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Behavioral Interactions of the Copepod *Temora turbinata* with Potential Ciliate Prey

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Key words: Copepod, Ciliate, Behavior, Swimming, Predator/prey interaction.

Planktonic food webs are complex, with large and variable numbers of species, trophic levels, and dynamic interactions between trophic levels. Copepods are key species in planktonic food webs, not only by being a link between primary producers and fish but as predators of other consumers (Wiadnyana and Rassoulzadegan 1989). Complex trophic interactions can be simplified by allocating copepods to functional groups or feeding guilds according to their different feeding mechanisms and types of food items (Polis and Holt 1992, Hwang et al. 2009b), their functional morphology (Anraku and Omori 1963, Paffenhöfer 1998), or their behavior (Jakobsen et al. 2005, Jiang and Paffenhöfer 2008, Hwang et al. 2009b). Copepod feeding guilds are commonly divided into categories like ambush feeders, cruising feeders, and suspension feeders (Gismervik et al. 1996, Dahms et al. 2006). Generalizations about these guilds might not be useful; for example, that filter feeders are typically algivores (feeding on small, slow-moving producers), and are not capable of capturing larger items or faster prey. Several studies showed that calanoid copepods can graze a significant proportion of ciliate production, either by filtering or by actively capturing individual prey items (Gismervik 2005). In studies of the ingestion of ciliates by calanoid copepods, ingestion rates were quite variable, but were generally < 50 ciliates/calanoid copepod/h, although values as

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high as 2700 ciliates/copepod/h were reported (Sanders and Wickham 1993).

Planktonic copepods of the family Temoridae are widely distributed in tropical, subtropical, temperate, and subboreal waters, and are common members of surface and near-surface mesozooplankton communities in estuarine, neritic, and oceanic waters (Ara 2002, Hwang et al. 2004a). *Temora turbinata* is widely distributed from tropical to temperate waters of the Atlantic, Pacific, and Indian Oceans, except for the eastern Pacific (Bradford-Grieve et al. 1999), and is often predominant in mesozooplankton communities of tropical, coastal, and oceanic environments of the Gulf of Mexico, Caribbean Sea (Ara 2002), and the western Pacific. It is also abundant in mesozooplankton communities in summer around Taiwan coastal areas (Hwang et al. 2004b, 2006, 2009a b c, Dur et al. 2007, Tseng et al. 2008a), affecting the food webs of waters surrounding Taiwan (Tseng 2008b c). *Temora turbinata*, like many calanoid copepods, generates a feeding current and filters suspended particles from the water (Hwang and Turner 1995, Hwang et al. 1998, Turner et al. 1998).

Copepods and ciliates may have an overlapping food size spectrum, although ciliates feed at the lower end of the size scale, with the most common naked ciliates grazing on organisms 3-7 μm in diameter, while small copepods of the genera *Acartia*, *Pseudocalanus*, and *Eurytemora* feed more efficiently on particles in a size range of 15-40 μm in diameter (Gismervik et al. 1996). Although several copepod species preferentially select larger food items, others are capable of feeding on small food items and can reach substantial population sizes when food abundance is high (Broglio et al. 2004). Because of the possible overlap in prey size, copepods feeding on ciliates would be preying on their competitors, a phenomenon termed intraguild predation (Polis and Holt 1992). Such trophic triangles are common in most aquatic food webs, but are ubiquitous in microbial food webs, because of the high plasticity in prey: predator size ratios and different feeding modes found among protozoa.

Oligotrich ciliates, such as those in the genera *Strobilidium* and *Strombidium*, are important components of the microzooplankton worldwide and are major grazers in planktonic food webs (Jonsson 1986). Densities of oligotrich ciliates commonly range 1-10 individuals/ml in marine waters (Lynn and Montagnes 1991), although mechanisms controlling their distribution and abundance are poorly understood. Predation by copepods may help control the abundance of ciliates (Nielsen and Kiørboe 1994, Gismervik 2006).

Ciliates play key roles in planktonic food webs, with substantial effects on carbon transport efficiencies, trophic interactions among protozoan grazers, their food, and their predators, and energy flows to higher trophic levels (Sherr and Sherr 2002). During eutrophication, and in the absence of copepods, ciliates may become abundant, and ciliates may be able to establish grazing control of algae (Gismervik 2006).

The majority of planktonic ciliates are within the 10-200 μm size range (Wickham 1995). Ciliates can either be small enough to be preferred as copepod prey, or too small to be detected or captured. Several studies showed that calanoid copepods can graze a substantial proportion of the ciliate production (Hwang et al. 2004a, Huo et al. 2008). Calanoid copepods feed either by filtering or actively capturing individual prey items (Jonsson and Tiselius 1990). Copepods particularly affect the structure of marine food webs by consuming ciliate grazers with higher growth rates and specific grazing rates (Vadstein et al. 2004). Some copepod species may selectively feed on ciliates over phytoplankton (Wiadnyana and Rassoulzadegan 1989).

