is often seen near the surface where it swims continuously in a relatively straight course. Recent studies by Shanks and Graham (1987) have shown that *S. meleagris* is capable of oriented swimming relative to directional cues.

Stomolophus meleagris medusae can reach a bell diameter of greater than 15 cm and exceed 1.5 kg in wet weight (Larson, unpublished data). The umbrella of *S. meleagris* is globular in shape (Fig. 1). Protruding from the subumbrellar cavity is the blunt and enlarged, gelatinous oral-arm cylinder. The oral arms trap prey as well as increase the velocity of the water jet by reducing the size of the bell opening. During swimming, the bell cavity contains water equivalent to 40–60% of the body weight, depending on the state of contraction (Larson, unpublished data). Numerous fin-shaped, gelatinous extensions protrude

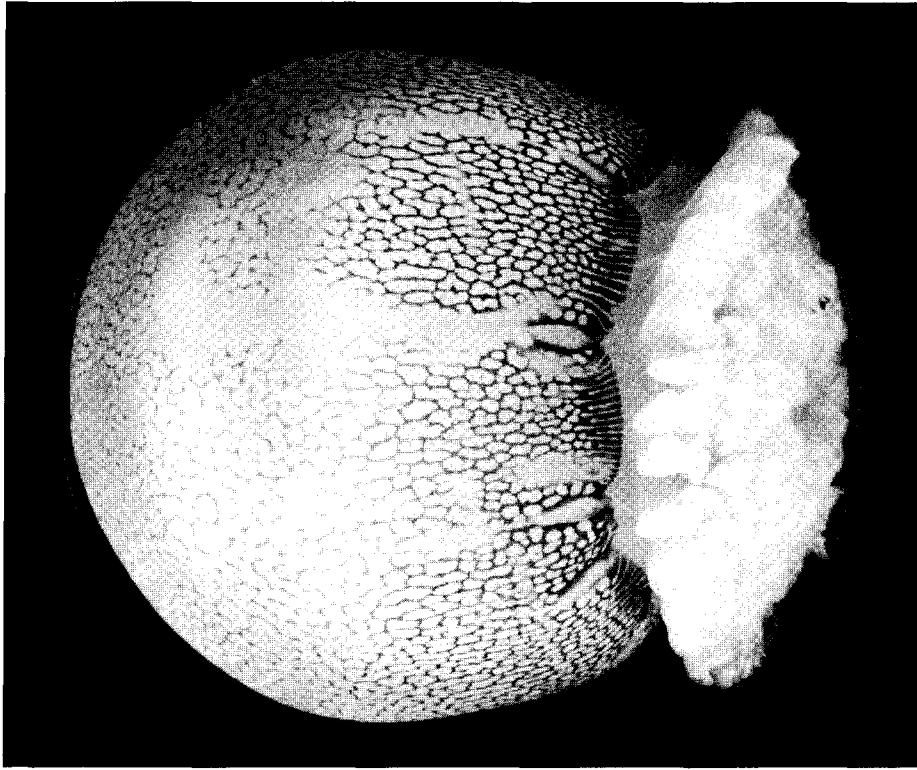


FIG. 1. Side view of *Stomolophus meleagris*, 6 cm in bell diameter.

outwards from the lateral edges of the distal portion of the oral-arm cylinder. These "fins" may help to maintain a straight swimming course.

Propulsive force is produced by circular muscles that cover about 80% of the subumbrellar surface, representing $\approx 1\%$ of the total body wet weight (WW) (0.7–0.9%, $n = 5$) (Larson, unpublished data). The muscles are divided into eight pairs of fields by gaps at the rhopalial radii. Each muscle field is roughly triangular, and is twice as tall as it is broad (Fig. 2). In medusae of less than 30 mm bell diameter, the muscles are flat sheets, but in larger specimens, which require greater propulsion, the muscles increase their cross-sectional areas with lateral folds. Gladfelter (1972*b*) gives further information regarding the histology of scyphomedusan muscles.

