Jumping Behavior in the Oligotrich Ciliates *Strobilidium velox* and *Halteria grandinella*, and Its Significance as a Defense Against Rotifer Predators

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Abstract. The jumping behavior of *Strobilidium velox* and *Halteria grandinella* was analyzed videographically. On average, undisturbed cells of these species jumped 1.7–3.6 and 8 times per minute and spent 0.8 and 1.0% of their time jumping, respectively. Both ciliate species initiated jumps after encounters with rotifer predators. *S. velox* jumped on contact with *Asplanchna girodi*, traveling a mean distance of 1.5 mm (33 body lengths) at a mean velocity of 7 mm/s (154 body lengths/s) at 17°C. *H. grandinella* jumped on contact or near contact with *Synchaeta pectinata*, traveling a mean distance of 0.37 mm (18 body lengths) at a mean velocity of 2.76 mm/s (131 body lengths/s) at 20°C. The maximum velocity recorded during these escape jumps was 16.07 mm/s for *S. velox* and 3.70 mm/s for *H. grandinella*. In *S. velox*, swimming velocity during jumps was not significantly correlated either with swimming velocity just before jumping (mean = 0.15 mm/s) or with distance traveled. In *H. grandinella*, jumping velocity and distance also were not significantly correlated. Jumping in *S. velox* and *H. grandinella* was calculated to require approximately 149% and 41% of total metabolic rate, respectively. Jumping seemed to be an effective defense against rotifer predation. Only 3% of 93 *S. velox* cells contacted by *A. girodi* were captured, and only 12% of 92 *H. grandinella* cells contacted or closely approached by *S. pectinata* were captured; all other cells jumped away. A predation experiment showed that *A. girodi* was about twice as, and significantly more, likely to ingest *Paramecium tetraurelia* as *S. velox* in a mixture of equal numbers of these ciliates. The swimming velocity of *S. velox* during jumps is the highest one so far reported for an oligotrich, and equals the highest one reported for any ciliate (*Mesodinium rubrum*).

Introduction

A variety of ciliates, most notably many oligotrichs and the holotrichs *Mesodinium rubrum* and *Askenasia*, exhibit intermittent jumps or bursts of very rapid swimming [3, 15, 19, 25]. However, most aspects of the so-called jumping behavior of these ciliates have received little or no attention.
Only a few studies on saltatory ciliates have involved direct observations of swimming velocities during jumps. Using cinematography, Lindholm [18, 19] discovered that *M. rubrum* moved several millimeters at a velocity of 5 mm/s and sometimes attained a speed of 8 mm/s. Similarly, using videography, Jonsson and Tiselius [15] found that this ciliate jumped at velocities reaching approximately 8.5 mm/s. No jumping velocities have been reported for oligotrichs, and no detailed data on jumping velocities and distances have been provided for any ciliate.

No information appears to be available on the proportion of time that saltatory ciliates spend jumping. This information is of interest, because swimming at the high velocities observed during jumping is energetically very costly [3].

Lastly, the ecological significance of jumping has rarely been considered, especially as a defense against predators. Tamar [24] noted that *Halteria bifurcata* sometimes “. . . jumped away from rotifers, larvae, and annelid worms when approached, but before these larger animals came into actual contact with the ciliates.” Also, he could induce jumping in this ciliate, and to a lesser extent in its congener *H. grandinella*, by moving the tip of a pin toward specimens. These observations suggest that *Halteria* could escape from potential predators by jumping away just before or after contact with them. Similarly, Taylor et al. [27] noted that *M. rubrum* avoided uptake by micropipette. Thus, this ciliate, too, may jump in response to water currents produced by approaching predators.

Several studies investigated more directly the significance of ciliate jumping as an escape response to predators. The first study, by Archbold and Berger [1], was a qualitative one. They found that five metazoans (two turbellarians, two cladocerans, and a cyclopoid copepod) ingested *Halteria grandinella*, and concluded that the jumping behavior of this ciliate “. . . must therefore be of only limited effectiveness in escaping from predatory metazoa.” However, they made no direct observations of interactions between these metazoans and the ciliate, and thus could not assess probabilities that the ciliate would escape from encounters with these predators. Furthermore, they did not compare the susceptibilities of *H. grandinella* and a comparable, nonsaltatory ciliate to any of these predators. Four studies found that saltatory ciliates were less susceptible to predators than nonsaltatory ones. Jonsson and Tiselius [15] showed that the copepod *Acartia tonsa* captured *M. rubrum* less efficiently than either the similarly-sized *Strombidium reticulatum* or the larger *Laboea strobila*, both of which swam at a more or less constant speed of approximately 0.5 to 1 mm/s. Jack and Gilbert [13] found that *Strobilidium gyrans*, which has a pronounced jumping response, was much less likely to be killed by the cladoceran *Bosmina longirostris* than the similarly-sized hymenostome, *Tetrahymena pyriformis*. Likewise, Gilbert and Jack [10] showed that *S. gyrans* was less susceptible than *T. pyriformis* to predation by three different rotifers (*Asplanchna girodi*, *Brachionus calyciflorus*, and *Synchaeta pectinata*). The difference in susceptibility was especially pronounced with *A. girodi*, whose clearance rates on *T. pyriformis* were about 13 times higher than those on *S. gyrans*. Similarly, Burns and Gilbert [2] found that the calanoid copepod *Diaptomus pygmaeus* cleared *S. gyrans* less efficiently than *T. pyriformis*.

The major goals of the present study were to investigate several questions concerning the jumping behavior of the oligotrichs *S. velox* and *H. grandinella*. What proportion of time do undisturbed cells of these ciliates spend jumping? What are the swimming velocities and distances traveled by these ciliates during jumps?