Outcomes of predator-prey interactions commonly depend on predator and prey swimming behaviors, speeds, and jumping behaviors, as well as size and palatability (Landry and Fagerness 1988). Because such behavioral traits are often taxon-specific, identification of key organisms and their functions in the marine pelagial is an important issue (Hwang and Turner 1995, Bathmann et al. 2001). If copepod behaviors vary with prey abundance and species composition, then these factors will affect the food web stability (Jakobsen 2002). It was proposed that food-switching copepods increase their clearance rate when the concentration of an alternative prey increases (Gismervik and Andersen 1997), whereas non-switching copepods sustain high predation pressures on ciliates even at low prey densities and may remove every ciliate from a location when resources are decreased. The ability of some ciliates to perform rapid jumps was suggested to decrease the probability of capture (Wiackowski et al. 1994, Broglio et al. 2001).

The objective of this study was to examine characteristics of ciliate protozoan and copepod behavioral interactions. Experiments using the calanoid copepod *Temora turbinata* were performed to assess the species-specific behavioral interplay of this copepod with 2 ciliate species of different sizes with different modes of locomotion.

MATERIAL AND METHODS

Collection of copepods and the culture of ciliates

Temora turbinata was collected from the Gulf of Mexico at Port Aransas, TX from July 29 to Aug. 4, 2004. Copepods were collected by a WP/2 net of 200 μm mesh size with a closed cod-end (Research Nets, Bothel, Washington, USA). The strobiliid *Strobilidium* sp. (54 × 40 μm) and an unidentified species of spinning ciliate (33 × 33 μm) were cultured in nonaxenic monocultures in the laboratory at 20°C in growth medium at a salinity of 30 psu, and held in dim light (24 $J/m^2/s$) in a 12 h light: dark cycle, feeding on an algal mixture of *Isochrysis galbana*, *Heterocapsa* sp., and *Rhodomonas* in a ratio of 1: 1: 1. Ciliates were identified from stained samples following the description of Lynn and Montagnes (1988), while one of the species could not be identified and was provisionally termed “spinning ciliate”.

Video equipment and recording

Observations of the behavior of the copepods and their ciliate prey were obtained by video-recording each ciliate species alone and together with females of the copepod predator *T. turbinata*. Filming was performed using dark-field illumination, in a dark room at a temperature of 23°C. A modified Schlieren optical system with an infrared (IR) LED lamp (peak wavelength 910 nm; 1.45 V) and an IR-sensitive camera (Sony XC-77, Japan) were used, and a DV recorder (Sony DCR-PC 120) recorded images on mini-DV tape. The experimental container was a 10 ml vessel (2 cm high × 4.5 cm long × 1.2 cm wide, with a lid) where 15 individuals of *T. turbinata* were kept at 30 PSU salinity. After transfer to the filming vessel, the ciliates were allowed to acclimatize for 15 min prior to filming at 23°C. Repeated observations were taken to elucidate the prey-capture behavior of the copepods, and subsequent responses by the ciliates. The video optical system, filming techniques, and film analysis were similar to those described by Hwang (1991). Some reviews of video optical technology for aquatic sciences can be found in Strickler and Hwang (1999) and Dahms and Hwang (2009).

Acquisition of trajectories and characterization of motility

Video sequences were analyzed using Track-It, a manual tracking software program to digitalize ciliate swimming trajectories (Nihongi et al. 2004). Before using the software, the video was transformed into image sequences using Adobe Premiere software (San Jose, CA, USA) to display images one by one. By successively clicking on the position of an object in each frame, a trajectory was numerically reconstructed.

Acquisition of swimming speed

We used the Pythagorean theorem, $C^2 = A^2 + B^2$ to obtain distance data in pixels to calculate a distance scale for the video analysis.

The distance, *d* (mm), traveled between 2 successive video frames was computed from the (*x*, *y*) coordinates as:

$d = [(xt - xt + 1)^2 + (yt - yt + 1)^2]^{1/2}$; (1)

where (*xt*, *yt*) and (*xt*+1, *yt*+1) are the positions of a copepod at times *t* and *t* + 1, respectively. The swimming speed, *v* (mm/s), was subsequently estimated as:

$v = d.f.$; (2)

where *f* is the sampling rate of the camera, i.e., *f* = 30 frames/s. Average swimming speeds and their standard deviations were calculated from complete individual tracks.

RESULTS

Swimming behaviors of *Strobilidium* sp. and the spinning ciliate without copepods

The swimming trajectory of *Strobilidium* sp. without the potential predator, *T. turbinata* (*n* = 20 tracks), showed a high frequency of lengthened helicoidal loops (Fig. 1A). The swimming trajectory of a spinning ciliate without the potential predator, *T. turbinata* (*n* = 19 tracks), exhibited much-broader helicoidal loops (Fig. 1B). The *Strobilidium* sp. swimming trajectory with the potential predator *T. turbinata* (*n* = 4 tracks) changed to an undulating trajectory (Fig. 1C). The spinning ciliate's swimming trajectory with the potential predator *T. turbinata* (*n* = 4 tracks) did not change (Fig. 1D compared to Fig. 1B).

Both ciliates, *Strobilidium* sp. and the spinning ciliate, showed different swimming patterns (Fig. 1, Table 1). When *Strobilidium* sp. was videotaped without *T. turbinata*, it slowly moved forward in a lengthening helicoidal trajectory (Fig. 1A). Swimming movements were interrupted by sudden short jumps or more rarely by long-distance jumps. We found only 2 long-distance jumps during a period of 5 min among a group of 10 ciliates. When jumping, *Strobilidium* sp. usually changed its swimming direction (Figs. 1A, C).