The exumbrellar mesoglea, which acts as an elastic antagonist to reexpand the bell after contraction, is up to 1 cm or more in thickness, is relatively rigid and dense, and probably has a high collagen content (Kimura *et al.* 1983). There are no joints in the mesoglea as occurs in *Cyanea capillata* (Gladfelter 1972*b*). A complex meshwork of anastomosing gastrovascular canals is located immediately below the muscles.

Methods and materials

Collection

Stomolophus meleagris medusae were collected from inshore waters of the Gulf of Mexico (St. Georges Sound) of northwest Florida (30° N 85° W), from June to August 1986. Surface water temperatures ranged from 28 to 31°C. Medusae were dipped from the surface, using nets, and were placed in 20-L plastic buckets. They were then transported to the Florida State University Marine Laboratory at Turkey Point where they were maintained in plastic pools (2–3 m in diameter; 0.3–0.5 m height) that had unfiltered seawater flowing into them. Only normal-appearing medusae were used in the experiments, within 4–24 h after collection. During this period, no mortality occurred.

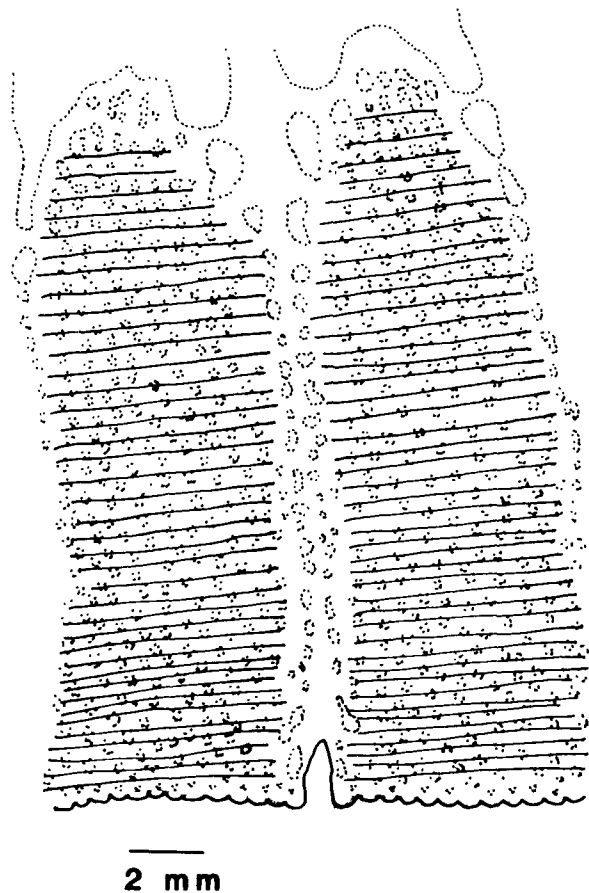


FIG. 2. View of subumbrella, showing two circular muscle fields with lateral folds (specimen 4 cm in bell diameter).

Mass measurements

For respiration experiments, wet weights were determined after the superficial water was drained off (all mass values are reported here as live wet weights). Weights of medusae (M , in g) used in swimming-speed measurements were estimated from the diameter (in cm) vs. weight relationship: $M = 0.24 (\text{bell diameter})^{3.23}$ ($r^2 = 0.99$, $n = 76$, range = 2–13 cm).

Size measurements

Plastic calipers were used to measure maximum bell diameters of medusae, held by hand horizontally, out of water.

Respiration rates

Oxygen uptake rates were measured at $30 \pm 1^\circ\text{C}$, using a polarographic oxygen sensor (POS), an oxygen meter (Yellow Springs Instrument model 57), and an x - y recorder. Medusae were placed individually into one of four clear acrylic chambers (0.7–8.4 L), fitted with a lid into which the POS was inserted through a hole. Water circulation around the POS was accomplished by a magnetic stir bar attached under the lid. This was accomplished by fitting two stir bars (each 8×25 mm) into opposite ends of a short PVC sleeve through which a small stainless steel bolt had been placed to attach the sleeve to the lid. To separate the POS from the medusa, an acrylic sheet with holes drilled through it was wedged into the chamber. The seawater used in the chambers was filtered (0.4- μm pore size) and saturated with air prior to use. Blank seawater controls were run at the beginning and end of each experimental day.

