Trophic interaction between copepods and ciliates: effects of prey swimming behavior on predation risk

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ABSTRACT: The transfer of matter and energy in planktonic food webs is determined by the encounter rate between predators and prey and subsequent attack and capture success. We tested if differences in swimming behavior and escape ability of 2 planktonic ciliates could explain differences in their susceptibility to predation from the calanoid copepod *Acartia clausi*. We chose 2 similarly sized ciliates, which exhibited very different swimming behavior: *Strobilidium spiralis* (Strobilidiina) and *Metacylis* sp. (Tintinnina). Behavioral analyses were combined with feeding incubations. The behavior of *S. spiralis* was characterized by slow upward and downward swimming interrupted by sudden jumps. *Metacylis* sp. showed a swimming pattern typical for many tintinnids, with steep helical trajectories and without jumps. Feeding experiments while *A. clausi* was incubated in a 1:1 mixture of both ciliate species showed a higher predation rate on *Metacylis* sp. According to behavioral observations, the copepod exhibited a 2-fold difference in ingestion rate between the ciliate species. Furthermore, film analyses revealed that *S. spiralis* escaped the attacking predator with rapid jumps while *Metacylis* sp. lacked any effective behavioral response to the approaching predator. We discuss the relative importance of velocities and dispersal rates in encounter processes and conclude that the escape response shown by *S. spiralis* significantly reduces the risk of predation. This study emphasizes the importance of mechanistic knowledge at the level of behavior and individual sensory abilities to improve present models of biogeochemical fluxes in the water column.

KEY WORDS: Predator-prey interaction · Swimming behavior · Ciliate · Copepod · *Acartia clausi*

INTRODUCTION

During the last 2 decades, ciliates have been shown to be an important food source for zooplankton in both marine (Stoecker & Capuzzo 1990, Verity & Paffenhöfer 1996) and limnic systems (Adrian & Schneider-Olt 1999). Ciliates may here act as a significant link between microbial food webs and the classical diatom-copepod-fish food webs (Cushing 1990) with implications for the flow of matter and energy in the pelagial (Azam et al. 1983, Sherr & Sherr 1986). Although the interest in this subject has increased during the past

years, an improved mechanistic approach is needed to understand the importance and magnitude of this link and to determine the factors involved in predator and prey dynamics. Studies of the interactions between copepods and ciliates have mostly focused on measurements of copepod clearance rates based on the disappearance of ciliates in laboratory and field incubations. Only few works have considered the encounter and post-encounter processes at the individual scale. For instance, using videography, Jonsson & Tiselius (1990) described the raptorial feeding behavior of the copepod *Acartia tonsa* when encountering planktonic ciliates. These authors showed that the escape response of the ciliate *Mesodinium rubrum* reduced pre-

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dation by *A. tonsa.* Similarly, in fresh water systems ciliates moving with jumps appeared to be less susceptible to predation by cladocerans (Jack & Gilbert 1993), rotifers (Gilbert & Jack 1993, Gilbert 1994) and copepods (Burns & Gilbert 1994). However, how changes in prey behavior can affect the outcome of both encounter and post-encounter processes is still scarcely known.

The aim of this work is to investigate if differences in swimming behavior of 2 similarly sized ciliates can affect the predation risk from the copepod *Acartia clausi*. First, we test for differences in ciliate swimming patterns and possible behavioral changes in the vicinity of a predator. Second, copepod attacks on the 2 ciliates are recorded and the capture success measured. Finally, the behavioral studies are combined with incubation experiments where *A. clausi* is offered a 1:1 mixture of both ciliates.