The average swimming speed of *Strobilidium* sp. was 0.36 ± 0.19 mm/s (including jumps). The swimming speeds of 100 ciliate tracks were held constant, until the protists suddenly jumped. From the trajectories of 10 ciliates, we calculated that the jumping frequency was 5.15 ± 1.07 jumps/min with an average jumping distance of 0.73 ± 0.24 mm and a jumping speed of 7.71 ± 3.86 mm/s (Table 1).

The swimming behavior of the spinning ciliate consisted of fast helicoidal swimming with an average swimming speed of 1.47 ± 0.32 mm/s (*n* = 20). This ciliate ceased swimming for short periods with an average resting time duration of 1.83 ± 0.5 s (Table 1, Fig. 1B). Before stopping its fast helicoidal swimming, some ciliates showed a straight-line trajectory (jump) for a few frames with an average jumping speed during 10 jumping events of 4.75 ± 1.38 mm/s, and an average jump distance of 0.54 ± 0.14 mm (Fig. 2, Table 1). Long-distance jumps were rare; 10 ciliates performed only 1 long-distance jump within 2 min. For the entire observation time, the jumping frequency was 7.86 ± 3.14 jumps/min (Table 1).

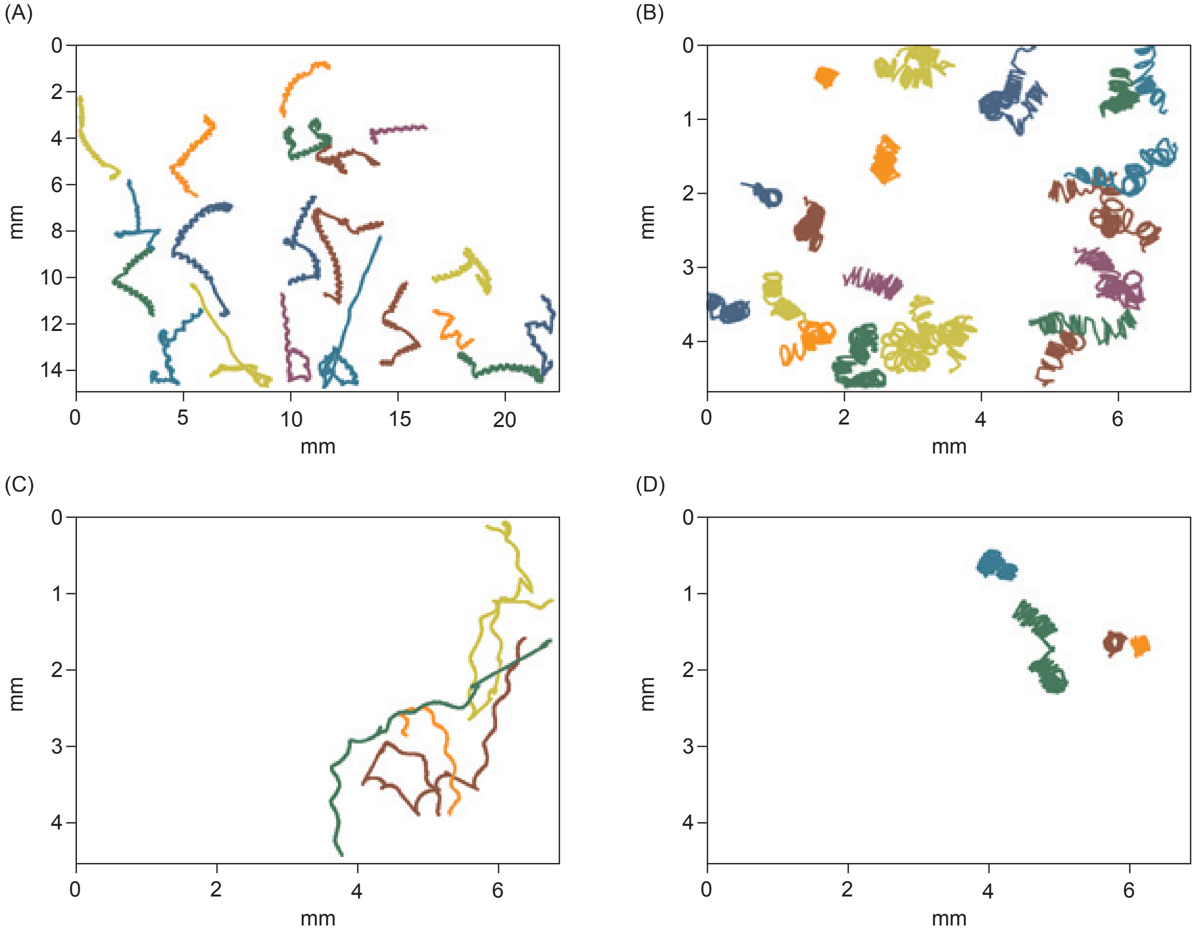


Fig. 1. Ciliate swimming trajectories with or without the potential predator, *Temora turbinata*. (A) *Strobilidium* sp. swimming trajectory without the potential predator, *T. turbinata* (*n* = 20 tracks). (B) Swimming trajectory of a spinning ciliate without the potential predator, *T. turbinata (n* = 19 tracks). (C) *Strobilidium* sp. swimming trajectory with the potential predator *T. turbinata* (*n* = 4 tracks). (D) Spinning ciliate swimming trajectory with the potential predator, *T. turbinata* (*n* = 4 tracks).

