Energetics of Swimming and Crawling in the Lion Nudibranch, *Melibe leonina*

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Abstract. The opisthobranch *Melibe leonina* both swims and crawls. Elective response between these two modes makes *M. leonina* a model organism for studies of gastropod locomotion. The effect of activity on the metabolic rate of *M. leonina* was investigated in three phases: (1) oxygen consumption rates were measured during alert, crawling, and swimming states; (2) anaerobic energy output was investigated by measuring whole-body levels of anaerobic enzymes; and (3) estimates of net cost of transport (COT_{net}) for swimming and crawling were established. *Melibe leonina* exhibited a two-fold increase in oxygen consumption between alert (234 μL O_2 h^{-1} for a 10 g animal) and crawling (477 μL O_2 h^{-1}) states, and a six-fold increase in oxygen consumption between alert and swimming (1380 μL O_2 h^{-1}) states. Opine dehydrogenases were not detected in whole body tissue and only low levels of lactate dehydrogenase (0.23 IU g wet tissue^{-1} min^{-1}) were found. This indicates that both swimming and crawling are supported aerobically in *M. leonina*. Swimming COT_{net} (6 mL O_2 kg^{-1} m^{-1}) and crawling COT_{net} (5 mL O_2 kg^{-1} m^{-1}) were similar to each other. However, when these values were compared to those of other swimming and crawling invertebrates, it was found that *M. leonina* displayed the typically high cost of gastropod crawling but swimming COT fell above the 95% confidence interval for energy costs associated with invertebrate swimming.

INTRODUCTION

Metabolic energy must be converted into mechanical energy to generate the forces and power required for locomotion. These expenses establish boundaries on foraging, larval dispersal, and reproduction, and ultimately influence an animal's ecology. Invertebrate running, swimming, and flying have been widely studied (see Full, 1997). However, some gastropods, among them *Melibe leonina* (Gould, 1853), swim as well as crawl, and the energetics of gastropod swimming have not yet been investigated.

Three general modes of opisthobranch swimming have been recorded: (1) parapodial or mantle flapping (*Gastropteron, Hexabranchus,* and *Aplysia*); (2) dorso-ventral undulation (*Tritonia* and *Pleurobranchaea*); and (3) lateral bending (*Melibe* and *Dendronotus*) (Farmer, 1970). Swimming in *M. leonina* can be evaluated in five parts. The behavior begins when (1) the oral hood closes and the anterior part of the foot detaches from substrate; (2) the sole of the foot folds in half while the body compresses laterally; and (3) lateral bending causes oral hood rhinophores to encounter the tail. The swimming bout

ends when (4) the anterior part of the foot locates suitable substratum and (5) the anterior foot attaches to the substratum, ensuring settlement (Hurst, 1968; Lawrence, 1997). Swimming bouts can last for a few seconds to well over an hour (Lawrence, 1997; personal observation). Individual animals often make several attempts to settle to the substratum but the foot does not stay attached (most often observed in animals 1 to 5 grams) (Hurst, 1968; Ajeska & Nybakken, 1976; Lawrence, 1997, personal observation) and animals will on occasion stop swimming without the foot being engaged on the substratum (Agersborg, 1923; Lawrence, 1997).

The function of swimming in *M. leonina* remains unclear. Agersborg (1919, 1921), having observed masses of *M. leonina* copulating, suggested that swimming is associated with reproduction. Swimming has also been linked to foraging (Hurst, 1968) and population dispersal (Mills, 1994). Swimming most often occurs at night in California populations where *M. leonina* individuals travel between stipes of the kelp *Macrocystis integrifolia* (Ajeska & Nybakken, 1976). Laboratory studies have shown that *M. leonina* spontaneously swims more than 20 times per hour during the night and approximately once per hour during the day (Watson et al., 2001). In Washington, *M. leonina* lives mainly on the eelgrass *Zos-*

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tera marina, and individuals have been observed swimming spontaneously between eelgrass blades (personal observation). Studies have shown that swimming can be readily elicited by chemical (1M KCl) and tactile stimuli (light, touch, change in water flow) (Hurst, 1968; Jing & Gillette, 1995; Lawrence, 1997, personal observation). As well, swimming can be stimulated by the predatory seastar *Pycnopodia helianthoides* (Lawrence, 1997).