MATERIALS AND METHODS

Culture and collection of organisms. The strobilidid *Strobilidium* (*Lohmanniella*) *spiralis* (Leegaard 1915) and the tintinnid *Metacylis* sp. were isolated from waters of Tjärnö Marine Biological Laboratory (TMBL), on the west coast of Sweden (58° 38′ N, 11° 45′ E). *Metacylis* sp. resembles *Metacylis jorgensenii* Cleve (1902) with a slightly pointed hyaline lorica. The ciliates were similar in size (measurements in 1 % Lugol's acid solution preserved specimens; *S. spiralis*: body length 59 ± 3.2 µm, width 55 ± 4.4 µm; *Metacylis* sp.: lorica and body length 52 ± 2.6 µm, width 49 ± 2.1 µm), and abundant at the site of collection. Ciliates were grown in a suspension of the microalgae *Isochrysis galbana* Parke 1949 (Prymnesiophycae) and *Pyramimonas disomata* Butcher 1959 (Prasinophycae) in filtered, autoclaved (120°C, 20 min) brackish seawater (15‰ S). Stocks of both ciliates were routinely kept in 50 ml culture flasks. Larger quantities of ciliates required for the experiments were grown in glass bottles (620 ml, Pyrex) kept on a plankton wheel (0.25 rpm) on the same diet. Approximately 100 ml of the culture was renewed with fresh medium every day to ensure a supply of exponentially growing algae for the ciliates. All cultures were maintained at room temperature (20°C) under a natural light cycle (17:7 h light:dark). Adult females of the copepod *Acartia clausi* (Giesbrecht 1889) were picked out from net tows (mesh size 160 µm) in coastal waters off TMBL. This copepod was dominant in the field and co-occurred with the isolated ciliates. Prior to each filming copepods were starved for 30 min in filtered, autoclaved, seawater (17.5‰ S).

Video recording. Observations of the behavior of the copepod and the ciliate prey were obtained by video recording the copepods in a suspension with a single prey species. For each recording, ciliates and approximately 20 adult females of *Acartia clausi* were added to an experimental aquarium (20 · 5 · 5 cm). The aquarium was placed inside a larger transparent tank (17 · 17 · 17 cm) filled with distilled water and fitted with a cooling device at the bottom in order to maintain the temperature as constant as possible (22 to 23°C) and to avoid convection currents. Observations were made using a horizontally mounted dissecting microscope (Wild M5A, 6 to 50·) equipped with a video camera (Minitron MTV-1802CB, 795 · 596 pixels, light sensitivity 0.01 lx) and recorded on VHS tape, at 50 frames s⁻¹. The field of view was 10 · 7.5 mm. Filming took place in a dark room and aquariums were illuminated by a back-transmitted red light (670 nm). The ciliates used for filming came directly from the cultures, and consequently they had ample supply of *Isochrysis galbana* and *Pyramimonas disomata*. Two cases were considered regarding the observations of ciliate behavior: sequences where no copepods appeared on the screen (called *undisturbed* hereafter), and those where an approaching copepod was present, sometimes leading to an attack against a ciliate. Frame-by-frame analysis of the video-recorded sequences was performed to quantify motility patterns of undisturbed ciliates and ciliates close to an approaching copepod. On the videotape, 10 to 15 individuals for each species were randomly selected and their positions traced onto acetate sheets frame by frame until out of focus. Ciliate positions on the acetate sheets were determined with a digitizing tablet and distances computed. Because filming was in 2 dimensions (XZ), we selected ciliates that were swimming perpendicular to the camera axis; hence displacement of the animals was measured in the XZ plane. Since measurements were based on 2-dimensional projections of 3-dimensional displacements, the estimates of swimming velocities and distances will be underestimated. However, we think that 2D analysis must not bias the comparison of swimming patterns between both ciliate species, as it does not seem likely that 1 ciliate species moves more in the XZ plane than in the YZ plane. Each sequence analyzed was ca 20 s for *Strobilidium spiralis* and 3 s for *Metacylis* sp. The difference in observation time between the 2 ciliates reflects the difference in swimming behavior: more positions per s had to be analyzed to describe the convoluted helical swimming path of *Metacylis* sp., while longer sequences were needed for *S. spiralis* in order to have appropriate resolution of its path (including sinking period and jumps). The mean swimming speed was calculated as the total length of the swimming path divided by the duration of the path. The overall mean swimming speed was computed by weighting the path means for

each ciliate by the observation time. Both average jump length and jump speed were weighted by the number of events (jumps) and observation time recorded for each individual ciliate. When ciliates were approached by a copepod, if they performed more than one jump to escape from the copepod, only the first jump was used for calculations.

As a rough estimate of differences in diffusion rate between both ciliates, a 2-dimensional dispersal rate coefficient (XY plane; area s^{-1}) was determined by measuring the time required for a ciliate to move to the periphery of a given circle centered on a random position in its swimming path. We used 2 circle areas (of 4 and 16 mm^2 respectively) to account for a possible scale dependence of the dispersal rates.