Interactions of *T. turbinata* with the spinning ciliate and *Strobilidium* sp.

The calanoid copepod *T. turbinata* is a suspension feeder. During our study, *T. turbinata* generated a feeding current that resulted in a slower swimming speed. When a stimulus was provided (such as from another copepod or prey in the same container), *T. turbinata* used its 1st antennae and swimming legs to kick back with a fast jump as a response.

Temora turbinata increased its average swimming speed in the presence of a ciliate (Table 2), generating a feeding current which resulted in slow gliding. The swimming speed of *T. turbinata* without a ciliate present was 1.69 ± 0.57 mm/s (*n* = 7). For *T. turbinata* with a spinning ciliate, the average swimming speed was 4.29 ± 1.53 mm/s (*n* = 5). When *T. turbinata* was kept together with *Strobilidium* sp., its swimming speed was 3.04 ± 1.8 mm/s (*n* = 7) (Table 2). However, the success of *T. turbinata* in capturing ciliates was limited (see below).

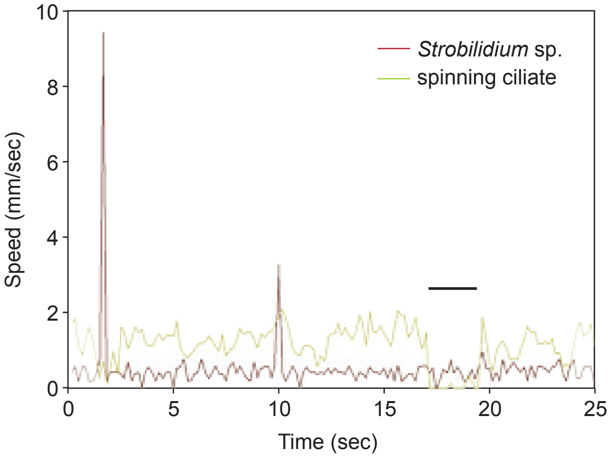


Fig. 2. Swimming speed of the ciliates, *Strobilidium* sp. and spinning ciliate. The average swimming speed of *Strobilidium* sp. was 0.5 mm/s, and the swimming speed was maintained at a constant speed, but sudden jumps were exhibited. The average swimming speed of the spinning ciliate was 1.17 mm/s. The black bar indicates a period of locomotory rest of the spinning ciliate.

In experiments with *Strobilidium* sp. and *T. turbinata*, the ciliate density was 1.91 individuals (ind./ml). Although the encounter rate with *Strobilidium* sp. was 47 times/h, only 2 capture events by *T. turbinata* were observed within a total observational period of 2 h. Once *Strobilidium* sp. perceived the feeding current of *T. turbinata*, it responded with an escape jump. Calibrating the shortest distance from the ciliate to the body of *T. turbinata*, we found an average distance of 0.64 ± 0.15 mm (*n* = 5)(Table 3, Fig. 3A), and the orientation when jumping was in a direction opposite to that of the predator. All jump positions occurred in front of the copepod. Since the copepod was swimming forward, this is a reasonable reaction (Fig. 3B). In 1 case, a *Strobilidium* sp. individual did not respond when the copepod was swimming close by; it simply followed the feeding track of the predator. In another case, *Strobilidium* sp. responded with an escape jump, but the jump was in the direction of the predator, *T. turbinata*, which subsequently captured it (Fig. 4).

In the experiment with the spinning ciliate and *T. turbinata*, the ciliate density was 3.19 ind./ml. Although the encounter rate was 162 times/h, only 3 ciliates were captured by *T. turbinata* within a total observational period of 2 h. Calculated from the escape position, the perception distance from the body of *T. turbinata* to the spinning ciliate was on average 0.73 ± 0.33 mm (*n* = 5) (Table 3, Fig. 3D). In the 3 cases observed, the spinning ciliate was captured while responding with an escape jump when *T. turbinata* came close. In all observed cases, the swimming ciliate jumped towards *T. turbinata*. This was similar to our

Table 1. Specifications of swimming behaviors of the 2 ciliates, *Strobilidium* sp. and a spinning ciliate

	Strobilidium sp.	Spinning ciliate
Swimming speed (mm/s)	0.36 ± 0.19	1.47 ± 0.32
Jumping distance (mm)	0.73 ± 0.24	0.54 ± 0.14
Jumping velocity (mm/s)	7.71 ± 3.86	4.75 ± 1.38
Frequency (jumps or rests/min)	5.15 ± 1.07	7.86 ± 3.14
Resting time (s)	Not observed	1.83 ± 0.50

observations with *Strobilidium* sp.

Although the escape distance of *Strobilidium* sp. was rather long (Fig. 3A), the ciliate was unable to successfully escape because it jumped directly towards the mouth of a 2nd copepod when it was trying to escape from the approaching 1st copepod. We concluded that in order to escape, both direction and speed were important.

