Ciliates can form an important link between the microbial loop and higher trophic levels primarily through consumption by copepods. This high predation pressure has resulted in a number of ciliate species developing rapid escape swimming behaviour. Several species of these escaping ciliates also possess a long contractile tail for which the functionality remains unresolved. We use high-speed video, specialized optics and novel fluid visualization tools to evaluate the role of this contractile appendage in two free-swimming ciliates, *Pseudotontonia* sp. and *Tontonia* sp., and compare the performance to escape swimming behaviour of a non-tailed species, *Strobilidium* sp. Here, we show that ‘tailed’ species respond to hydrodynamic disturbances with extremely short response latencies (less than or equal to 0.89 ms) by rapidly contracting the tail which carries the cell body 2–4 cell diameters within a few milliseconds. This provides an advantage over non-tailed species during the critical first 10–30 ms of an escape. Two small, short-lived vortex rings are created during contraction of the tail. The flow imposed by the ciliate jumping can be described as two well-separated impulsive Stokeslets and the overall flow attenuates spatially as $r^{-3}$. The high initial velocities and spatio-temporal arrangement of vortices created by tail contractions appear to provide a means for rapid escape as well as hydrodynamic ‘camouflage’ against fast striking, mechanoreceptive predators such as copepods.

1. Introduction

Ciliates are recognized as playing a key role in aquatic ecosystems and act as top ‘predators’ in microbial food webs [1,2]. They are extremely abundant and often exist at densities of thousands of cells per litre [3]. Consequently, ciliates form a critical link in the transfer of energy from the ‘microbial loop’ to higher trophic levels, often through consumption by copepods. It has been shown that ciliates make up approximately 30% of a copepod’s diet which globally translates to 2.0–2.4 Gt of ciliate-derived C yr$^{-1}$ [4]. It has been estimated that copepods alone can clear 25–40% of the ciliate population from surface waters daily [3]. Some ciliate species have evolved effective escape swimming behaviour in response to hydrodynamic signals generated by approaching predators. Studies have shown this to be an effective adaptation as species incapable of escaping fast are two to 15 times more likely to be consumed by copepods compared with species that exhibit rapid escape swimming behaviour [5,6]. In order to successfully employ such escape behaviour, prey require an ability to detect hydrodynamic disturbances of the surrounding fluid. With larger metazoans, specialized structures are designated for detecting fluid signals of potential predators. These structures are capable of detecting signals with only nanometres of fluid displacement [7]. For unicellular protozoans, mechanoreceptors appear to be embedded directly in the cell membrane [8]. This strategy does not appear to reduce the sensitivity of fluid signal detection in ciliates as the critical deformation thresholds for escape vary between 2 and 3.5 s$^{-1}$ [6]. This is within the range of many copepods which are considered highly sensitive to fluid deformation [9]. Jakobsen [6] showed that once a signal has
been detected, both *Mesodinium pulex* and *Strobilidium* sp. can swim rapidly at speeds up to 100 bodylength s\(^{-1}\) (2.1 and 5.2 mm s\(^{-1}\), respectively).

Ciliary propulsion is one of the most ancient means of locomotion as the eukaryotic cilium originated over 800 Ma [10]. For ciliated swimming microorganisms, inertia is negligible and fluid viscosity is the dominant force affecting locomotion in this low Reynolds number regime. The cilium is the principle feature of motile protists and consists of nine pairs of microtubules arranged in a ring around a single central pair. Cilia move through the sliding of microtubules, caused by the formation of transient bridges between dynein arms of adjacent microtubules resulting in sliding [11]. However, sliding is constrained due to other attachments which convert applied force into bending. This rapid motility is characterized by asymmetric waveforms where an effective stroke provides thrust and the accompanying recovery stroke returns the cilium to its starting position with limited viscous resistance. Many ciliated swimmers use energetically efficient [12] coordination of many closely opposed cilia (metachronal patterning).

Some ciliates are characterized by the presence of a contractile ‘tail’ [13]. The structure of the ‘tail’ that some planktonic ciliate species possess differs markedly from cilia in structure and movement pattern. The tail contains numerous parallel membranous tubes with many invaginations that are thought to be derived from the smooth endoplasmic reticulum and containing many mitochondria [14]. These are connected to small bundles of microfilaments which probably function in the rapid contraction of the tail. While the structure of the tail of these ciliates is unique, there are certain similarities to the stalk of the Tintinella and also to the motile extension of the dinoflagellate *Erythropsidinium* [14]. The presence of the contractile tail of some ciliates has been known since the early 1900s [15], and researchers have speculated that it contributes to the cell’s movement and/or stabilizes the cell during feeding [16]. However, the details on the function and potential advantages of the contractile appendage remain unknown. In this study, we use high-speed video and specialized optics to evaluate the role of the contractile appendage in two free-swimming ciliates, *Pseudotontonia* sp. and *Tontonia* sp., and we compare the performance to escape swimming behaviour of a non-tailed species, *Strobilidium* sp.