Crawling is the other form of locomotion used by *M. leonina.* Gastropods locomote by generating rhythmic waves on the ventral surface of their pedal musculature, and wave patterns differ among species (Miller, 1974). These patterns are determined by the direction the wave travels and the portion of the foot it occupies. *Melibe leonina* uses monotaxic, indirect waves for crawling (Bickell-Page, 1991). In this case, the waves cover the entire foot and travel in the direction opposite of snail movement. A thin film of mucus is secreted by pedal glands to allow gliding over and adhesion to the substratum, and this probably explains the generally high energetic costs of this form of locomotion (Denny, 1980).

While there are many marine gastropods that utilize both swimming and crawling for movement, the energy costs associated with swimming and how they compare to that of crawling in these organisms is unknown. In this study, the energetics of *Melibe leonina* were investigated in three phases. In the first phase, the rate of oxygen consumption of *M. leonina* was measured during alert, crawling, and swimming activity states to determine aerobic energy costs. Second, anaerobic energy sources were investigated by measuring the levels of enzymes which regularly contribute to anaerobic metabolism in invertebrates. Last, estimates of the cost of transport for both swimming and crawling for *M. leonina* were established.

METHODS

Experimental Animals

Melibe leonina individuals were collected from Padilla Bay, Washington along with eelgrass from collection sites. They were gathered by snorkeling or SCUBA when population distributions were patchy and low in abundance and by hand dipnets when numerous. They were maintained at Shannon Point Marine Center, Anacortes, Washington, held in sea-tables with a constant flow (500 mL min^{-1}) of fresh seawater. Ambient temperature at which the nudibranchs were held ranged from 8 to 12°C with an average temperature of 10°C and an average salinity of 30.7 ppt. The sea-tables were located under a window, establishing photo-periods of ambient light regime.

The animals were fed with associated eelgrass fauna and with supplemental weekly feedings of *Artemia* sp. Experiments were conducted within 2 days of collection for determination of aerobic energy expenditure and cost

of transport. Nudibranchs survived beyond 30 days in sea-tables.

Aerobic Energy Consumption

For each oxygen consumption trial, *M. leonina* (n = 19; 1.15–24.17 g range in wet body mass) were placed individually in one of two round, perspex respirometers (140 mL or 650 mL depending on animal size). An oxygen electrode (Cameron Instrument Company, Pt. Aransas, Texas) was placed in the respirometer chamber and the chamber was placed in a temperature controlled cooling jacket. The electrode was connected to an oxygen monitor (DI 2000, Cameron Instrument Company) which in turn was connected to a data acquisition system (DataQ, Akron, Ohio) allowing the oxygen tension in the respirometer to be monitored continuously. Oxygen consumption rates were determined during three states of activity for each animal: alert (the nudibranch was stationary and displayed no obvious contractions of the oral hood when the oral hood was expanded), crawling (hood was extended while the foot of the nudibranch was attached to the substratum with apparent forward movement), and swimming (posterior portion of foot was detached from substratum and body exhibited lateral undulations). Swimming and crawling were initiated through tactile stimulation. Only animals that exhibited all three states for a minimum of 5 minutes each were used for analysis.

Anaerobic Energy Consumption

In order to determine which pyruvate reductase endproducts might be produced by *M. leonina* during anaerobiosis, whole tissue samples of the nudibranch (n = 3) were analyzed for a range of pyruvate reductase enzymes. The nudibranchs were individually homogenized in a 2 mL buffer: 1 g animal ratio (50 mM imidazole-HCl buffer, 1 mM EDTA, 1 mM dithiothreitol, pH 7.2) with an Ultra-Turrax homogenizer. Homogenates were centrifuged for 2 minutes at 3000 rpm and 25°C. Supernatants were placed on ice and assayed within 1 hr. Pyruvate reductase activity was determined by following the reduction of NADH at 340 nm using a spectrophotometer at 25°C. Controls lacking substrate were run to allow for non-specific activity.

The compositions of the reaction mixtures for the various pyruvate reductases were as follows: lactate dehydrogenase, 2.5 mM pyruvate, 0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0; tauropine dehydrogenase, 80 mM taurine, 2.5 mM pyruvate, 0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0; octopine dehydrogenase, 20 mM arginine, 2.5 mM pyruvate, 0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0; strombine dehydrogenase, 200 mM glycine, 2.5 mM pyruvate, 0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0; lysopine dehydrogenase, 100 mM lysine, 2.5 mM pyruvate,

0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0; alanopine dehydrogenase, 100 mM alanine, 2.5 mM pyruvate, 0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0; β-alanopine dehydrogenase, 100 mM β-alanine, 2.5 mM pyruvate, 0.15 mM NADH, 50 mM imidazole-HCl buffer, pH 7.0.