Temora turbinata captured and ejected non-food particles

After handling captured particles for 1.5-2 s, *T. turbinata* was able to differentiate between ciliate prey and inert particles. Inert particles were rapidly ejected. When *T. turbinata* detected any particle (prey or non-food particle), it usually reoriented its body towards the particle. When swimming close to the particle, the particle usually followed the feeding current of *T. turbinata*. Then *T. turbinata* handled the particle with its maxillae (Strickler 1984, Jiang et al. 2002) for 1-2 s as if testing whether the particle was suitable food or not. When handling a non-food particle, *T. turbinata* ejected the particle toward the posterior end of its body (Fig. 5). Because the experiment was performed in a dark room, using infrared light for illumination, *T. turbinata* could not have used visual aids to discriminate particles, since there is no indication of infrared sensing in copepods.

Table 2. *Temora turbinata* swimming speed in the presence and absence of potential ciliate prey

	Swimming speed (mm/s)
Temora turbinata alone	1.69 ± 0.57, *n* = 7
Temora turbinata with spinning ciliate	4.29 ± 1.53, *n* = 5
Temora turbinata with *Strobilidium* sp.	3.04 ± 1.80, *n* = 7

n, number of observations.

DISCUSSION

In the interaction experiment with either ciliate species, *T. turbinata* showed higher swimming speeds. With *Strobilidium* sp., the copepod's swimming speed was 4.29 ± 1.53 mm/s (*n* = 5) (Table 2). *Temora turbinata* with the spinning ciliate swam at 3.04 ± 1.8 mm/s (*n* = 7) (Table 3).

Swimming speed

In the interaction experiment with either ciliate species, *T. turbinata* showed a higher swimming speed than when the copepod was alone. We interpreted this as an adaptation to increase the encounter rate. *Strobilidium* sp. decreased its swimming speed in the presence of the copepod, possibly in order to decrease the encounter rate with a potential predator or to decrease its hydrodynamic signal making it more difficult to be detected. The swimming speed of the spinning ciliate did not change in the presence of the copepod. The spinning ciliate exhibited a different escape strategy; its high swimming speed and helicoidal swimming pattern may make it more difficult for the copepod to detect and capture.

Density

Comparing the 2 ciliates within the predator interaction experiment, the spinning ciliate density (3.19) was higher than with *Strobilidium* sp. (1.91) by 1.7 times. However, the encounter rates with the spinning ciliate (162 times/h) were 3.4 times higher than those with *Strobilidium* sp. (47 times/h). In a 2 h experiment, we observed a spinning ciliate

Table 3. Details of interactions of *Temora turbinata* with the spinning ciliate and *Strobilidium* sp.

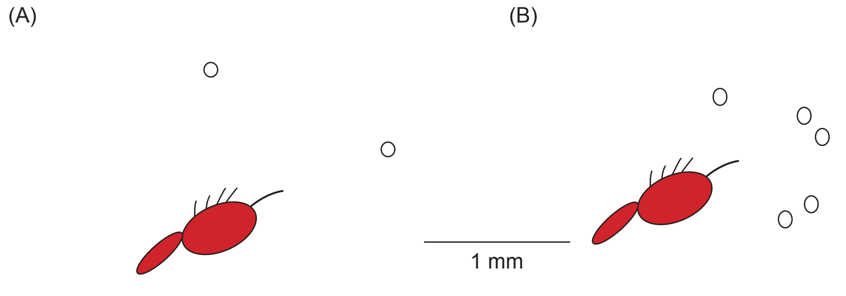
	Strobilidium sp.	Spinning ciliate
Ciliate speed (mm/s)	0.15 ± 0.04 (*n* = 4)	1.36 ± 0.47 (*n* = 4)
The nearest distance of ciliate before being captured (mm)	0.41 (*n* = 2)	0.96 (*n* = 3)
Distance of ciliate detection (mm)	0.64 ± 0.15 (*n* = 5)	0.73 ± 0.33 (*n* = 5)
Encounter rate between the copepod and ciliate	47/1 h	162/1 h
Incidences of ciliates being captured	2/2 h	3/2 h
Ciliate density	1.91 individuals/ml	3.19 individuals/ml

n, number of observations.

to be captured 3 times, a higher incidence than the 2 captures of *Strobilidium* sp. Considering both the density and encounter rates, the spinning ciliate may have had a better strategy to avoid predation.