2. Material and methods

(a) Ciliate cultures

Ciliates were isolated from a whole water sample (S approx. 32 psu) collected at Port Aransas, TX (27°35’59.11” N, 97°13’47.97” W). Cultures were enriched with phytoplankton (*Isochrysis galbana*, *Rhodomonas* sp. and *Heterocapsa* sp.) and placed into 50 ml tissue culture flasks with a few drops of each food. Flasks were then covered and placed in an incubator at 20°C on a 12 L:12 D cycle. Cultures were transferred weekly and fed every 3–4 days.

(b) Experimental set-up

Videos were recorded in a darkroom at room temperature using a Photon SA6 high-speed camera at 1125 frames per second and 1920 × 1440 pixel resolution. Recordings were performed in an optical glass film vessel (10 × 20 × 40 mm) and illumination was provided from a 150 W fibre optic illuminator with an attached collimator. Magnification was provided by 10× or 40× Nikon Extra Long Working Distance objective lenses depending on the species and desired field of view. Long working distance objectives allow the user to focus further away from the front of the lens and into the middle of the volume of interest. Thus, cells that are swimming in focus are free from any ‘wall effects’ that may impact locomotion [17].

The hydrodynamic stimulus to elicit an escape response of ciliates was produced by the vertical movement of a small sphere (4 mm in diameter) connected by a stainless steel rod to a piezoelectric pusher, which was lowered into the chamber and situated in the middle of the water column. A signal generator provided the stimulus pulse and was synchronized to both the high-speed camera and piezoelectric pusher. Once triggered, the camera saves half the video frames from before and half from after the stimulus. The stimulus was manually activated when a ciliate was in focus and close to the sphere. Approximately 20 escapes were recorded for each experimental condition.

(c) Data analysis

High-speed videos were imported into ImageJ (v. 1.48) software that was used to obtain kinematic information. Escape sequences were manually checked for any escape tracks that travelled out of the field and were not included in our analysis to avoid underestimating swimming kinematics. Additionally, to avoid including rapid jumps that were not a direct result of the prescribed stimulus, if a ciliate began an escape jump more than 15 ms before or after the stimulus, it was not included in our analysis. In total, 27 swimming sequences were analysed for *Pseudotontonia* sp., 16 for *Strobilidium* sp. and 13 for *Tontonia* sp. Escape response latencies were determined for *Pseudotontonia* sp. and *Tontonia* sp. by identifying the initial contraction movements of the tail after stimulus onset, and for *Strobilidium* sp. by identifying distinct changes in ciliary movement/structure associated with rapid swimming. Statistical comparisons between species were performed using SigmaPlot (v. 13.0) software. We compared the difference in escape performance parameters using a one-way ANOVA or Student’s t-test (when only two groups were compared). All data were log-transformed and checked for normality using a Shapiro–Wilk test. In a few cases when normality was not achieved through transformation, the non-parametric Mann–Whitney test was used to compare means between two treatment groups.

(d) Micro-particle image velocimetry

The larger (i.e. *Pseudotontonia* sp.) of the tailed ciliate species investigated in this study was chosen for this analysis because it provided a better ratio between organism and tracer particle size. To quantify fluid motion around *Pseudotontonia* sp. during rapid escape behaviour, we used high-speed micro-particle image velocimetry (µPIV) described in [14]. Briefly, this method uses long working distance objective lenses (40×) to create a thin ‘optical sheet’ for resolving tracer particles in the fluid surrounding the organism. Seeding particles consisted of unicellular microalgae, *Nannochloropsis oculata*, which are approximately 2 μm in diameter. Fluid velocity vectors from motion of particles within the focal plane were determined from sequential images analysed using a cross-correlation algorithm (LASIKEN software v. 8.2). Image pairs were analysed with shifting, overlapping interrogation windows of a decreasing size of 64 × 64 to 32 × 32 pixels. Subsequently, the instantaneous vorticity field, \(ω(x, z, t)\), was calculated from the instantaneous velocity vector field, where \(x\) and \(z\) are, respectively, the horizontal and vertical coordinate of the focal plane, and \(t\) is time.

