

### *Short Communication*

## **COST OF TRANSPORT IN THE SWIMMING BIVALVE *LIMARIA FRAGILIS***

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Measurements of cost of transport (the amount of energy needed to transport a unit mass over a unit distance) have been determined for a wide range of invertebrates including those that run, fly, crawl, and swim. Measurements for paddling swimmers include those for crabs, shrimp, amphipods, mysids, and euphausiids, while measurements for swimmers that use jet propulsion include salps, squid, nautilus, and jellyfish (see Full, 1997 for references). Thus far, cost of transport for a swimming bivalve has not been determined.

The file shell *Limaria fragilis* (Gmelin), Family Limidae, is a small free-swimming bivalve with thin, ovate equivalves. It is easily collected subtidally from shallow sand burrows beneath coral boulders on tropical reef flats of the Great Barrier Reef, Australia. At rest, the long red tentacles on the mantle margins cannot be accommodated fully within the valves, which

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abut only at the anterior hinge. When disturbed, file shells are capable of slow sustained swimming for periods of at least 15 min (Baldwin and Lee, 1979). Swimming is powered by contractions of the single phasic adductor muscle that moves the valves together into the vertical plane, expelling water from the mantle cavity past the hinge and propelling the animal forward and upward with the hinge hindmost. This form of locomotion is in marked contrast to scallops (Pectinidae) that swim with the valves in the horizontal plane and with the hinge hindmost, and can only sustain short bursts of very rapid valve closures predominantly powered by anaerobic metabolism (Grieshaber and Gäde, 1977; Baldwin and Opie, 1978; De Zwaan *et al.*, 1980; Livingstone *et al.*, 1981).

The energetics of swimming by *Limaria* have been well documented. Baldwin and Lee (1979) determined the aerobic energy expenditure of animals swimming at different velocities (measured in no. valve snaps  $\text{min}^{-1}$ ) and concluded that little energy was derived anaerobically. However, with the subsequent identification of the newly discovered pyruvate reductases strombine dehydrogenase and alanopine dehydrogenase in the file shell adductor muscle, and with a better understanding of the effect of captivity on arginine phosphate levels in resting animals, it was established that swimming did in fact involve a significant contribution from anaerobic metabolism (Baldwin and Morris, 1983).

After reviewing these *Limaria* studies, it became evident that cost of transport for swimming *Limaria* could be calculated if aerobic energy expenditure during swimming could be correlated with velocity, expressed as a distance per unit time rather than in valve snaps  $\text{min}^{-1}$  as had been reported in Baldwin and Lee (1979). Thus, the purpose of this paper was to determine the relationship between swimming velocity, measured as distance per minute, in *Limaria fragilis* and number of snaps per minute, which would allow the cost of transport for a swimming *Limaria* to be calculated.

*Limaria fragilis* of a size range similar to those used in previous studies (Baldwin and Lee, 1979; Baldwin and Morris, 1983; Baldwin and Hochachka, 1985) were collected from beneath small coral boulders at low tide on the reef flat at Heron Island, Queensland, Australia. All swimming experiments were then carried out immediately at the site of capture. In the first series of experiments, *Limaria* ( $N=5$ ; 2.0–4.3 cm length) were placed individually in clear sand areas and allowed to swim freely without further manipulation. Time of swimming, distance covered, and number of valve snaps were recorded. To control the effects of tidal flow better, a second series of experiments were conducted in which *Limaria* ( $N=11$ ; 3.1–4.4 cm length) were placed individually into a shallow plastic container

(55 × 30 × 15 cm) filled with fresh seawater and floated on the sea surface. Swimming sessions (4–8 for each animal) were conducted in which swimming time, distance covered, and number of valve snaps were recorded.

In the first series of experiments, freely swimming *Limaria* moved at a mean velocity of 296 cm min<sup>-1</sup> with a mean snap distance (distance travelled in one valve snap) of 4.7 cm snap<sup>-1</sup>.

In the second series of experiments, mean velocity ( $v$ ; cm min<sup>-1</sup>), mean snap frequency ( $f$ ; no. snaps min<sup>-1</sup>), and mean snap distance ( $d$ ; cm snap<sup>-1</sup>) were calculated for each individual *Limaria* swimming in the container. Mean velocity ranged from 267 to 640 cm min<sup>-1</sup>, mean snap frequency ranged from 53 to 104 snaps min<sup>-1</sup>, and mean snap distance ranged from 4.7 to 6.9 cm snap<sup>-1</sup>. Both mean snap frequency and mean snap distance increased linearly with increasing mean velocity, with regression equations of  $f = 13.6 + 0.136v$  ( $r^2 = 0.96$ ,  $t = 15.44$ ,  $p < 0.001$ ) and  $d = 4.7 + 0.003v$  ( $r^2 = 0.47$ ,  $t = 2.80$ ,  $p = 0.02$ ), respectively. As there was no relationship between *Limaria* length and mean snap distance over the size range in this series of experiments ( $r^2 = 0.02$ ,  $t = 0.42$ ,  $p = 0.68$ ), the data were pooled for a grand mean of 5.9 cm valve snap<sup>-1</sup> ± 1.1 sd.