Cost of Transport (COT)

Total cost of transport (COT_{tot} mL O_2 kg^{-1} m^{-1}) is used as a measure of aerobic energy expenditure per unit of distance traveled and is defined as the total amount of oxygen needed to move a unit of animal mass over a unit of distance. Cost of transport is calculated by dividing the mass-specific oxygen consumption of a moving animal by its speed (Schmidt-Nielsen, 1972). In comparison, net cost of transport (COT_{net}) is calculated by subtracting standard oxygen consumption (alert) from active oxygen consumption rates (swimming or crawling) before dividing the result by the speed of locomotion.

Since it was impossible to simultaneously measure mass specific oxygen consumption and swimming speed in the respirometer, an estimate of the net cost of transport during swimming was determined in the following manner. Average speed of *M. leonina* swimming in the respirometer was estimated by placing *M. leonina* (n = 10; average mass 10.06 ± 1.46 g) individually in a respirometer and counting the number of undulations during an approximately 5 min swimming session. The distance each animal was able to travel during the swimming session was then estimated by placing the same animal in a glass aquarium with motionless water and measuring the distance covered in 1 minute while counting the number of undulations. The average distance covered in one undulation (from the tank) was then integrated with the number of undulations in the respirometer to give an average speed. COT_{net} was then calculated by subtracting the alert rate of oxygen consumption from the swimming rate of oxygen consumption for a 10 g animal (see Results) and dividing by the average swimming speed.

Crawling COT_{net} was estimated in a similar manner. To determine the average speed of *M. leonina* in the respirometer, two 1 cm grids were used. The first was fixed to the outside of the respirometer so the entire chamber was covered. The second was hand-held and used to trace the route the animal was able to travel. *Melibe leonina* (n = 10; average mass 10.27 ± 0.69 g) were placed individually in a respirometer, and the route the animal traveled was traced on the hand-held 1 cm grid while the time spent crawling was recorded. The distance traveled was then calculated from the traced route and divided by the crawling time to determine crawling speed. COT_{net} was then calculated by subtracting the alert rate of oxygen consumption from the crawling rate of oxygen consumption for a 10 g animal (see Results) and dividing by the average crawling speed.

RESULTS

Aerobic Energy Consumption

Oxygen consumption increased with increasing animal mass for all three activity states (Figure 1). The slopes of the regression equations were not statistically different ($F_{0.05,51} = 0.123$, $P > 0.5$; ANCOVA) which indicates that mass affects metabolic rate in the same manner for all three states. The intercepts, however, were statistically different ($F_{0.05,53} = 52.18$, $P < 0.001$; ANCOVA), with each intercept falling into its own subgroup (all $P < 0.05$; Tukey's multiple comparison test) indicating that the swimming state was metabolically more expensive than crawling, which was in turn more expensive than alert.

Oxygen consumption for a representative 10 g *Melibe leonina* was calculated from these regression equations. Swimming oxygen consumption rates were the highest (1380 μL O_2 h^{-1}) followed by crawling oxygen consumption (447 μL O_2 h^{-1}) and alert oxygen consumption (234 μL O_2 h^{-1}). Thus, aerobic expansibility (the ratio between maximal sustainable oxygen consumption and inactive oxygen consumption) was 5.9 for a 10 g swimming *M. leonina* and 1.9 for a 10 g crawling *M. leonine.*

Anaerobic Energy Consumption

All known opine dehydrogenases were absent from *M. leonina* body tissue, and only small amounts of lactate dehydrogenase were present (Table 1).

Cost of Transport

To compare the two modes of locomotion (crawling and swimming), COT_{net} for a 10 g *M. leonina* was calculated for each. Average speed of crawling was 4.3 ± 3.1 m h^{-1} and of swimming was 19.8 ± 6.7 m h^{-1}. From these average speeds and from the differences in active and alert oxygen consumptions, COT_{net} was estimated to be 5 mL O_2 kg^{-1} m^{-1} during crawling and 6 mL O_2 kg^{-1} m^{-1} during swimming.

