

Original papers

Cost and speed of locomotion for rotifers

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Summary. The hypothesis that the ciliary locomotion of rotifers is size limited and that it accounts of a significant portion of the energy budget was investigated using the genera *Brachionus* and *Asplanchna*. Speed of movement was measured among clones of different size in *Brachionus*, which shows little size variation through development. The same tests were done among individuals of different size within a clone of *Asplanchna*, which shows significant post-embryonic size increase. In both cases, relative speed (body lengths per second) decreased significantly as body size increased. On this basis, an ecologically limiting size for ciliary locomotion is proposed. The actual cost of locomotion was measured for *Brachionus*; it is 62% of total metabolism, even though the theoretical (calculated) power requirements are well below 1% of total metabolism. Ciliary locomotion in the Rotifera thus appears to be extremely inefficient (low ratio of theoretical to actual power requirements). This hypothesis is supported indirectly by the sensitivity of speed to total metabolic rate in *Brachionus*: both plateau over the temperature range 20–32° C and decline in parallel outside this range. Unexpectedly high actual cost of locomotion is proposed as an important disadvantage of the Rotifera, partly offsetting the advantages accruing to them from small body size.

Introduction

The rotifers are among the largest of the actively swimming metazoans to rely on simple cilia for locomotion. Absence of ciliary locomotion in animals larger than the rotifers suggests that the rotifers are approaching the upper body size limits at which ciliary locomotion is evolutionary feasible. The possible size constraints on ciliary locomotion include performance (speed) and energy efficiency. Performance limitation occurs if cilia are unable to move an organism at velocities necessitated by its ecological requirements. Because of structural considerations, including limitations on the length and rigidity of the cilia (Sleigh and Blake 1977), cilia may be unable to fulfill certain performance requirements irrespective of energy efficiency. Decreasing energy efficiency with increasing body size might also preclude the use of cilia as a locomotion mechanism in large organisms. Our recent study of physiological aspects of sexual dimorphism in the Rotifera suggests that

both constraints are important in this group (Epp and Lewis 1979).

Brachionus plicatilis and the rotifers in general show a great degree of sexual dimorphism. The males are smaller than the females in most planktonic species and they are specially adapted for finding females. The males are able to swim faster than the females; this increases the probability of contact with a female. We have hypothesized that the higher swimming speed of males is a direct adjunct of their smaller size (Epp and Lewis 1979). We have also calculated the theoretical power requirements for swimming and have found that, despite their higher swimming speeds, males have a lower theoretical power requirement than females (Epp and Lewis 1979). The theoretical power requirements are, however, low in both males and females in relation to total metabolism. Theoretical power represents only the energy required per unit time to overcome the resistance of water to an object of specific size moving at a specific velocity. Theoretical power does not include inefficiencies in translating stored energy into movement. Energy may be lost through intermediary metabolism, coupling of metabolic pathways to ciliary movement, or inefficiency of cilia in translating metabolic power to movement. Thus even though the theoretical power required for movement is low, energy expenditure on movement may be adaptively significant if the ratio of theoretical to actual power requirement for movement is low. Unfortunately, the actual cost of movement in small invertebrates has very seldom been measured. In this paper we examine the performance of six clones of *Brachionus plicatilis* and one clone of *Asplanchna sieboldi*. We also determine the actual cost of movement in one clone of *B. plicatilis* and compare this to the theoretical power requirements.

Materials and methods

Six clones of *Brachionus plicatilis* were used for determination of speed of movement. Clone GP-1 originated in Boulder County, Colorado (Epp and Lewis 1979). Other clones of *B. plicatilis* were from the following locations (the accompanying symbols preceding the source are used throughout this paper): Austria (Aus), Spain (Sp), France (Fr), Los Angeles (La), MaCay Bay, Fla. (MB). One clone of *Asplanchna sieboldi* (10C6) was used to determine the performance-size changes accompanying development.

Body lengths of both *B. plicatilis* and *A. sieboldi* were determined with a filar-type ocular micrometer. All animals

were lightly anesthetized with MS-222 (tricaine methanesulphonate) prior to this measurement. This treatment prohibited movement without causing retraction of the rotifer. Total body length was measured from the base of the body (base of the foot in *Brachionus*) to the base of the coronal cilia, thus excluding the length of the coronal cilia and the foot. For *Asplanchna*, each experimental animal was measured. For *Brachionus*, pre-ovigerous females were randomly selected from each of the *Brachionus* clones for determination of body length.