Aspects of the foraging behavior of *Acartia clausi* preying on the 2 ciliates were also measured. 'Reaction distance' for the copepod was determined by measuring the shorter distance between the ciliate and the copepod head immediately prior to an attack. We defined 'attack' as the jump (or the last jump in case of a chase) shown by the predator towards the ciliate, usually with a change in the orientation of the copepod. Attacks were divided into 3 groups depending on the final outcome: escaped, missed and captured. 'Escaped' was the case when the ciliate jumped away from the predator; 'Missed' was when the copepod failed to accurately locate the prey. The group 'Captured' consisted of 2 subgroups: the attacks where the ciliate was eaten ('Eaten') and attacks where the prey was lost after being handled ('Lost').

Incubation experiments. Prey selection by the copepod *Acartia clausi* was tested in incubation experiments where copepods were offered a 1:1 mixture of the ciliates *Strobilidium spiralis* and *Metacylis* sp. Two incubation experiments were run with an identical protocol but with different ciliate concentrations: for each species, 14 ciliates ml^{-1} and 5 ciliates ml^{-1} respectively. Ten glass bottles (620 ml, Pyrex) were filled with suspensions of the 1:1 ciliate species at desired concentrations. Two of the bottles were used to determine the initial ciliate concentration (100 ml aliquots preserved in 1% Lugol's acid solution). Four bottles (without copepods) were used as control and 4 bottles were filled with 4 to 5 adult females of *A. clausi* each. All bottles were sealed with plastic film and capped, then incubated on a plankton wheel (0.25 rpm) at room temperature (20°C). The experiment was run for 24 h and the contents of the bottles were gently filtered through a submerged mesh (180 μm) to collect the copepods, and 100 ml of the screened water which were fixed in Lugol's acid solution. Ciliates concentration were determined in 50 ml aliquots of the preserved samples settled in Utermöhl chambers and counted under a microscope. A total of 300 to 600 ciliates were counted per sample. Ingestion and clearance rates were calculated according to the equations of Frost (1972).

Statistical analysis. All means are presented with the standard error of the mean (SE) and the sample size. Ciliate swimming speeds were analyzed in a 2-factor analysis of variance (ANOVA) with species and the presence/absence of a predator as fixed factors. Differences in ciliate jump length and velocity during spontaneous jumps and jumps performed when approached by a copepod, and during copepod attack were tested with a 1-factor ANOVA and Student-Newman-Keuls (SNK) means comparison test. The hypothesis of a difference in escape capability between the ciliate species was tested with a *G*-test (Sokal & Rohlf 1994) using the clearance rates in Table 3. The difference in predation mortality between the ciliate species was tested in a 2-factor ANOVA using the results on clearance rates in the feeding experiments (see Table 4). The 2 experiments were analyzed jointly where each experiment was regarded as 2 levels in a random factor and the 2 ciliate species as a fixed factor. Since the interaction term was highly non-significant it was pooled with the residual term. The data analyzed with ANOVA were first tested for homoscedasticity using Cochran's test (Winer et al. 1991). In all tests a type-I error (α) of 0.05 was used.

RESULTS

Prey swimming behavior in undisturbed situations

The ciliates *Strobilidium spiralis* and *Metacylis* sp. showed very different swimming patterns (Fig. 1). Like many other species in the Strobilidiidae family, *S. spiralis* moved forward slowly while generating a strong feeding current. When not disturbed by the raptorial copepod *Acartia clausi* (undisturbed ciliates), *S. spiralis* alternated between periods of slow upward swimming interrupted by sudden jumps involving very rapid swimming and periods of helical downward swimming. Mean swimming speed was 0.33 ± 0.02 mm s^{-1} (n = 11). Jump frequency was 5.7 ± 1.6 jumps min^{-1} and mean jump length and velocity were 0.36 ± 0.05 mm and 3.93 ± 0.39 mm s^{-1} respectively (Table 1).

Metacylis sp. showed a swimming pattern with steep helical trajectories interrupted with occasional ciliary reversals (only 3 events observed). No jumps were observed for this species. When away from any approaching copepod, the tintinnid *Metacylis* sp. moved at a mean speed of 0.78 ± 0.06 mm s^{-1} (n = 15).