Respiration measurements were taken for 15–30 min, depending on the uptake rate. After the routine O_2 uptake rate was measured, the standard (inactive) uptake rate was obtained. During the routine O_2 uptake rate, activity was monitored by recording the bell pulsation rates at 2–5 min intervals. To obtain the standard rate, swimming was inhibited by disrupting the nervous input from the swimming muscle pacemakers. This was done by crushing the eight marginal ganglia, using fine forceps.

Swimming velocities

The speed of swimming medusae was estimated by measuring (using a stopwatch) the time required for medusae to swim across a pool (2 or 3 m in diameter). Since the medusae did not always swim in a straight line, the estimated speeds are probably conservative.

Results

Pulsation rates

Pulsation rates (PR) measured for medusae in the pools ranged from 1.7 to 3.6 Hz (pulsations/s) over a 10–1000 g mass range. The rates were a negative power-function of weight ($\text{PR} = 4.07 M^{-0.12}$) (Fig. 3). Pulsation rates measured in respiration chambers were similar, except those of larger specimens, which had somewhat lower and more variable rates than pool specimens. This variability was probably because the medusae in the chambers were more stressed, thus becoming fatigued since they were swimming very forcefully. As discussed by Trueman *et al.* (1984), pulsation rates may not necessarily be correlated with power production owing to the variability in the degree of bell contraction.

Swimming velocities

Measured speeds in the pools ranged from 4 to $16 \text{ cm}\cdot\text{s}^{-1}$. Below 70 g, mean velocities increased from about $5 \text{ cm}\cdot\text{s}^{-1}$ at 2 g to $12 \text{ cm}\cdot\text{s}^{-1}$ at 70 g and were described by the power function $V = 4.5 (\text{WW})^{0.22}$, where V is in $\text{cm}\cdot\text{s}^{-1}$ and WW in g (Fig. 4). Above 70 g, speed remained nearly constant at $12.3 \text{ cm}\cdot\text{s}^{-1}$.

During swimming, there was no noticeable acceleration or deceleration between pulsations, although there must be some change in velocity during a jet cycle. The Reynolds number (the ratio of inertial to viscous forces, where $\text{Re} = (\text{TL})V/k$, TL = total length, V = velocity, and k = kinematic viscosity (k herein

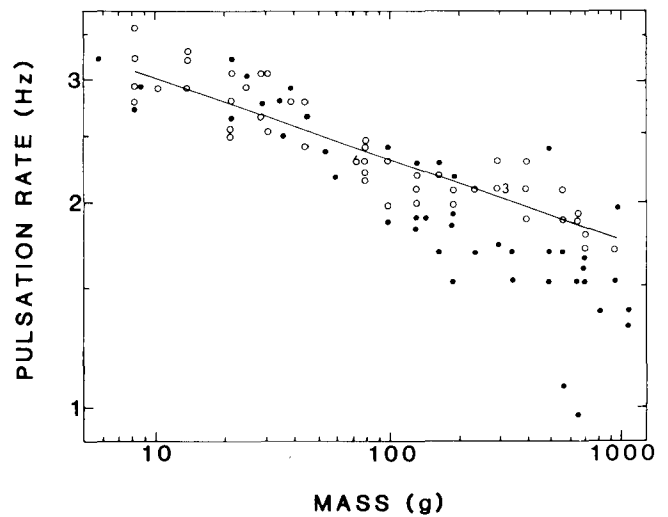


FIG. 3. Scatterplot and regression line of mass vs. pulsation rate. Open circles, medusae in pools; solid circles, medusae in respiration chambers.