Activity was determined with a substage grid system (Epp and Lewis 1979). The substage was coupled to a water bath whose temperature could be controlled within 0.025° C. Temperature within the test chamber was obtained with a micro-thermistor probe and was found to be within 0.25° C of that in the water bath.

Most activity measurements lasted 1 min and were conducted at 22.5° C, the temperature of acclimation. One experiment concerned the effect of temperature on speed of movement. This experiment involved activity measurements of *Brachionus* clone GP-1 at temperatures ranging from 14 to 34° C in increments of 2° C. Experimental animals were placed in the test chamber for 3 to 5 h of acclimation prior to the measurements.

Respiration measurements were made at acclimation temperature (22.5° C) with a Cartesian diver micro-respirometer (Epp and Lewis 1979). Only the open-necked variety was used. Total gas volume per diver was less than 1 microliter. Individual *Brachionus plicatilis* males were placed in the divers with and without anesthetization with MS-222. The difference between metabolism of anesthetized and unanesthetized males is taken as a direct estimate of the actual cost of movement. The males of *Brachionus* are desirable test animals for this type of experiment, as they lack a digestive system and accompanying structures such as mouthparts and digestive glands. Thus the difference in metabolic expenditure between anesthetized and non-anesthetized males will most closely reflect the cost of movement as distinct from metabolic costs associated with feeding that might also be affected by anesthetization.

Results

Mean body lengths of the six *Brachionus plicatilis* clones were compared by one-way analysis of variance in which the null hypothesis was that body size is uniform (Table 1). This hypothesis was rejected, indicating a significant difference in body size among clones (d.f. 5,114; $P < 0.001$). Absolute speeds ($\mu\text{m}\cdot\text{sec}^{-1}$) of the different clones were also tested by analysis of variance in which the null hypothesis was that speed is uniform among clones (Table 1). This hypothesis was rejected, indicating a difference in absolute speed among clones (d.f. 5,144; $P < 0.001$). Size and speed (means for each clone) were then tested for relationship by Model II regression after log transformation of both variables. There is some suggestion of a positive relationship with a slope well below 1.0, but it is not significant ($P = 0.15$). Whether there is a positive relationship of slope < 1.0 or no relationship, relative speed (body lengths per second) decreases with increasing size, which is the main point of interest here.

Activity of *A. sieboldi* is shown in Fig. 1. Body length and speed are fitted to the allometric equation $\log Y = b \log X + \log a$ in which X represents length in μm and Y

Table 1. Lengths and absolute speeds for six clones of *Brachionus plicatilis*. Values for both size and speed represent mean values for 25 individuals per clone

Clone	MB	LA	AUS	FR	GP-1	SP
Length, μm						
mean	183	189	266	286	290	292
Std. error	3.1	5.0	4.6	4.9	4.3	5.3
Speed, $\mu\text{m}\cdot\text{sec}^{-1}$						
mean	620	650	720	770	690	610
Std. error	30	30	30	20	20	20

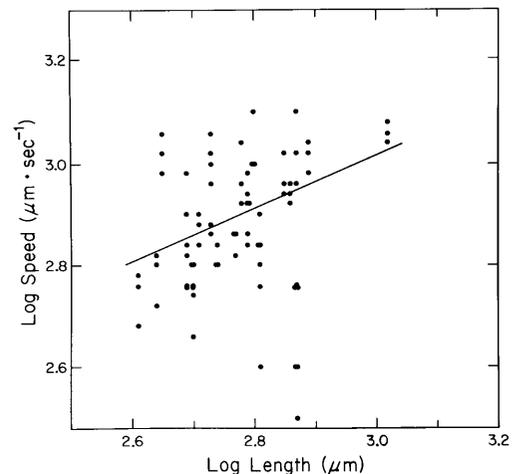


Fig. 1. Points and regression lines showing the relation of swimming speed to body size in *Asplanchna sieboldi*