Although *Strobilidium spiralis* showed a lower mean speed than *Metacylis* sp., the differences in swimming behavior (i.e. upward and downward swimming, and jumps for *S. spiralis*, continuous helical paths for *Meta-*
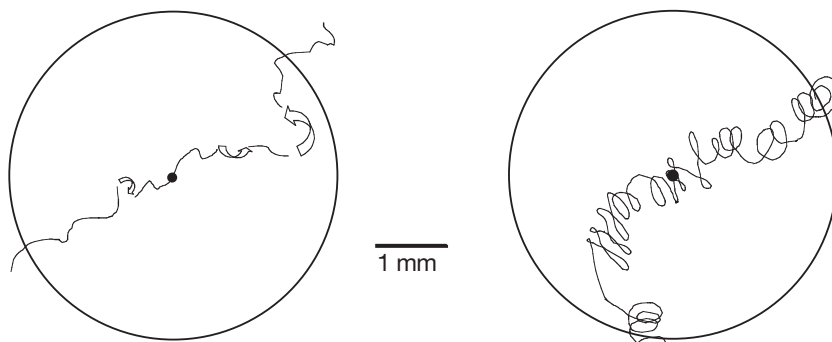
Strobilidium spiralis

Length of the path: 7.85 mm
Duration of the path: 23 s

Metacylis sp.

Length of the path: 11.56 mm
Duration of the path: 20 s

Fig. 1. Swimming patterns of (A) *Strobilidium spiralis* and (B) *Metacylis* sp. Arrows indicate jumps. The 4 mm^2 circle used to calculate the dispersal rate is shown. The dispersal rate was estimated measuring the time required for the ciliate to move to the periphery of the circle, centered (black point) on a random position in the swimming path

cylis sp.) resulted in a 1.5 times higher dispersal rate for *S. spiralis* (small sample area: 1.18 ± 0.09 mm^2 s^{-1}; large sample area: 2.14 ± 0.18 mm^2 s^{-1}, n = 23) than for *Metacylis* sp. (small sample area: 0.74 ± 0.08 mm^2 s^{-1}; large sample area: 1.50 ± 0.15 mm^2 s^{-1}, n = 19).

Prey-predator interactions

When a sinking copepod detected a ciliate, it reoriented its body towards the prey and attacked. There was no need for physical contact between the copepod and a ciliate to trigger an attack. When the attack resulted in a successful capture, the ciliate was handled for a very short period of time before being ingested (<1 s).

Although true detection distances cannot be estimated from our observations, a minimum estimate can be obtained from the distance at which the prey triggered an attack from the copepod. Reaction distance differed for the 2 ciliates. Thus, the *Acartia clausi* average attack distance for *Strobilidium spiralis* was 0.69 ± 0.11 mm (n = 16) measured from the head tip, while the distance was 0.40 ± 0.05 mm (n = 21) for *Metacylis* sp. Despite the higher reaction distance of the copepod for *S. spiralis*, the capture success was much lower than for *Metacylis* sp. (*G*-test, p < 0.05). In the case of *S. spiralis*, only 32% of the observed attacks resulted in successful captures and ingestion; the per-

centages of the attacks where the ciliate was lost, missed, or it jumped away escaping the predator are shown in Table 2. When *A. clausi* attacked *S. spiralis*, the reaction distance was significantly greater (*t*-test, p < 0.05) for unsuccessful attacks (0.81 ± 0.12 mm) than for attacks resulting in eventual capture of the ciliate (0.52 ± 0.20 mm).

Although for *Metacylis* sp. a higher proportion of the attacks resulted in capture and ingestion (64%, Table 2), the percentage of missed prey (32%) was also higher in comparison to *Strobilidium spiralis* (16%). Frequently, the copepod slowly approached the tintinnid before lunging into attack, to assure the capture. After being captured, the capacity of *Metacylis* sp. to avoid ingestion was very low (4% of the observed attacks).

Measurements of swimming behavior of *Strobilidium spiralis* and *Metacylis* sp. differed when in close vicinity of a copepod compared to observations well away from any copepod. When approached by a copepod, the mean swimming speed of *S. spiralis* increased from 0.33 ± 0.2 to 0.51 ± 0.15 mm s^{-1} (n = 5). Escape jumps were longer and faster than jumps performed by undisturbed ciliates (ANOVA, $F_{2,28} = 16.8$, p < 0.05) (Table 1) and the frequency of jumps increased after a copepod attack (18.5 ± 4.2 jumps min^{-1}). We also observed that in the proximity of the copepod, *S. spiralis* often initiated a jumping response at a mean distance of 0.53 ± 0.07 mm from the copepod head (n = 10), indicating that the ciliate may detect the presence of the copepod in advance of an attack. Ciliate jumps initiated by an approaching copepod were also longer and more rapid compared to jumps in the absence of any copepod (1-factor ANOVA, $F_{2,28} = 16.7$ and SNK test, p < 0.05; Table 1).