(e) Flow data analysis

The flow imposed by the ciliate *Pseudotontonia* sp. jumping by tail contraction consists of two opposite signed viscous vortex rings:
Subsequently, the temporal decay phase of the impulsive Stokeslet model has a spatial decay of spatial decay rate of the imposed flow. Note that the theoretical circulation based on the impulsive Stokeslet model [18,19]:

\[ \Gamma_\text{in}(t) = \frac{I_{\text{in}}(t)}{4\pi v(t - t_0)} , \]

where \( I_{\text{in}} \) is the fitted hydrodynamic impulse of the vortex, and \( v \) is the kinematic viscosity.

Spatial extension of the flow imposed by the ciliate jumping may be used to quantify the risk of the ciliate being detected by mechanoreceptive predators. To quantify the spatial extent of the imposed flow, we computed the area (\( S \)) within which the flow velocity exceeds a threshold magnitude (\( U^* \)) for the time instant when the flow reaches its maximum spatial extent. We then calculated the radius of an equivalent circular area, defined as \( r = (S/\pi)^{1/2} \). By choosing a series of magnitudes for \( U^* \), we plotted the resulting \( r \) as a function of \( U^* \), to determine the spatial decay rate of the imposed flow. Note that the theoretical impulsive Stokeslet model has a spatial decay of \( r^{-3} \).

### 3. Results

The escape swimming behaviours of three ciliate species were investigated. Two species have contractile appendages (i.e. tails) (\( Tontonia \) sp. and \( Pseudotontonia \) sp.) and one species (\( Strobilidium \) sp.) does not. Results from high-speed recordings show that both ‘tailed’ species rapidly contract the tail which pulls the cell body forward resulting in the tail contraction and body jumping motion being oppositely directed inwards towards the same location. After contraction, the escape continues in tailed species which swim in the same direction as the cell body has been pulled using cilia to ‘push’ the organism forward. By contrast, \( Strobilidium \) sp. (without a tail) performs escape swimming cilia-first and ‘pulls’ itself through the water. Both tailed species exhibit several morphological differences from each other. At 898 \( \mu \text{m} \) (s.d. 97), the tail length is nearly 11\( \times \) the longitudinal cell length in \( Pseudotontonia \) sp. but in \( Tontonia \) sp. the tail is only one-third this length and represents only 5\( \times \) the length of the cell (figures 1 and 2 and table 1). In addition, \( Pseudotontonia \) sp. has paired tentacles that extend approximately 150 \( \mu \text{m} \) from the cell body and contain prey-derived chloroplasts. These structures do not contribute to propulsion and are rapidly contracted within 8 ms after the onset of escape behaviour (figure 1).

During escapes, all species were observed to swim in a straight trajectory but cell bodies rotated about the longitudinal axis up to 700 r.p.m. In addition, the ciliary metachronal waves responsible for locomotion were observed to travel at more than or equal to 2000 r.p.m. around the adoral polykinetid zone and peristomial collar. When propelled by cilia alone, \( Strobilidium \) sp. was observed to swim with the greatest absolute speed (mm s\(^{-1}\)) and relative speed (cell lengths [cl] s\(^{-1}\)) followed by \( Pseudotontonia \) sp. and \( Tontonia \) sp. (table 1). Unlike \( Strobilidium \) sp. however, both \( Pseudotontonia \) sp. and \( Tontonia \) sp. have elongate contractile appendages and exhibit significantly higher velocities (\( p < 0.001 \)) during the initial phase of escape swimming as the ‘tail’ contracts (figure 3 and table 1). Tail contractions resulted in \( Tontonia \) sp. exhibiting the greatest absolute and relative speeds.
(88 mm s\(^{-1}\); 1450 cl s\(^{-1}\)). This high-velocity phase of the escape lasts only for a few milliseconds and transports the cell 2–4 cell lengths, which is roughly the same relative distance a copepod travels per repositioning jump [19]. Tail contraction velocities in Tontonia sp. reach speeds of 225 mm s\(^{-1}\) (s.d. 38), while Pseudotontonia sp. contracts the tail more slowly with peak speeds of 72 mm s\(^{-1}\) (s.d. 9). The combination of the higher tail contraction speeds and shorter tail length in Tontonia sp. resulted in switching to cilia-driven propulsion after only 3.6 ms (s.d. 1.1), whereas Pseudotontonia sp. takes 11.5 ms (s.d. 2.4) before switching to purely cilia-driven propulsion. The Reynolds number of escape swimming in ciliates ranged from 0.24 (Tontonia sp.) to 5.1 mm s\(^{-1}\) (s.d. 0.7) but was not significantly different (\(p = 0.06\)). Peak fluid velocities created by the tail were 5.1 mm s\(^{-1}\) (s.d. 0.7). The temporal decay of the circulation of the vortices fits very well to the impulsive Stokeslet model (equation (2.2); figure 4b). The imposed flow attenuates with distance, \(r\), as approximately \(r^{-3}\) (figure 4c), conforming to the prediction from the impulsive Stokeslet model.