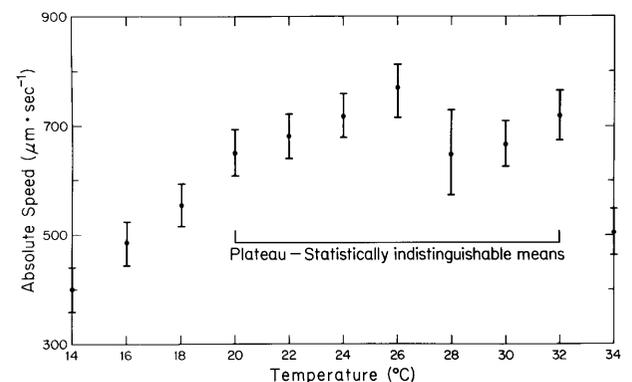


Fig. 2. Absolute speeds of *Brachionus plicatilis* and 95% confidence intervals for mean speed at different temperatures. Mean absolute speeds over the temperature range 20–32° C are statistically indistinguishable at $P = 0.05$

is speed in $\mu\text{m}\cdot\text{second}^{-1}$. The relation between log speed and log length is statistically significant (Model II regression: $P = 0.01$; $b = 0.41$). Thus absolute speed increases with increasing body size, but at a rate less than the rate of increase in size. Relative speed therefore decreases with increasing size within clone 10C6 of *Asplanchna*, just as it does among the six clones of *Brachionus*.

The effect of temperature on activity in *Brachionus* was analyzed by one-way analysis of variance in which the null hypothesis was that absolute speed is uniform across temperatures. This hypothesis was rejected (d.f. 10, 284; $P < 0.01$). There is evidence of a plateau in speed over the tem-

perature range 20° to 32° C and a decrease in speed below 20° and above 32° C (Fig. 2). The method of a posteriori contrasts (Snedecor and Cochran 1976) shows that mean speeds between 20 and 32° C are not distinguishable at $P=0.05$.

Metabolic rates of anesthetized and unanesthetized male *Brachionus* were compared using the Mann-Whitney test (Snedecor and Cochran 1976). The mean metabolic rate for unanesthetized males was $6.69 \times 10^{-4} \mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}$ (Standard error, 0.6). Metabolic rate of the anesthetized males was 62% of the rate for unanesthetized males ($4.17 \times 10^{-4} \mu\text{l ind}^{-1} \text{ h}^{-1}$; Standard error, 0.2) and the difference is significant ($P < 0.001$).

Discussion

Speed of movement

Speed among the six *Brachionus* clones ranged from 600 to $800 \mu\text{m} \cdot \text{sec}^{-1}$. Absolute speed increases with size through development in clone 10C6 of *Asplanchna sieboldi* and the mean speed is $800 \mu\text{m} \cdot \text{sec}^{-1}$. Sleigh and Blake (1977) have shown that organisms which move by means of simple cilia (principally protozoans) move at a fairly uniform rate of 1 mm/sec, which is close to that observed in the rotifers. Cilia in the Rotifera are restricted to the head region in contrast to the more widely distributed ciliation found in many ciliated protozoans. Despite the restriction of cilia to the head region, the rotifers are capable of achieving absolute speeds which are nearly equivalent to those of the protozoans, but the relative speed (body lengths/sec) of rotifers will of course be lower.

It is possible to view the decrease in relative speed with size as a reduction in performance. For *Brachionus*, relative speed decreases from 3.4 body lengths per second for the smallest clones (MB and LA) to only 2.1 body lengths per second in the largest (Sp and Gp-1). The decrease in relative speed must be explained by the increase in size rather than other morphological variation, as the clones are morphologically identical except for size. The relative speed of the smallest *Asplanchna* used in this study (411 μm) was only 1.6 body lengths per second. Gilbert (1977) has reported *A. sieboldi* reaching lengths of 1.5 mm. Based on the length-speed equation for *Asplanchna* (Fig. 1) we calculate the speed of such an animal as only 0.8 body lengths per second. Obviously, there is a finite limit on size above which the relative speed is no longer capable of sustaining a non-sessile organism. The rotifer *A. sieboldi* may be approaching this limit, which is set ecologically and evolutionarily by food gathering and predator avoidance.