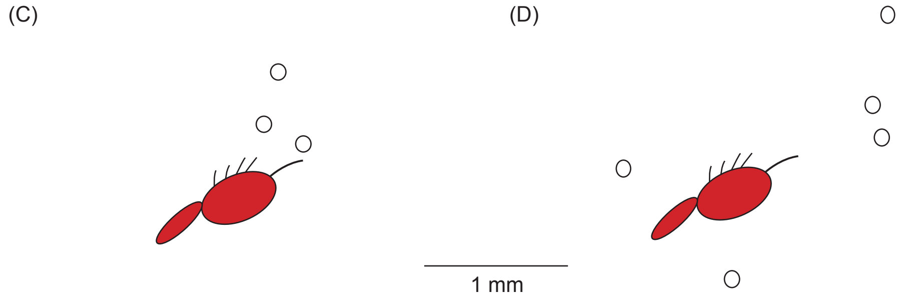
Copepod feeding strategies are commonly divided into the categories of suspension feeders, ambush feeders, and cruising feeders. Although these groupings may be justified for behavioral reasons, the conclusions derived from these groupings might not be accurate. A common perception is that suspension feeders are typically algivores (feeding on microscopic and non- or slow-moving phytoplankton), with the generalization that these copepods are not capable by eating other prey. However, the present study with *T. turbinata*, as well as others (Fessenden and Cowles 1994, Jakobsen et al. 2005), showed that suspension-feeding species are also able to exploit comparatively larger moving prey like ciliates. A suspension-feeding copepod will trap a ciliate in its feeding current, if the current velocity is greater than the escape velocity of the ciliate (Jakobsen et al. 2005). This finding illustrates the problems involved in extrapolating our preconceptions that suspension-feeders are not able to capture faster-moving ciliates.

In the present study, both ciliate species seemed to be trapped, although at very low rates, in the current generated by *T. turbinata*. In a study by Gismervik (2006), *Pseudocalanus* sp. had a considerably higher clearance rate for the ciliates, *Lohmaniella oviformis* and *Strombidium* sp., than for *S. conicum*. As none of the examined ciliates displayed jumping or other escape responses in Gismervik's study (2006), the different clearance rates observed must be related to other factors. Despite their differences in size, both the small *L. oviformis* and the larger *Strombidium* sp. were removed at the same rate by *Pseudocalanus* sp. At the same time, clearance rates of the very similarly sized *S. conicum* and *Strombidium* sp. differed. Gismervik (2006) concluded that size did not seem to be the most important discriminant for this copepod. Differences in feeding effort may have been related to the nutritional status of the ciliates, as previously noted by Pérez et al. (1997). In their study, heterotrophic species were consumed at higher rates than mixotrophic species. The low numbers of captured ciliate specimens and a lack of knowledge about the nutritional requirements precluded any interpretation of this aspect in the present results.



Strobilidium sp. by captured distance

Strobilidium sp. Escape distance



Spinning ciliate by captured distance

Spinning ciliate Escape distance

Fig. 3. (A) *Strobilidium* sp. and spinning ciliate (small circles) interactions with *Temora turbinata*. A, B, Ciliate capture distance where ciliates significantly changed swimming direction or jumped shortly before they could have been captured by *T. turbinata*; C, D, ciliate escape distance when they jumped away when they perceived *T. turbinata* approaching.

In experiments by Hwang and Turner (1995), *T. turbinata* continuously swam for extended periods, with almost no periods of rest and, therefore, almost no transitions from swimming to non-swimming. Both *T. turbinata* and *Undinula vulgaris* are primarily suspension feeders on phytoplankton and other particles (Hwang and Turner 1995). Both species, therefore, can produce strong feeding currents. In the case of *T. turbinata*, this current continuously pulled the copepod forward so that it cruised through the water. The congeneric *T. longicornis* generated a feeding current by which food particles were collected; and it spent nearly 100% of its time slowly cruising or hanging stationary while moving its feeding appendages (van Duren and Videler 1995). The feeding current flow field of *T. longicornis* is strong and wide, and the motion of fluids is maximal at the tip of the feeding appendages (van Duren and Videler 2003). Feeding *T. longicornis* showed no response to *Strobilidium* sp. that were performing escape jumps, or to those *Strobilidium* that came very close to the copepod. This may indicate that *T. longicornis* did not detect prey from the hydrodynamic signals it produced. *Temora* longicornis produced a strong hydrodynamic signal while feeding, and its feeding current increased the fluid deformation around the anterior part of the copepod with fluid deformation rates of up to 10.2/s (Kiørboe et al. 1999). This deformation could provide early warning signals to trigger escape responses in protists. The success of escape may depend on the speed of the filtering current at the point of detection compared to the escape jump speed. Maximal feeding currents in *T. longicornis* were reported to vary 3-8 mm/s (van Duren and Videler 2003). At a certain point, the fluid deformation in the feeding current exceeded the critical deformation, and the ciliate escaped by jumping. It is therefore necessary to determine whether the escape velocity of entrained ciliates is sufficient to overcome the feeding current velocity of the copepod, as further detailed by Jakobsen et al. (2005).