DISCUSSION

Melibe leonina appears to be a typical opisthobranch with respect to standard rates of aerobic and anaerobic energy expenditure. Carefoot (1967) reported a standard V_{O2} of 960 μL O_2 h^{-1} for 30 g *Archidoris pseudoargus*, 720 μL O_2 h^{-1} for 30 g *Aplysia punctata*, and 135 μL O_2 h^{-1} for 3 g *Dendronotus frondosus*. Ajeska & Nybakken (1976) measured respiration rates for *Melibe leonina* from Monterey Bay, California. Their largest animals (8–9 g) consumed approximately 162 μL O_2 h^{-1} (temperature not specified), comparable to 234 μL O_2 h^{-1} for a 10 g *M. leonina* found in this study. Ajeska & Nybakken (1976) concluded that juvenile *M. leonina* consume more oxygen per unit body mass than adults and attributed this to an increased activity level for juveniles. However, this study
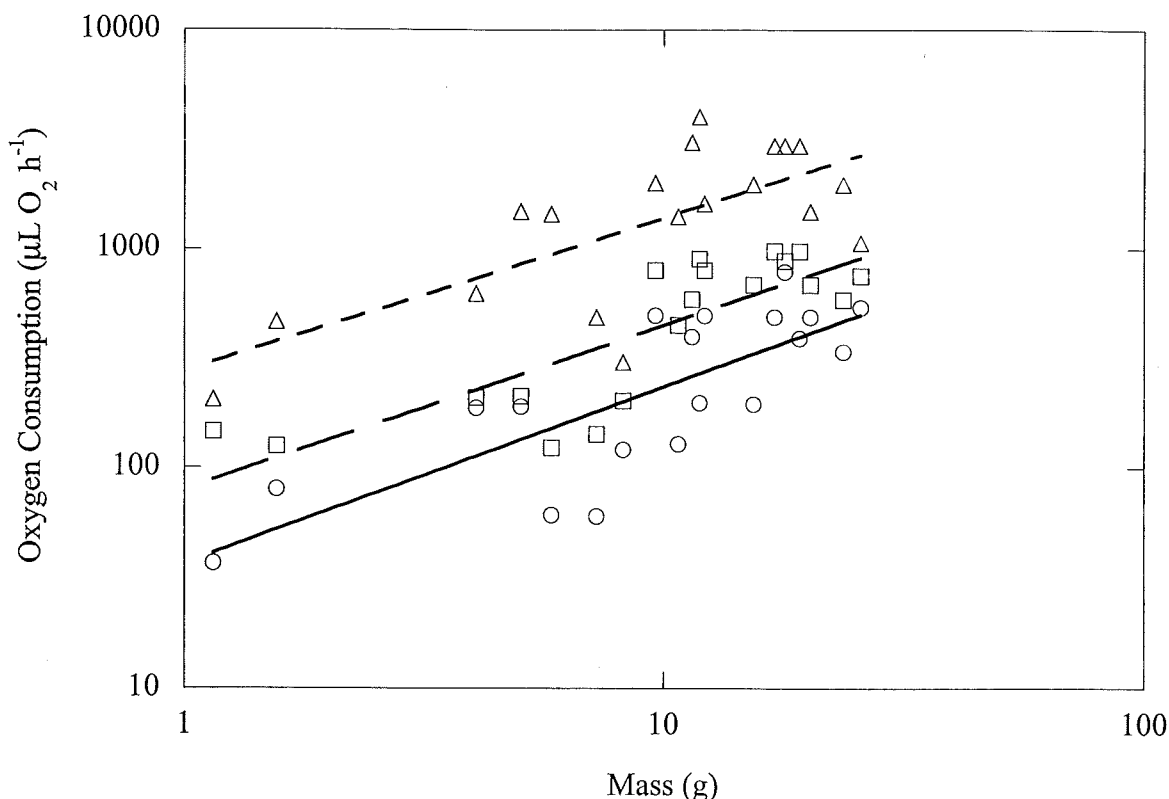
Figure 1.   Regression of oxygen consumption (μL O_2 h^{-1}) on mass (g) for *Melibe leonina* in the alert (circle), crawling (square), and swimming (triangle) states. The regression equations for each state of activity were: *log alert* V_{O2} = 1.56 + 0.81 *log mass*, r^2 = 0.61; *log crawling* V_{O2} = 1.90 + 0.75 *log mass*, r^2 = 0.67; and *log swimming* V_{O2} = 2.44 + 0.70 *log mass*, r^2 = 0.51.

shows that smaller *M. leonina* consume relatively more oxygen than larger *M. leonina* on a per-gram basis (indicated by the log V_{O2} vs. log mass slopes of 0.70 to 0.81) even when activity levels are accounted for, as would be expected from simple scaling principles.