The relationships between mean snap frequency and mean snap distance vs. mean velocity indicate that *Limaria* increase both the frequency and power output of snaps in order to increase velocity. However, the contribution of these two parameters is very disparate. Specifically, in order to increase swimming velocity from 15 to 150 cm min<sup>-1</sup> [roughly the range of velocity for the oxygen consumption data of Baldwin and Lee (1979)], the average *Limaria* doubled snap frequency from 16 to 34 snap min<sup>-1</sup> while the distance covered in an average snap increased from 4.7 to 5.2 cm snap<sup>-1</sup>. Thus, increasing the number of snaps appears to be the primary method of increasing velocity in *Limaria fragilis*.

Assuming the increase in power output with increasing velocity is minor compared to the increase in snap frequency, the mean value of 5.9 cm snap<sup>-1</sup> can be used to convert the oxygen consumption relationship ( $\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  vs. no. valve snap min<sup>-1</sup>) of Baldwin and Lee (1979) to a relationship between energy consumption and velocity of swimming (Fig. 1, open circles and solid line). This can then be used in calculating cost of transport. Oxygen consumption, expressed in  $\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , was converted to  $\text{J kg}^{-1} \text{ h}^{-1}$  using the oxygen equivalent for the metabolism of carbohydrates 21.1  $\text{mJ } \mu\text{l O}_2^{-1}$ ; Elliot and Davison, 1975), as glycogen is the major fuel utilized during locomotion in bivalves (De Zwaan, 1983; Hochachka *et al.*, 1983).

The form of the relationship between aerobic energy expenditure and velocity in swimming animals is not the same for all organisms. A linear

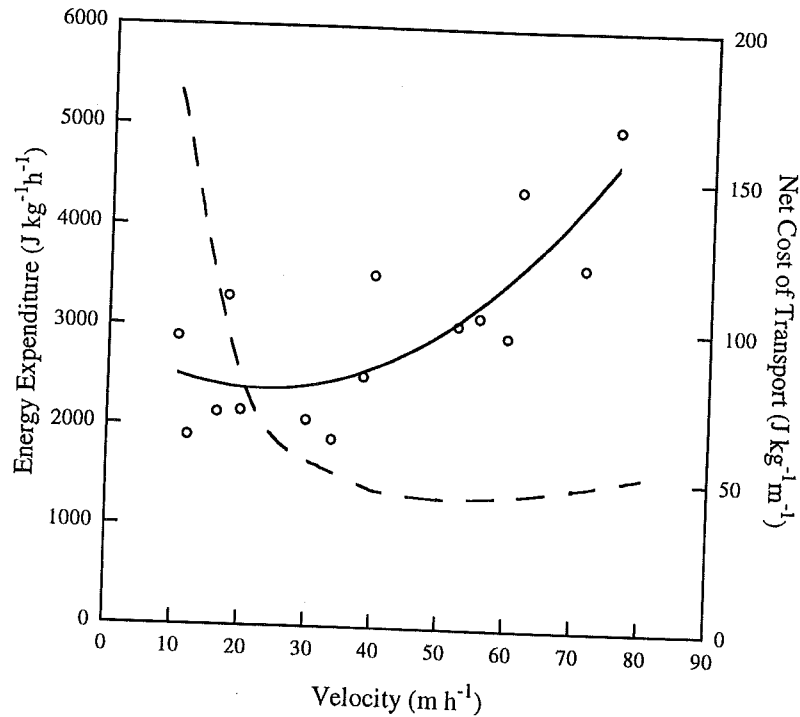


FIGURE 1 The open circles and solid line represent the mass specific aerobic energy expenditure ( $\text{J kg}^{-1} \text{h}^{-1}$ ) of swimming *Limaria* as a function of velocity ( $\text{m h}^{-1}$ ). Data originally from Baldwin and Lee (1979). Regression statistics can be found in the text. The dashed line represents the net cost of transport ( $\text{J kg}^{-1} \text{m}^{-1}$ ) for swimming *Limaria* as a function of velocity ( $\text{m h}^{-1}$ ). Points on the line were calculated by first subtracting resting weight-specific aerobic energy expenditure from the aerobic energy expenditure at a given velocity (calculated from the regression of aerobic energy expenditure on velocity), then dividing by that velocity.