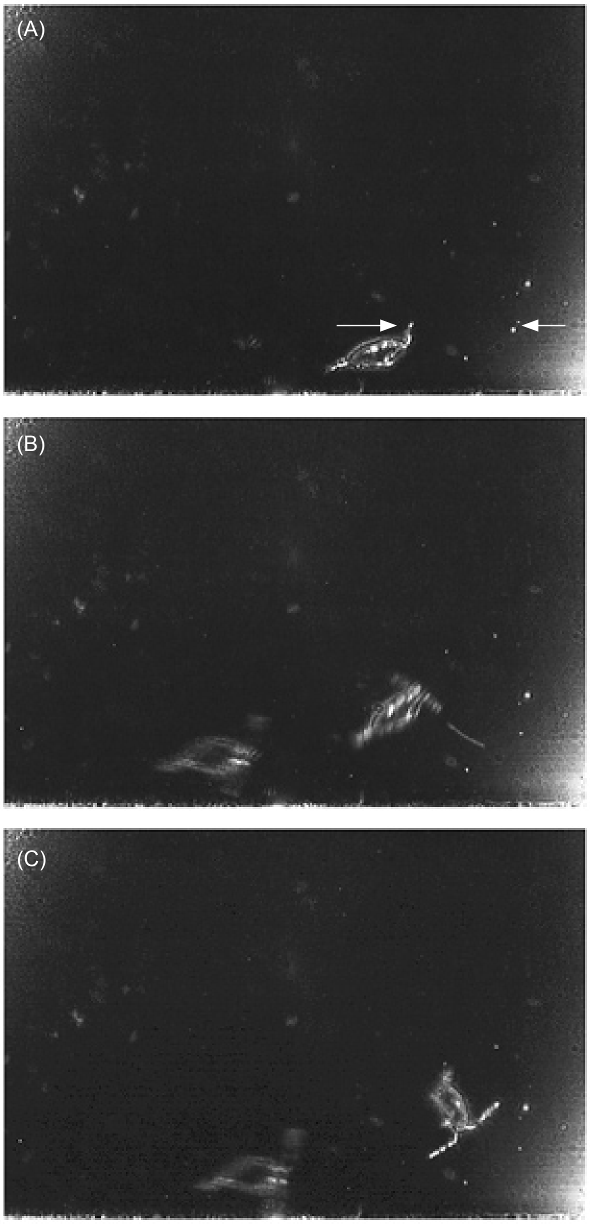


Fig. 4. Predator-capturing process of a *Strobilidium* sp. ciliate sequence. (A) *Temora turbinata* and the ciliate swimming towards each other (arrow indicates the swimming direction). (B) *Temora turbinata* jumps first (1 frame 1/30 s before), triggering the ciliate to escape by jumping (arrow indicates the swimming direction). (C) *Temora turbinata* capturing a ciliate.

Differences in the behavioral interplay between the copepod predator and ciliate prey may be a result of several factors. An ambushing copepod reacts to hydromechanical signals from a swimming ciliate and attacks. In a study by Tiselius and Jonsson (1990), the ciliate detected a copepod and escaped if its jumping/swimming speed was fast enough (see also Broglio et al. 2001). Different ciliate species may have different vulnerabilities to copepod predators, according to their behavior (Wiackowski et al. 1994). There also might be other factors involved, such as size and morphological differences on both sides of the predator-prey system (Jakobsen 2002, Dahms and Qian 2005).

A filter-feeding copepod like *T. turbinata* that swims constantly, greatly differs from a slowly sinking ambush predator that has the advantage of not being detected until it attacks. The cruising ambush predator *Centropages typicus*, in contrast, feeds selectively on ciliates (Wiadnyana and Rassoulsadegan 1989). If a mixed feeder like the calanoid *Acartia* sp. switches from an ambush-feeding mode to filter feeding when ciliate abundance decreases and algal abundance increases, the vulnerability of ciliates will decrease as well. In a study by Gismervik (2006), the stereotypical suspension feeding of *Pseudocalanus* sp. even led to the elimination of ciliates in the experimental container, as this copepod did not decrease its clearance rate at low food concentrations.

Turbulence

Predator-prey interactions are also affected by environmental factors such as turbulence (Hwang 1991, Hwang et al. 1994, Hwang and Strickler 1994 2001, Saiz and Kiørboe 1995). Feeding rates in the ambush mode of some species like *A. clausi* may be enhanced with certain levels of turbulence (Saiz and Kiørboe 1995). There are no such studies as yet on suspension-feeding species.

Effects of turbulence on prey/predator interactions are complex issues (Hwang 1991, Hwang et al. 1994, Hwang and Strickler 1994, 2001, Saiz and Kiørboe 1995). These complexities include factors such as sensitivity to prey behavior, habituation to prey behavior, and the encounter rate of prey. In a study by Waggett and Buskey (2007), *T. turbinata* showed a smaller reactive distance in response to turbulent conditions, suggesting that turbulence may have a greater effect on the copepod's ability to detect hydrodynamic signals such as those produced by a prey item. Copepods can hydromechanically differentiate external disturbances from their own feeding currents (Hwang and Strickler 2001).

The present study showed a wide variance in the measured reaction distances (0.64 ± 0.32 mm) of *T. turbinata* in response to a swimming ciliate.