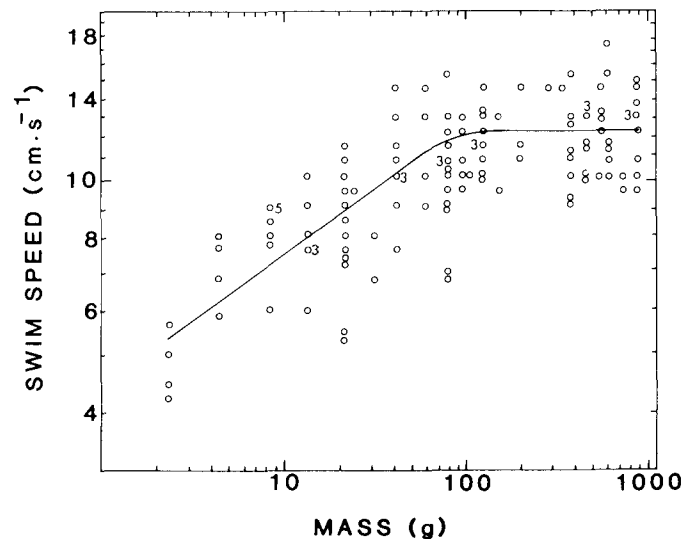


FIG. 4. Scatterplot and regression line of mass vs. swimming speed (data from medusae in pools).

estimated from water temperatures and salinities)) increased from 900 at 2 g to 13 000 at 1 kg.

Net costs of transport

The estimated net metabolic costs of transport per unit mass and distance ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$) were estimated from respiration rates and swimming speeds. Oxygen uptake rates of actively pulsating medusae were almost directly proportional to mass ($\text{mL O}_2\cdot\text{h}^{-1} = 0.05 M^{0.99}$, for M in g, $r^2 = 0.97$, $n = 71$), increasing from $0.5 \text{ mL}\cdot\text{h}^{-1}$ at 10 g to $45 \text{ mL}\cdot\text{h}^{-1}$ at 1 kg (Fig. 5). Because medusae in the respiration chambers were active and swimming very forcefully, these rates probably are near maximum and most likely are higher than rates for medusae swimming at cruising speeds. Oxygen uptake rates for inactive medusae (standard rates) were about half those of active specimens (weight-specific respiration rates of active medusae = 48 ± 2 ($\bar{x} \pm \text{SE}$) $\text{mL}\cdot\text{h}^{-1}\cdot\text{kg}^{-1}$, $n = 71$; rates for inactive medusae = $24 \pm 1 \text{ mL}\cdot\text{h}^{-1}\cdot\text{kg}^{-1}$, $n = 42$). After maceration of the rhopalia there was little or no contraction of the subumbrellar muscles,

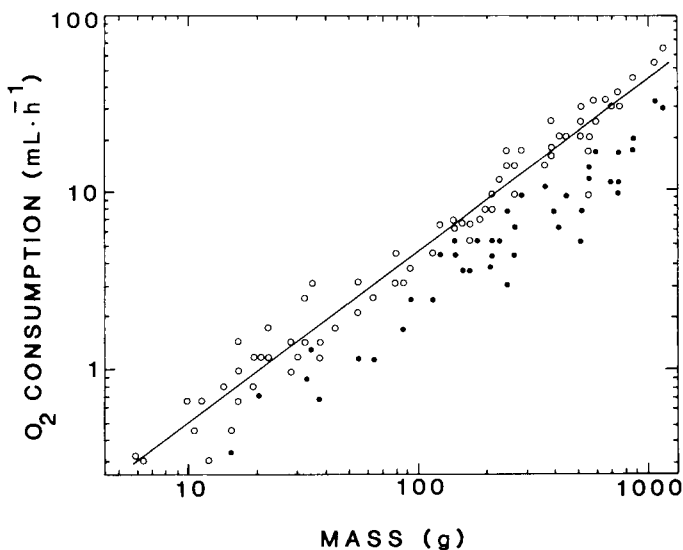


FIG. 5. Scatterplot and regression line of mass vs. oxygen consumption for individual medusae. Open circles and regression line, routine (active) rate; solid circles, standard (inactive) rate.