relationship of the form  $Y = a + bX$  has been found in mysids (Cowles and Childress, 1988), amphipods (Halcrow and Boyd, 1967), euphausiids (Torres and Childress, 1983), and hydromedusas (Daniel, 1985), while a semi-log model ( $\log Y = \log a + bX$ ) has been used for crabs (Houlihan *et al.*, 1985), squid (O'Dor, 1982), and nautilus (O'Dor *et al.*, 1990) and an exponential model ( $\log Y = \log a + b \log X$ ) for shrimp (Ivlev, 1963). All three of these models gave significant correlation coefficients for the relationship between aerobic energy expenditure ( $E$  in  $\text{J kg}^{-1} \text{h}^{-1}$ ) and velocity ( $v$  in  $\text{m h}^{-1}$ ) for swimming *Limaria* ( $r^2 = 0.52, 0.51,$  and  $0.38$  and  $p = 0.002, 0.003,$  and  $0.015$  for the linear, semi-log, and exponential models, respectively). On this basis, the linear model provides the best fit. However, a better fit to the

linear model was obtained by adding a quadratic term (linear model:  $E = 1767 + 30v$ ;  $r^2 = 0.52$ ,  $F_{0.05,1,13} = 14.4$ ,  $p = 0.002$ ; quadratic model:  $E = 2811 - 38v + 0.8v^2$ ,  $r^2 = 0.64$ ,  $F_{0.05,2,12} = 10.8$ ,  $p = 0.002$ ). This resulted in a U-shaped curve with a minimum aerobic energy expenditure of  $1619 \text{ J kg}^{-1} \text{ h}^{-1}$  occurring at a velocity of  $24 \text{ m h}^{-1}$  (Fig. 1, solid line), a value two times larger than the resting weight-specific aerobic energy expenditure for *Limaria* ( $738 \text{ J kg}^{-1} \text{ h}^{-1}$ ; Baldwin and Lee, 1979). *Limaria* are capable of swimming at speeds much greater than those measured in the respirometer by Baldwin and Lee (1979), and this U-shaped curve may not adequately describe the energy requirements of swimming at higher speeds. However, we would expect aerobic energy expenditure to increase greatly at higher speeds, since drag forces increase with  $v^2$ , so our estimation of minimum aerobic energy expenditure should be valid despite the low range of velocities over which aerobic energy expenditure was measured.

Net aerobic cost of transport (transport cost above resting metabolic rate) was calculated by first subtracting resting weight-specific aerobic energy expenditure from the aerobic energy expenditure at a given velocity (calculated from the regression of energy expenditure on velocity), then dividing by that velocity. A minimum aerobic cost of transport of  $43 \text{ J kg}^{-1} \text{ m}^{-1}$  was obtained at  $50 \text{ m h}^{-1}$  (Fig. 1, dashed line). It is interesting that this was the average velocity of free swimming *Limaria* observed by Baldwin and Lee (1979) but it was much slower than the average velocity of  $178 \text{ m h}^{-1}$  obtained for free swimming *Limaria* in the present study.

The anaerobic contribution to the cost of swimming can be estimated from the data of Baldwin and Hochachka (1985). In that study, the average *Limaria* weighed 10 g (excluding shell) and animals were allowed to swim for five minutes before anaerobic metabolites were measured. An average *Limaria* swimming for five minutes used  $20.2 \mu\text{mol g adductor muscle}^{-1}$  of arginine phosphate,  $2.22 \mu\text{mol g adductor muscle}^{-1}$  of ATP, and accumulated  $0.8 \mu\text{mol g adductor muscle}^{-1}$  of strombine and alanopine. Since the adductor muscle accounts for 5.4% of wet mass (excluding shell) (Baldwin and Morris, 1983), a 10 g animal would have a 0.54 g adductor. Thus, a 10 g animal hydrolyzes  $10.9 \mu\text{mol}$  of arginine phosphate,  $1.2 \mu\text{mol}$  of ATP, and accumulates  $0.4 \mu\text{mol}$  of strombine and alanopine during 5 min of swimming. This converts to  $10.9 \mu\text{mol ATP}$ ,  $1.2 \mu\text{mol ATP}$ , and  $0.6 \mu\text{mol ATP}$  for the arginine phosphate, ATP, and strombine/alanopine, respectively, for a total of  $12.7 \mu\text{mol ATP}$  from anaerobic sources.

The aerobic contribution to swimming can be estimated from Baldwin and Lee (1979) who found a difference of  $105.6 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  between active and resting *Limaria*. This means a 10 g animal (excluding shell) consumes

3.9  $\mu\text{mol}$  of oxygen while swimming for five minutes, which is equivalent to 23.4  $\mu\text{mol}$  of ATP.