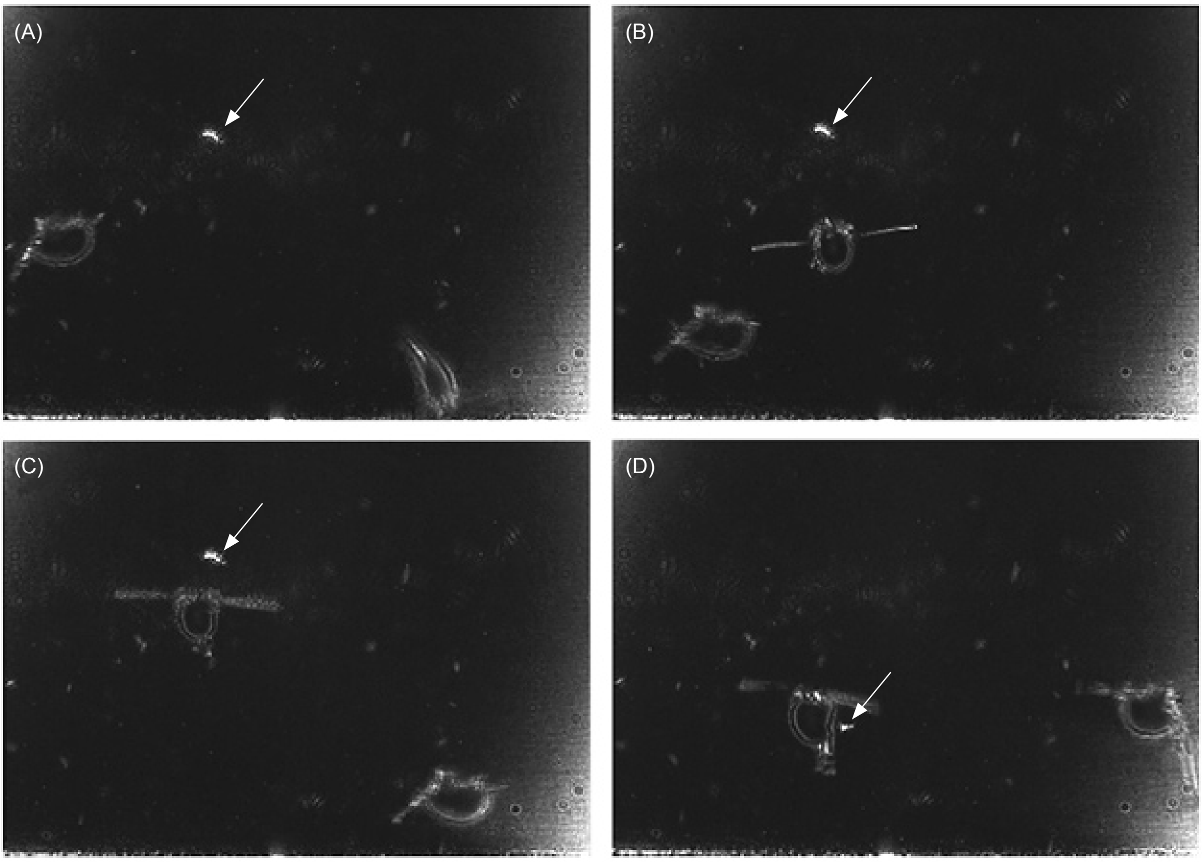


Fig. 5. *Temora turbinata* can differentiate between live and inert food particles. (A) Horizontal swimming of *T. turbinata*. (B) *Temora turbinata* detecting a particle and changing its swimming direction. (C) *Temora turbinata* swimming towards the particle and pausing to capture it. (D) *Temora turbinata* holding on to a particle for about 1 s before discarding it.

Svensen and Kiørboe (2000) found a similar variation in the mean reaction distance of 0.14 ± 0.07 mm for *O. similis* using its 1st antenna to detect the dinoflagellate, *Gymnodinium dominans*. They used the mean of the measured reaction distances for an encounter-rate model (Svensen and Kiørboe 2000), which implied that the predator displayed behavioral responses to a prey item when a threshold signal strength was exceeded.

Escape

We interpreted spinning and other evasive behaviors such as jumping as predator-deterrent strategies by ciliates. Wickham (1995) found that while cyclopoids were capable of having a very considerable impact on ciliate populations, some ciliate species appear to have behavioral, morphological, or chemical defenses that reduce their vulnerability. Escape jumps commonly involve a change in swimming direction followed by a drastic increase in swimming velocity (Jakobsen 2002). The escape of the ciliate did not trigger an attack response by *T. longicornis* in any of the interactions viewed by Jakobsen (2002). This is in contrast to other studies on interactions between copepods and their prey, in which prey-escape responses elicited an attack response from the predator (Yen and Strickler 1996). A possible explanation for the lack of a copepod attack response may be that the hydromechanical signals generated by the escaping *Strobilidium* sp. were too weak to be detected and the fact that *T. longicornis* showed low sensitivity to motile prey. A self-propelled particle moving in a fluid generates an anterior fluid wake (Visser 2001). The mechanosensory setae on the 1st antenna of copepods may sense such a wake and warns the predator about the presence and spatial location of the prey (Yen et al. 1992). The prey size, prey swimming velocity, and distance to the copepod at which the prey escapes determines the magnitude of the wake signal perceived by the copepod (Kiørboe et al. 1999).

Available studies show that jumping by protozoans like ciliates appeared to enhance survival from predators that generate a feeding current (Jakobsen 2002). Ciliates are eaten by copepods although the same ciliates may feed on flagellates entrained in the copepod's feeding current. Only a few studies demonstrated ciliate behavior relating to predator-prey encounters (Stoecker 1995).

In conclusion, we found that the spinning ciliate was able to sense the copepod from a longer distance and escaped from the feeding current with a faster response than did *Strobilidium* sp. We suggest that spinning and other evasive behaviors such as jumping are predator-deterrent strategies by ciliates. We demonstrated that *T. turbinata* can differentiate between living and non-living organisms and ejects non-ingestible particles.

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