4. Discussion

Despite long-standing knowledge of the presence of contractile appendages in some ciliate species [15], the function of this unique sub-cellular structure has not previously been investigated. This is in large part due to the need to observe these organisms alive and free swimming as the tail remains contracted when cells are disturbed or killed [20]. Their small size also requires specialized optical, illumination and camera systems to resolve details of the free-swimming cells. By satisfying these requirements, we are able to explore the details of ciliate escape behaviour.

The response latency between the onset of the stimulus (threat) and the behavioural response is a critical component of an organism’s ability to successfully escape predation. Shorter response latencies to predatory signals will increase the effectiveness of an escape response. The response latencies to a hydrodynamic disturbance for all three ciliate

### Table 1. Comparison of species characteristics and escape swimming performance of the three ciliates in the study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Cell size ((\mu)m)</th>
<th>Tail length ((\mu)m)</th>
<th>Escape response latency (ms)</th>
<th>Mean swimming speed (mm s(^{-1}), (cl s(^{-1}))</th>
<th>Peak swimming speed (mm s(^{-1}), (cl s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudotontonia sp.</td>
<td>83.0 ± 5.5</td>
<td>898 ± 97</td>
<td>≤0.89</td>
<td>9.1 ± 1.6, 109 ± 19</td>
<td>54.8 ± 11, 653 ± 170</td>
</tr>
<tr>
<td>Tontonia sp.</td>
<td>60.5 ± 3.3</td>
<td>310 ± 31</td>
<td>≤0.89</td>
<td>3.9 ± 0.8, 65 ± 13</td>
<td>88.2 ± 9.7, 1470 ± 154</td>
</tr>
<tr>
<td>Strobilidium sp.</td>
<td>76.4 ± 6.2</td>
<td>n.a.</td>
<td>≤1.78</td>
<td>22.4 ± 4.3, 295 ± 57</td>
<td>27.6 ± 6.4, 363 ± 84</td>
</tr>
</tbody>
</table>
species investigated in this study are among the shortest recorded for any organism. Both *Pseudotontonia* sp. and *Tontonia* sp. began to contract the tail within 0.89 ms of onset of the stimulus and the response latency for *Strobilidium* sp. was also very short (less than or equal to 1.78 ms). For *Tontonia* sp., the response latency may even be substantially shorter than 0.89 ms as the tail was often more than 50% contracted after a single video frame (figure 2), but temporal resolution of the video was limited to 1125 frames per second. In comparison copepods, which have one of the shortest response latencies of any animal and are important ciliate predators, can only respond to hydrodynamic disturbances in less than or equal to 3 ms [21,22].

Such short response latencies in ciliates are required to successfully escape from predatory copepods. Here, it is important to consider the spatial scale in which this predator–prey interaction occurs. Given that ciliates can detect strain as low as 2–3.5 s\(^{-1}\), we can infer where this threshold is in a copepod feeding current. Jakobsen [23] determined that in the feeding current of *Temora longicornis*, the ciliate *Strobilidium* responds on average 620 mm away from the copepod. With a response latency of less than 2 ms and escape speeds that exceed the feeding current velocity, these ciliates appear well suited to avoid this copepod feeding mode. It should also be noted that while strain rate magnitudes are appropriate for considering prey detection of predators, it has been numerically demonstrated that prey perception by predators more likely depends on the absolute magnitude of the fluid velocity generated by the moving prey [9].