Table 1. Length and velocity of jumps performed by *Strobilidium spiralis*. Jumps are classified into 3 scenarios: 'undisturbed' (i.e. when ciliates were far from predators), 'in danger' (i.e. when jumps were triggered by the predator presence) and 'escape' (i.e. when ciliates were escaping from the predator). n = sample size. When more than one jump was performed as a response to the predator, only the first one was measured

Scenario	n	Jump length (mm)	Jump velocity (mm s^{-1})	Maximum jump velocity (mm s^{-1})
Undisturbed	20	0.36 (± 0.05)	3.93 (± 0.39)	6.37
In danger	15	2.19 (± 0.37)	6.48 (± 0.50)	10.45
Escape	7	2.80 (± 0.40)	9.46 (± 0.51)	11.85

Table 2. Behavioral analysis of copepod-ciliate interactions. Frequencies (as %) of the different outcomes of the interaction. For *Strobilidium spiralis* and *Metacylis* sp., 19 and 22 attacks were analyzed, respectively

Species	Escaped	Missed	Captured	
			Lost	Eaten
S. spiralis	36	16	16	32
Metacylis sp.	0	32	4	64

Metacylis sp. did not show any escape (jump) response triggered by an approaching or attacking *Acartia clausi*. However, the swimming speed increased after an unsuccessful attack by the copepod (1.05 ± 0.18 mm s^{-1}, n = 5) and the ciliate seemed to move in a steeper helical path. The increased swimming velocity may have contributed to the unsuccessful attacks performed by the copepod. Interestingly, we observed that some individuals of *Metacylis* sp., when lost after being handled by the copepod became motionless for a few seconds before resuming swimming again and were no longer pursued by the predator after the first attack. This behavior was not observed for *Strobilidium spiralis*.

Feeding experiments

Both feeding experiments of *Acartia clausi* incubated in 1:1 mixture of ciliate suspension showed an unequal consumption of the 2 ciliate species (2-factor ANOVA, pooled $F_{1,13} = 12.0$, p < 0.05), with much higher clearance rates for *Metacylis* sp. in comparison with *Strobilidium spiralis*. This effect was most evident at the lowest ciliate concentration, where consumption rates on *S. spiralis* were sometimes below detection. Averaged over both experiments the copepod clearance rate for *Metacylis* sp. was almost 7-times higher than for *S. spiralis* (Table 3).

DISCUSSION

In coastal and oceanic environments the populations of marine planktonic ciliates are frequently limited by high predation rates by mesozooplankton (Stoecker & Capuzzo 1990, Nielsen & Kiørboe 1994). However, small-scale predation and eventual capture depend on specific predator and prey behavior. Planktonic ciliates show a wide diversity of swimming patterns including different helical trajectories, rapid jumps, ciliary reversals and periods of inactivity and sinking (e.g. Buskey et al. 1993). The main hypothesis tested in the present paper is if differences in swimming behavior between

Table 3. Summary of the 2 feeding experiment where the copepod *Acartia clausi* was offered a 1:1 mixture of the 2 ciliates *Strobilidium spiralis* and *Metacylis* sp. Copepod clearance rates (mean ± SE, n = 4) for the 2 ciliate species are based on 24 h incubations and corrected for ciliate growth. Two experimental bottles resulted in negative clearance rates due to very low consumption rates and they were rounded up to zero

Experiment	Ciliate prey	Copepod clearance (ml copepod^{-1} d^{-1})
Expt 1 (28 cil. ml^{-1})	*S. spiralis*	12.2 ± 4.4
	Metacylis sp.	40.1 ± 20.6
Expt 2 (10 cil. ml^{-1})	*S. spiralis*	6.6 ± 6.0
	Metacylis sp.	73.8 ± 15.9

2 ciliates result in higher survival rates in the presence of the copepod *Acartia clausi*. The ciliates *Strobilidium spiralis* and *Metacylis* sp. were selected because they are of similar size but differ in their swimming paths and in their ability to react to fluid disturbances. *S. spiralis* has a richer repertoire of swimming behavior with upward and downward swimming and jumps, while *Metacylis* sp. swims upwards in helical trajectories and lacks jumps, as is typical for many tintinnids. In our experiments, both ciliate species, *S. spiralis* and *Metacylis* sp., were attacked and could be ingested by *A. clausi*.