Cost of locomotion

A number of determinations of theoretical power requirements have been made in small planktonic invertebrates. Using excess density and distance of vertical migration, Hutchinson (1967) concluded that a copepod would require oxidation of less than 0.5% of the organic matter in its body in order to migrate 50 meters. This assumes, without supporting data, an efficiency of approximately 1% in translating stored energy into movement. Vlymen (1970) calculated the theoretical power required for locomotion in copepods based on drag, velocity, and Reynolds number. His conclusion was that locomotion requires less than 0.1%

of the energy budget, but this assumes theoretical power and actual power are equal. The cost of normal activity in the rotifer *Brachionus plicatilis* was calculated from the velocity, drag, and Reynolds number by Epp and Lewis (1979), who found that the theoretical power of locomotion in both the male and female was much less than 1% of the total energy budget. Thus published reports of the theoretical power requirement in small planktonic invertebrates suggest that it should be only a small fraction of the total energy utilized by the animals.

Few direct measurements have been made of the actual cost of locomotion in aquatic invertebrates. Lasker (1966) determined that oxygen consumption of euphausiid shrimps was essentially unchanged in going from a state of rest to normal swimming activity. Zeuthen (1971), on the other hand, found a doubling of metabolic rate between resting and swimming veliger larvae.

In the present study, the metabolic rate of the non-moving male *B. plicatilis* is only 62% of the rate in the moving animals. Since these animals lack a functional digestive system, the observed difference between active and resting rates would appear to be attributable to the actual cost of locomotion. Since the theoretical power requirement is quite small (Epp and Lewis 1979), while the actual power requirement is quite high, the efficiency of movement must be very low. Because of the similarity in intermediary metabolic pathways in all animals, it seems unlikely that the low energy efficiency of movement is due to peculiarities in the metabolic machinery of the rotifer. We therefore conclude that the mechanism of movement (simple cilia) is energetically inefficient. Zeuthen's study (1971) showing a doubling of metabolic rate in swimming veligers of approximately the same size as *Brachionus* did not include a computation of theoretical power, but the theoretical power would almost certainly be very close to the one we have obtained for *Brachionus*, since the size and speed of veliger are close to those of *Brachionus plicatilis* (Sleigh and Blake 1977). Thus Zeuthen's study supports our hypothesis that movement by cilia is very inefficient among the larger organisms that use this mode of locomotion.

Our conclusion that the actual cost of movement in *Brachionus* is exceptionally high is further supported by the data on temperature and movement. These data indicate the presence of a plateau in the movement rate over the temperature range 20–32° C. The rate of movement decreases both above and below this temperature plateau. These results parallel our recent conclusions concerning the effect of temperature on metabolism (Epp and Lewis 1980). We have shown that, contrary to the common belief that invertebrate metabolism increases as a function of temperature, metabolism of *Brachionus* shows a plateau over the temperature range 20 to 28° C. We have speculated that the plateau in metabolism represents an optimal level of metabolism which the rotifers are adapted to maintain over a temperature range which is typical of their normal environment. This constant level of metabolism also allows the rotifers to maintain a constant rate of movement. Below a temperature of 20° and above 32° C, the animals are no longer able to maintain the constant level of metabolism. This results in a decrease in available energy for locomotion and a corresponding decrease in movement rate. If movement were not costly, it is unlikely that movement would so closely parallel total metabolism.

The relatively high cost of movement has important im-

plications concerning resource use by rotifers. While an energetic inefficiency in movement has not blocked the success of the Rotifera, it may have had a significant impact on the evolution of rotifer life histories. Of particular interest in this respect is resource allocation among life stages. In a zooplankton community analysis, Lewis (1979) found that the birth rates and absolute production values for zooplankton species were proportional to the mean body weights of the adults. Larger species are forced to sustain a higher birth rate to compensate for the much longer period of pre-reproductive mortality, and a tendency toward greater predation losses. This results in the apparent anomaly that copepods can under field conditions have average birth rates higher than the much smaller rotifers in the same habitat. This begs a question: what prevents the rotifers from realizing much higher birth rates? Under ideal resource conditions (r_{max}) it would appear that the rotifers have the advantage (Allan 1976), but this advantage is clearly not realized in most lakes, despite the lower vulnerability of rotifers to vertebrate predation. We now suggest that this may be partially explained by energy inefficiency of movement in the rotifers. If the rotifers spend a greater percent of their energy budget on movement than do larger zooplankton, it follows that resource stress will occur more easily, suppressing realized birth rates. Further support for this hypothesis awaits quantification of actual power requirements in large zooplankton.

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