Ambush feeding copepods may present a greater challenge to fast escaping ciliates because these copepods only strike at their prey when it is within approximately 0.3 mm and copepods can cover this short distance in only a few
milliseconds [24]. This translates to a strike speed of approximately 100 mm s$^{-1}$ which interestingly is only marginally faster than the peak escape speeds of the tailed ciliates (table 1). Thus, even when factoring in a loss of approximately 1 ms in response time, tailed ciliates can travel over 100 µm in only 2 ms (figure 3b). The unicellular nature of ciliates probably allows for the sub-millisecond responses required to gain an advantage during predation attempts because there are no neurons or gap junctions that signals must travel through. Investigations of *Paramaecium* sp. by Naitoh & Eckert [25] suggest mechanoreceptors rapidly hyperpolarize the cell which results in an increase in cilia beat frequency, thus accelerating the swimming velocity. Fluid deformation may uniformly stretch the entire protist cell, hence activating both the posterior and the anterior mechanoreceptors which could hyperpolarize the cell membrane potential almost simultaneously, inducing a shift in the cilia beat direction and frequency. Therefore, while bipolar mechanoreceptors may provide a mechanism for rapid response and fine-scale sensitivity, the ability of the ciliate to perceive the directionality or location of the stimulus may be negatively impacted because deformation is caused by a simultaneous activation of uniform stretching of the whole cell body [23]. This is supported in this study as we found escape trajectories were related to the initial orientation of the cell and not observed to be directed away from the stimulus.

The contractile appendage has an important impact on escape performance. Once a stimulus has been detected and a response initiated, propulsive structures must effectively remove the prey species from the immediate vicinity of the predator. The tails of *Pseudotontonia* sp. and *Tontonia* sp. appears well suited to meet this need. During tail contractions, *Pseudotontonia* sp. reaches speeds that are six times greater than peak speeds obtained through cilia-driven propulsion, and 20 times greater for *Tontonia* sp. Compared with *Strobilidium* sp., a non-tailed species, speeds are significantly higher for both tailed species during those first critical milliseconds of an escape (figure 3a). Even though the cilia-driven propulsion phase in *Strobilidium* sp. was found to be significantly faster than the cilia-driven swimming phase of *Pseudotontonia* sp. and *Tontonia* sp., the use of the contractile tail appendage in the latter two species provides a speed and cumulative displacement advantage during initial stages of the escape (figure 3b). Mean escape speeds of *Pseudotontonia* sp. and *Tontonia* sp. exceed those of *Strobilidium* sp. over the first 30 and 10 ms, respectively. Given that the predatory strike of a copepod takes only several milliseconds and covers a distance of only 0.3–0.5 mm, the short duration of the propulsive advantage in the tailed species may result in greater escape success.

Even between the two-tailed species investigated in this study, there are noteworthy differences. *Pseudotontonia* sp. contains elongate, chloroplast-containing, paired structures just below the apical membranelles [20] (figure 1). These structures are rapidly contracted during initial stages of the escape but probably still contribute to increased drag during the first few milliseconds and may partially account for lower peak escape speeds compared with the smaller *Tontonia* sp. Copepods are well known as one of the fastest animals relative to body size and escape with peak speeds exceeding 500 bodylengths s$^{-1}$ [26]. However, both species of tailed...
ciliate investigated in this study can attain relative speeds that match or exceed copepods which are an order of magnitude larger (table 1).

Another obvious difference is the tail lengths of the two ciliate species. The tail is approximately 11 times the maximum cell dimension in *Pseudotontonia* sp. versus only five times in *Tontonia* sp., yet the relative distance travelled during tail contraction is similar (approx. 2 cell diameters). However, when tail lengths are considered in terms of cell volume, which is directly proportional to the mass being pulled by the tails, the ratio becomes nearly the same for both species. This is important to consider as tail length may need to increase relative to body size and thus would impose physical limits on the size of organisms that could obtain similar propulsive performance. Based on relationships from the two-tailed species, a cell double the size of *Pseudotontonia* sp. may need a tail length of 14.4 mm or 90 times the cell diameter to provide enough drag-based surface area to compensate for the increase in cell mass and drag force due to the greater surface area. A similar type of problem can be found in ‘ballooning’ behaviour of small spiders (2–3 mm) where animals extrude a strand of silk into the wind which carries them to a new location. Here, animals often require filament lengths over 1 m in length and wind speeds exceeding 0.8 m s\(^{-1}\) \[27,28\] to provide sufficient drag force to be carried an appreciable distance. Larger spiders are rarely observed to perform this wind-driven relocation because the length of silk needed becomes so long that it is more likely to tangle than provide enough drag [28]. Such long structures would probably also become impractical as a constantly deployed anti-predator mechanism in larger organisms. Response latency was not significantly different for either tailed species (both 0.89 ms) despite *Pseudotontonia* sp. having nearly three times the volume of *Tontonia* sp. However, it is likely that one or both species can respond faster than this as the response latency may be shorter than the temporal resolution of the camera (1125 fps or 0.89 ms). We hypothesize that the smaller cell volume of *Tontonia* sp. may allow for faster signal propagation and shorter response times. This is supported by the fact that *Tontonia* sp. can detect a stimulus, respond and almost fully contract its tail in less than 0.89 ms (figure 2).