Melibe leonina is capable of periods of sustained swimming (one animal swam for 1.5 hr in the respirometer, and was still swimming when the run was terminat-

Table 1

Pyruvate reductase activities in whole body tissue of *Melibe leonina* (n = 3). Enzymes which were not detected are designated by nd.

Enzyme	Activity (IU g^{-1} min^{-1}; 25°C) (mean ± SE)
Lactate dehydrogenase	0.23 ± 0.02
Tauropine dehydrogenase	nd
Octopine dehydrogenase	nd
Strombine dehydrogenase	nd
Lysopine dehydrogenase	nd
Alanopine dehydrogenase	nd
β-Alanopine dehydrogenase	nd

ed). This can lead to functional hypoxia which arises when oxygen is present in the environment but insufficient amounts are being transported to working muscles. In addition to aerobic energy sources, many invertebrates rely on anaerobic energy during periods of functional hypoxia, and many gastropods rely on pyruvate reductases during sustained functional hypoxia when compared to other anaerobic sources during environmental hypoxia (de Zwaan, 1983). *Melibe leonina*, however, appears to rely solely on aerobic energy sources since only minimal levels of lactate dehydrogenase (LDH) and no other known pyruvate reductases were present in whole animal tissue (Table 1). This LDH value is one to two orders of magnitude smaller than that of other marine invertebrates that readily utilize LDH for anaerobic metabolism. For example, the foot of the abalone *Haliotis kamtschatkana* was found to contain 20.1 IU g wet muscle^{-1} min^{-1} of tauropine dehydrogenase (TDH) and 9.1 IU g wet muscle^{-1} min^{-1} of LDH while the adductor muscle contained 29.0 IU g wet muscle^{-1} min^{-1} and 1.2 IU g^{-1} wet muscle^{-1} min^{-1} of TDH and LDH, respectively. Combined, these enzymes contribute 21% of the energy needed for abalone to locomote (Donovan et al., 1999). The low levels of LDH and the absence of opine dehydrogenases in

M. leonina tissues are consistent with levels found in other nudibranchs (Livingstone et al., 1983; Livingstone et al., 1990; Sato et al., 1993). This indicates that nudibranchs in general may rely on aerobic energy sources for locomotion.

It was determined that swimming is a relatively expensive form of locomotion for *Melibe leonina,* which required more aerobic energy to swim than to crawl (Figure 1). Oxygen consumption increased nearly six-fold during swimming when compared to the alert state, in contrast to a nearly two-fold increase for crawling. Past studies have indicated that gastropod crawling is expensive relative to other forms of locomotion, possibly because of mucus production. The terrestrial slug *Ariolimax columbianus* expends large amounts of energy to crawl (Denny, 1980) as do marine gastropods (Houlihan & Innes, 1982; Innes & Houlihan, 1985; Donovan & Carefoot, 1997). However, it appears that lateral bend swimming exhibited by some nudibranchs is just as costly.

Net costs of transport for crawling and swimming in *M. leonina* were similar to each other, but remarkable was how these two modes of locomotion compared with other crawling gastropods and swimming invertebrates (Figure 2). *Melibe leonina* crawling COT_{net} (5 mL O_2 kg^{-1} m^{-1}) fell within the range of other marine gastropods. However, swimming COT_{net} for *M. leonina* (6 mL O_2 kg^{-1} m^{-1}) was greater than that of other swimming invertebrates, falling above the 95% confidence interval for the regression equation of log COT vs. log mass for swimming invertebrates (Figure 2; data for the regression from Full [1997]). This indicates that swimming, generally the least costly mode of locomotion, is very costly for the *M. leonina* used in this study. In fact, a 10 g invertebrate swimmer would be expected to have a COT of 0.75 mL O_2 kg^{-1} m^{-1} based on Full's (1997) regression of log swimming V_{O2} on log mass. The high cost of *M. leonina* swimming is probably due to the high levels of aerobic energy needed to produce the relatively slow swimming speeds.

It is important to mention, however, that costs of transport are generally measured by oxygen consumption rates and thus reflect aerobic energy expenditure only. While adequate for the highly aerobic *M. leonina,* this may not hold true for other marine invertebrates that readily use anaerobic energy sources for metabolism. Therefore, to attain a more complete picture of COT, particularly for marine invertebrates, some assessment of anaerobic contribution to COT must be made (Donovan & Carefoot, 1997; Donovan et al., 1999).