Combining the aerobic and anaerobic energy expenditures gives a minimum cost of transport for swimming *Limaria* of  $66 \text{ J kg}^{-1} \text{ m}^{-1}$ . (Since aerobic energy only accounted for 65% of the energy expended during swimming,  $43 \text{ J kg}^{-1} \text{ m}^{-1}$  is an underestimation of the minimum cost of transport.) This value is well above the regression of  $\log_{10}$  cost of transport vs.  $\log_{10}$  mass for other swimming invertebrates (Fig. 2; regression line from Full, 1997; the value for *Limaria* was converted to  $3.12 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$  for comparison). It is, in fact, four times larger than the average cost of transport for an equal-sized swimmer [ $0.75 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ; calculated from the regression equation  $\log_{10} \text{COT}_{\min} = 0.12 - 0.25 \log_{10} m$ , where  $\text{COT}_{\min}$  is the minimum cost of transport in  $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$  and  $m$  is mass in g; standard error of the estimation = 0.16; regression points from Full (1997, Figure 12.13)] and is beyond two standard errors of the estimation for this regression line.

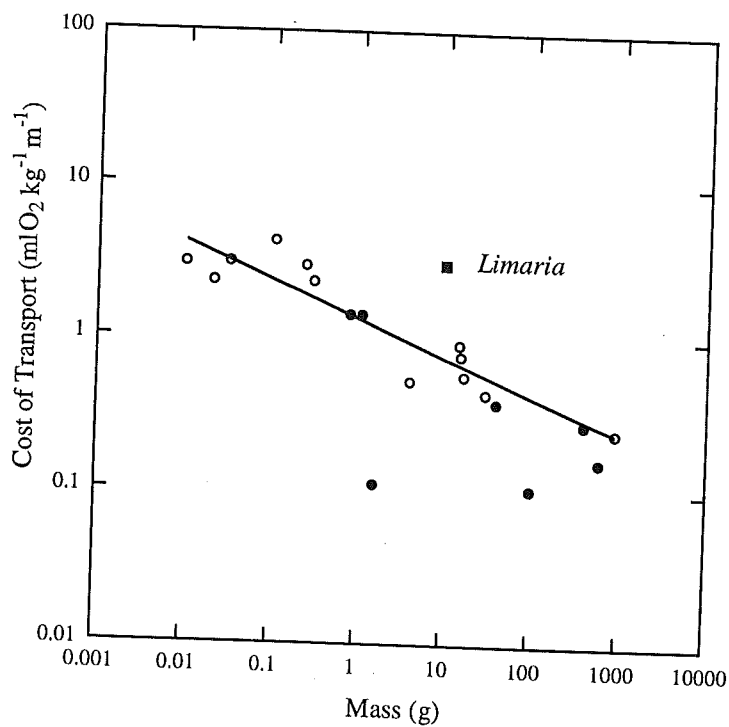


FIGURE 2 Minimum cost of transport of *Limaria* compared with that of other swimming invertebrates. The regression line for paddling swimmers (open circles) and the data points for jetting swimmers (closed circles) are from Full (1997).

The reasons for this large cost of transport are probably multiple. Unlike all of the values in the regression from Full (1997), our measure of cost of transport incorporated both aerobic and anaerobic energy expenditure. Donovan *et al.* (1999) found that anaerobic metabolism accounted for 54% of minimum cost of transport in the abalone *Haliotis kamtschatkana*, and they argued that transport costs for many invertebrates are probably underestimated if anaerobic energy sources are not incorporated. However, even our estimate of aerobic cost of transport ( $43 \text{ J kg}^{-1} \text{ m}^{-1}$ , which converts to  $2.04 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) is beyond two standard errors of the estimation for the swimming invertebrate regression line, indicating that other factors must be at work. The cost of carrying a shell, no matter how reduced, must be a factor. As well, unlike the shelled nautilus whose cost of transport is small (O'Dor *et al.*, 1990), *Limaria* is not neutrally buoyant and must therefore expend energy to generate lift as well as to overcome drag. O'Dor (1988) found that 30–90% of the total force generated by swimming squid went for compensating negative buoyancy. However, freely moving squid exhibit "climb and glide" swimming, in which they swim at an upward angle then coast downward, which reduces total cost of transport by 35% (O'Dor, 1982; 1988). *Limaria* may also employ such a tactic as demonstrated by their undulating swimming. Last, by swimming hinge-hindmost, *Limaria* swim with their extensive tentacles facing forward. This is contrary to other jetters, such as squid and octopus, which swim with their arms trailing behind them, presumably decreasing drag (O'Dor, 1982).

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