Propulsion of large organisms such as fishes display characteristics such as reverse Von Karman vortex shedding during self-propulsion by oscillating the propulsive structure [29]. This occurs as a result of near inviscid conditions at high Reynolds number. For small swimmers (less than 1 mm), viscosity dominates and alternative strategies for self-propulsion must be employed. Despite being at least one order of magnitude smaller than the copepod *Acartia tonsa* [19], the ciliate *Pseudotontonia* sp. creates similar viscous vortex rings during rapid escape swimming. In *Pseudotontonia* sp., the tail contraction and the body jumping motion are oppositely directed inwards towards the same location, while in *A. tonsa*, the beating motion of the swimming legs and the jumping motion of the body are oppositely directed outwards away from each other. Thus, the two vortex rings created in the ciliate jumping rotate in directions different to those created in the copepod jumping. Despite this apparent difference, in both situations, the two vortex rings are arranged spatiotemporally in a near mirror image fashion. Such an arrangement is likely to bring a hydrodynamic ‘camouflage’ to the jumping ciliate, similar to that discussed previously for the jumping copepod [30]. Consider that a mechanoreceptive predator a short distance away can only strike at one side of the two vortices; this may effectively reduce the probability that the ciliate prey gets caught. Thus, even if a copepod senses the hydrodynamic disturbance of an escaping ciliate, the strike speed is only marginally faster than the tail-driven escape speed of the ciliate but it may also have, at best, a 50% chance of choosing the right direction to strike.

The impulsive swimming behaviour of small organisms has been described using one of two unsteady viscous vortex ring models (an impulsive Stokeslet and impulsive stresslet) [19,31–33]. Velocity fields scale as \(u \sim r^{-3}\) for the impulsive Stokeslet and \(u \sim r^{-4}\) for impulsive stresslet models [18]. In other words, the velocity magnitude of the hydrodynamic signal generated by jumps falls off more rapidly than for a continuously swimming or feeding organism. For *Pseudotontonia* sp., in order to generate a strong enough impulse to pull the cell body rapidly forward, the tail needs to be long enough and deployed far enough from the cell body. Thus, the imposed tail-bound vortex and body-bound vortex are well separated and evolve rather independently after creation. For the copepod (*A. tonsa*) repositioning jump [19], the separation distance between the two vortices when their vorticities reach maximum was approx. 1 body length of the copepod. For the ciliate jumping, the separation distance was approx. 2 body lengths of the ciliate (figure 4a, 3.56 ms). This study shows that the flow imposed by the ciliate jumping is well described by the flow due to two well-separated impulsive Stokeslets, and that the overall flow attenuates spatially as \(r^{-3}\) as theoretically predicted (figure 4b,c). By contrast, the repositioning jump of *A. tonsa* creates two viscous vortex rings that are separated by only a shorter distance, and therefore the overall flow is better described by an impulsive stresslet with a spatial decay of \(r^{-4}\).

The flow imposed by the *Pseudotontonia* jumping has a slower spatial decay \(\left( r^{-5}\right)\) than that achieved by a copepod repositioning jump \(\left( r^{-4}\right)\). However, a spatial decay of \(r^{-3}\) remains to be the fastest spatial decay we have identified so far for protist imposed flows. Comparably, the jumping ciliate *Mesodinium rubrum* also achieves an \(r^{-3}\) spatial decay rate by beating the equatorially located propulsive ciliary belt to impose a potential dipole-like flow [34,35]. Despite adopting different propulsive morphologies and strategies, both ciliates jump rapidly with imposed flows attenuating as fast as achievable at these small scales. In so doing their suitability to rheotactic predators will presumably be reduced.

In conclusion, factors that can alter the outcome of predator–ciliate interactions are important given the trophic position of these protists within the microbial loop and widespread abundance in aquatic ecosystems. The rapid response and use of contractile appendages in some ciliate species appears to provide an advantage during those first critical milliseconds of an escape.

Data accessibility. The experimental data have been deposited at Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.r5f7m).

Authors’ contributions. B.J.G. conducted the experiments, and B.J.G. and H.J. analysed the data. All authors interpreted the results and wrote the manuscript.

Competing interests. The authors declare no competing interests.

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