If anaerobic energy contribution were included for swimming invertebrates, the regression line of log COT vs. log mass determined by Full (1997) would be higher. We can speculate about the increase for a 10 g swimmer based on some comparisons with other known invertebrate swimmers. For example, if the expected 0.75 mL O_2 kg^{-1} m^{-1} COT for a 10 g swimming invertebrate rep-

resented 65% of the total contribution to swimming as seen in the highly aerobic *Limaria fragilis* (Baldwin & Morris, 1983), the observed COT would be 1.15 mL O_2 kg^{-1} m^{-1}. If the 10 g swimmer relied heavily on anaerobic energy, as does the scallop *Placopecten magellanicus,* the 0.75 mL O_2 kg^{-1} m^{-1} may represent only 6% of the total energy expended (Livingstone et al., 1981), and the observed COT would be 12.5 mL O_2 kg^{-1} m^{-1} which falls above the COT_{net} of *M. leonina.* However, organisms comprising Full's (1997) regression for swimming invertebrates are generally long-range swimmers (i.e., squids, salps, copepods), so the rise in intercept of the line would probably be in the range of *Limaria* rather than *Placopecten,* a short-range, quick-burst swimmer. In this case, even if anaerobic energy were accounted for, *M. leonina* COT represents a higher value than other swimming invertebrates.

Although Lawrence (1997) reported that *M. leonina* has some control over swimming direction despite currents, it is important to note that long-distance movement of *M. leonina* likely involves the passive use of currents (Willows, 2001) and this would drastically reduce COT. When *M. leonina* begins a swimming bout it first swims up then proceeds in a lateral direction (Lawrence, 1997) and this may be typical of lateral bend swimmers (Jing & Gillette, 1995). This would serve to propel them into the water column where they would likely catch a current. Mills (1994) noted that swimming *M. leonina* was most often observed in Washington during winter months when there had been two consecutive high tides with very little drop between them. In this case, it was speculated that flushing of shallow bays had transported *M. leonina* individuals some distance as there were no known local populations. That *M. leonina* can move long distances is well established. Along with Mills's (1994) observations noted above, Ajeska & Nybakken (1976) observed a large population of *M. leonina* (20,000 individuals) that subsequently disappeared from a kelp bed within a short period of time, with no apparent signs of mortality. This population was replaced 2 months later by another 2000 individuals. Thompson & Crampton (1984) report that *Melibe fimbriata* of the Indian Ocean migrated to the Mediterranean Sea, via the Red Sea, by means of its lateral bend swimming. Migrations associated with *M. leonina* swimming, along with the aid of currents, may provide for earlier patch exploitation (Agersborg, 1921; Hurst, 1968; Lawrence, 1997). Population dispersal and escaping from predation are also activities that appear to be augmented by *M. leonina* swimming.