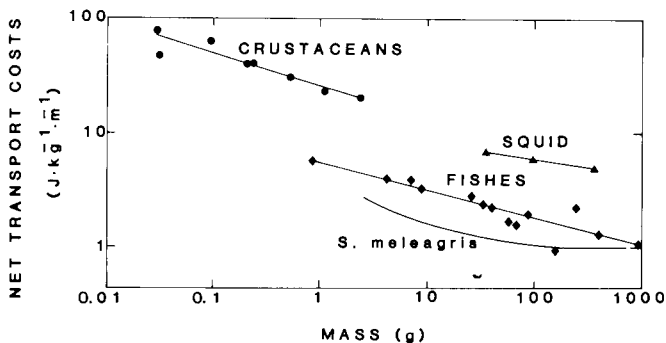


FIG. 6. Regression lines of mass vs. net costs of transport for various aquatic exotherms including *Stomolophus meleagris*. Data for crustaceans from Torres (1984), for fishes from Beamish (1978), and for squid from O'Dor and Webber (1986).

suggesting that the inactive rates are equivalent to standard rates.

The amount of energy liberated by metabolism during swimming can be estimated from oxygen uptake rates (active – inactive rates) and the oxycaloric equivalent. It is unlikely that anaerobic respiration is significant in these medusae since they swim constantly and lack glycogen stores (carbohydrate values for medusae are low (Percy and Fife 1981) and mostly consist of polysaccharide components of the mesoglea (Gardner and Zubkoff 1978)). Since *Stomolophus* feeds primarily on zooplankton (Larson 1978), protein is the major metabolic substrate. Oxidation of protein liberates approximately $19 \text{ J} \cdot \text{mL}^{-1} \text{ O}_2$ (Elliot and Davidson 1975).

The net costs of transport were calculated for *S. meleagris* that weighed between 5 and 1000 g using swimming speed data (predicted values from regression: $V = 4.5 (\text{WW})^{0.22}$, where V is in $\text{cm} \cdot \text{s}^{-1}$ and WW in g, for medusae < 70 g and using a mean velocity of $12.3 \text{ cm} \cdot \text{s}^{-1}$ for medusae > 70 g) and values for metabolic energy released during activity (using an O_2 uptake value of $24 \text{ mL} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$). The results suggest that the energy costs for locomotion decrease nonlinearly with increasing mass, i.e., from $2 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ at 5 g to $1 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ at 1 kg (Fig. 6).

Discussion

The net costs of transport for small swimming animals range from about $1 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ in *Stomolophus* and fishes to $50 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$ or more in small crustaceans (Fig. 6). Although the costs are comparable in fish and *Stomolophus* of 1 kg mass, medusae of < 10 g have transport costs equal to about one-half those of comparably sized fishes.

Low transport costs ($1.1 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$) have been previously reported for nonfeeding salps by Trueman *et al.* (1984). However, feeding salps would have significantly higher costs due to the pressure drag of the internal mucus filter.

Only one other worker has reported the cost of transport for medusae. Daniel (1985) reported the costs of transport for two species of small (1 g) hydromedusae, i.e., *Gonionemus vertens* and *Stomotoca atra*. Comparing his results to those of Schmidt-Nielsen (1972), Daniel concluded that transport costs for these medusae were high, being equivalent to flying animals. However, using his data (mean velocity = $5 \text{ cm} \cdot \text{s}^{-1}$, and O_2 uptake at $5 \text{ Hz} = 0.05 \text{ mL} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$), I calculated that gross transport costs are about $5 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$, which is very close to $6 \text{ J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$, the extrapolated transport costs for a 1-g *Stomolophus meleagris* (mean velocity = $4 \text{ cm} \cdot \text{s}^{-1}$, O_2 uptake = $0.05 \text{ mL} \cdot \text{h}^{-1} \cdot \text{g}^{-1}$). These estimates suggest that the cost of transport for medusae is relatively low and is similar to that for fish.

The primary reason for the cost-efficient transport in medusae and salps, relative to other aquatic animals, is their low specific metabolic rates. Although, on a carbon basis, gelatinous zooplankton have respiration rates similar to those of crustaceans and fish (Cetta *et al.* 1986; Kremer *et al.* 1986; Larson 1987), on a wet-weight basis, gelatinous forms have oxygen uptake rates 2–3 orders of magnitude less. Furthermore, the ratio of active to standard metabolism is much higher in crustaceans, fish, and squid, exceeding 3 in most species studied, and reaching 10 or more in others (Jones and Randall 1978; Newell 1979; DeMont and O'Dor 1984; Torres 1984; Davenport and Trueman 1985; Webber and O'Dor 1985), whereas in salps and medusae, this value is ~ 2 or less (Kuzmicheva 1980; Davenport and Trueman 1985; Larson 1985; data presented herein).