Ajeska & Nybakken (1976) reported that *M. leonina* in Monterey Bay, California regularly swims short distances between kelp stipes. In this case, currents may not be as much help and energy expenditure may be substantial. However, given that crawling COT is as expensive as swimming COT for *M. leonina,* and given that the distance a *M. leonina* must crawl to travel to a comparable
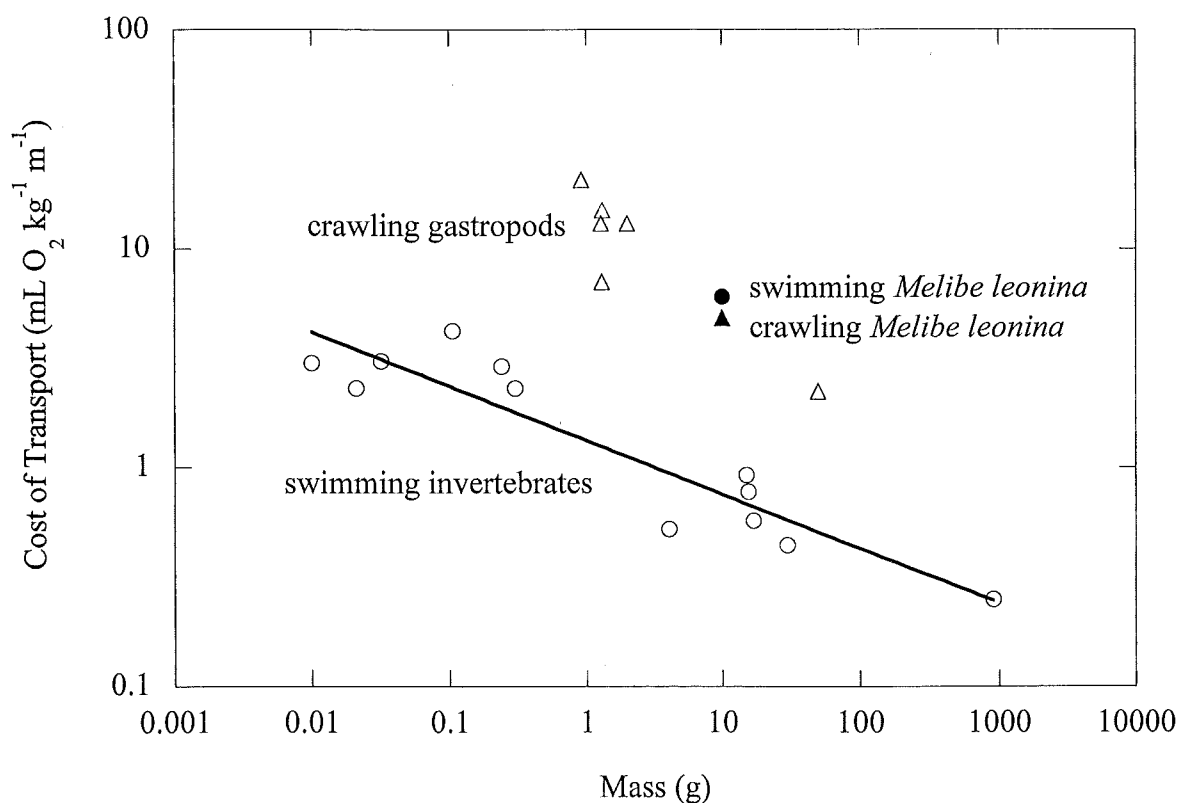
Figure 2. Cost of transport of crawling (closed triangle) and swimming (closed circle) *Melibe leonina* compared to those of other crawling (open triangle) and swimming (open circle) invertebrates. Data points for crawling marine gastropods are from Houlihan & Innes (1982), Innes & Houlihan (1985), and Donovan & Carefoot (1997). The regression line for swimming invertebrates is from Full (1997).

height on another stipe (several meters down one stipe, over to the next kelp, several meters up the next stipe), swimming is undoubtedly the most economic form of transportation in this case. This may also hold true for *M. leonina* traveling between eel grass blades in Puget Sound, Washington.

It is interesting that *M. leonina* apparently relies on aerobic energy sources for locomotion, but not surprising given its ability to swim for extended periods. Since *M. leonina* lacks the appearance of any oxygen uptake mechanism, it may rely on simple diffusion of oxygen from the environment to the working muscles which are closely associated with the surface epithelium (Lawrence, 1997). Hurst (1968) reported that the body wall is well vascularized, with haemal sacs occurring throughout the muscle network. As well, blood is redistributed to the dorsal cerata during swimming, which may aid in oxygen uptake. *Melibe leonina* in this study was collected in a channel where there was high water flow exchange allowing the ready uptake of oxygen across the skin during its highly aerobic swimming.

Currents notwithstanding, lateral bend swimming may be expensive due to energy expended in both accelerating

and decelerating the animal's mass and its added mass as it moves through water. This swimming behavior is considered unsteady, non-directional swimming (Daniel, 1984). Such swimming produces a thrust that results in higher costs of transport than steady directional swimming (Daniel, 1985). *Melibe leonina* can somewhat minimize energy expended during swimming in a few ways. Lateral compression of the body and oral hood during swimming produces an increase in lateral surface area which would produce more thrust (Lawrence, 1997). As well, asymmetrical swimming resulting in a foot sculling motion may serve to propel the nudibranch through the water column (Daniel, 1984). These changes in morphology, along with periodic suspended motionless floating during swimming (Lawrence, 1997), may provide some energy savings and increase locomotion efficiency for *M. leonina*.

There are other opisthobranchs with swimming forms that are more directional than that of *Melibe leonina*. It would be of interest to evaluate energy costs of these taxa to determine if gastropod swimming is truly a more expensive form of locomotion than the swimming of other invertebrates.

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