Low respiration rates in medusae and other gelatinous forms are primarily a result of the paucity of metabolically active tissues. Salps and *Stomolophus* have swimming muscles that represent only 1% or less of body mass (Bone and Trueman 1983; data presented herein), whereas in fishes, this value may exceed 50% (Bone 1978). Such a large muscle mass can produce fast accelerations, but is inefficient at lower, routine swimming speeds (Webb 1975). In contrast, the muscles of *Stomolophus* are probably operating at optimum efficiency at normal cruising speeds but, consequently, the medusae have limited ability to accelerate. In fact, the highest-measured swimming speeds for *Stomolophus* were only 30% above the average routine speed.

An additional factor, which makes gelatinous zooplankton relatively cost-efficient swimmers, is the lack of respiratory and circulatory organs. Webb (1975) estimates that in salmonoid fishes, 20% of the active metabolism can be attributed to respiratory and circulatory demands.

Although medusae and other jet-propelled gelatinous zooplankton are hydrodynamically inefficient when compared with fishes and squid, the disparity does not compensate for the great difference in metabolic rates. For example, underyearling sockeye salmon, *Oncorhynchus nerka*, swimming at $10 \text{ cm} \cdot \text{s}^{-1}$, consume about $150 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ (Jones and Randall 1978), whereas *Stomolophus*, swimming at the same speed,

consume only 1 mL O₂·kg⁻¹·min⁻¹. Thus, to cover the same distance, the salmon consumes 150 times more O₂ per unit body weight. Squid have even higher respiration rates at a given speed (Webber and O'Dor 1985; O'Dor and Webber 1986), and thus have high transport costs.

The cost of transport for *S. meleagris* decreased with increasing size. This relationship appears to be the norm for aquatic animals (Schmidt-Nielsen 1972; Beamish 1978; Torres 1984; Morris *et al.* 1985; O'Dor and Webber 1986). Nonetheless, in *S. meleagris*, the relationship between log-mass and log-transport cost is apparently not linear as it is in other animals; instead, it is curvilinear, and is asymptotic for weights between 0.1 and 1 kg. This is apparently due to an insufficiently powerful muscle mass in larger *S. meleagris* medusae. Consequently, the relationship between swimming speed and biomass is inconstant. The significance of this is that there is little transport-related metabolic gain for *S. meleagris* to exceed weights of 0.1–0.5 kg.

It is likely that some gelatinous zooplankton have even lower costs of transport than *Stomolophus*. This is because *S. meleagris* depends on turbulence produced during swimming to bring prey into contact with the oral arms (Larson 1978). The lowest drag and the lowest cost of transport for gelatinous zooplankton probably would be for nonfeeding individuals where drag produced by tentacles, oral lobes, oral arms, internal mucus nets, etc. would be reduced due to contraction of drag inducing structures. Ctenophores may have the lowest locomotory costs of any metazoan; some species have very low respiration rates (<10 mL·h⁻¹·kg⁻¹, Kremer *et al.* 1986), and they can reach modest speeds when disturbed (to 2 cm·s⁻¹, Larson, unpublished data). Furthermore, since ctenophore ciliary propulsion is steady, ctenophores do not expend energy to constantly accelerate, as do jet-propelled forms. Consequently, it is possible that the cost of transport in ctenophores may be significantly less than 1 J·kg⁻¹·m⁻¹.

Reducing the costs of transport has probably been an important factor during animal evolution. Yet most animals must also be able to escape predators. This may mean rapid but inefficient locomotion. For some gelatinous zooplankton rapid escape swimming may be adaptive (Roberts and Mackie 1980; Mills *et al.* 1985). However, for others this may not be important and these species can therefore reduce locomotory costs. Further studies are needed to determine how gelatinous zooplankton reduce their swimming costs and how this affects their ecological success.

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