Analysis of the encounter and post-encounter processes can provide possible explanations of the mortality differences found for the 2 ciliate species. According to our estimated dispersal rates *Strobilidium spiralis* had a higher probability of encounter with the predator (1.5 times) than *Metacylis* sp. Previous encounter models have proposed algorithms to calculate the encounter rate using some detection distance and assuming a random motility of predator and prey, e.g. Gerritsen & Strickler (1977) and Tiselius at al. (1997). Gerritsen & Strickler's model defines encounter rate as a function of the area over which the interaction occurs, the abundance of the prey and the relative velocities of predator and prey. Under the presence of a cruising predator, the swimming speed of the prey has little effect on encounter if the velocity of the predator is higher than that of the prey. However, when the predator is an ambush feeder, as in the case of *Acartia clausi* feeding on ciliates, the swimming velocity of the prey may have a strong effect on the encounter rate. Tiselius et al. (1997) incorporated into that model the hydrodynamic signaling produced by a jumping prey as a mechanism to increase the perceptive distance of the predator, and consequently the encounter rate. Using our data on swimming speed and jump behavior, and applying the model of Tiselius et al. (1997), we find that the encounter rate of *Meta-*

cylis sp. with the predator is expected to be higher (1.6-times) than for *S. spiralis*. This result contrasts with our observation (i.e higher dispersal of *S. spiralis* than *Metacylis* sp.) and is mainly a consequence that their model takes into account only the velocity of the prey (which in our case is higher for *Metacylis* sp.) but not the structure of the prey swimming path (more convoluted trajectories for the ciliate *Metacilys* sp. while displacement is higher for the ciliate *S. spiralis* mainly because of the jumping behavior).

On the other hand, although we would predict a higher encounter rate of *Acartia clausi* with *Strobilidium spiralis*, our behavioral observations conducted for each species separately indicate that *Metacylis* sp. would be the preferred prey. Our feeding incubation experiments on a mixture of the 2 ciliates confirm this observation (Table 4).

From our study, it appears that the susceptibility to predation on ciliates is very dependent on their escape ability (either before being detected or while being attacked by the predator), becoming more determinant than differences in encounter rates mediated by their swimming (cruising velocity, dispersal rate). In the present study, *Strobilidium spiralis* showed an effective jump response to copepod attacks. The escape jumps shown by *S. spiralis* reached velocities above 10 mm s^{-1} (ca 200 body lengths s^{-1}) with an average length of 2.8 mm. In contrast, the investigated tintinnid *Metacylis* sp. does not jump during swimming and does not show escape reactions to an approaching predator. Jump behavior in response to hydrodynamic signals have been described for some other ciliates, e.g. *Mesodinium rubrum* (Lindholm 1985, Jonsson & Tiselius 1990) and the freshwater ciliates *Strobilidium velox* (Jack & Gilbert 1993, Gilbert 1994) and *Halteria grandinella* (Tamar 1974, Gilbert 1994), but is probably more widespread as indicated in some descriptions of

ciliates (e.g. Kahl 1932). Therefore, although jumps could act as a mechanism to avoid capture by a predator, it has been suggested that the strong hydrodynamical signals generated by jumps could alert the predator and facilitate the detection and eventual attack by the predator (Tiselius et al. 1997). Actually, using our data and applying the encounter model presented in Tiselius et al. (1997) that assumes a random motion, about 40 % of the encounters with a predator like *Acartia clausi* should occur during jumps despite that the ciliates only spend ca 1 % of the time jumping. It can only be speculated that the jump behavior also serves other functions, maybe to efficiently shed the envelope of water around the ciliate that may be depleted of food particles and replete with excretion products. However, we need to remark that although previous results and our experiments suggest that escape can be considered an efficient way to avoid capture by a potential predator, rates of copepod predation on ciliates can vary considerably for different combinations of copepod and ciliate species (Wickham 1995). For instance, Burns & Gilbert (1993) found that copepods efficiently preyed on the jumping ciliate *S. velox*, indicating that the escape response may only give protection against slower predators. Moreover, Jonsson & Tiselius (1990) found high clearance rates for *A. tonsa* when feeding on *S. spiralis* despite its jumping behavior, suggesting that *A. tonsa* is a more efficient predator on fast-moving prey than *A. clausi.* The lack of escape responses and the presence of a dense lorica around the cell body suggest a different defense strategy for the tintinnid *Metacylis* sp. It can be speculated that the lorica may protect motionless tintinnids against some predators, causing rapid sinking during the attack and making capture and handling more difficult. The lorica may also shield the diffusion of chemical substances that may be required by some

Table 4. Overview of relative susceptibilities of the 2 ciliate species as estimated from behavioral observations and from feeding incubation experiments. Relative susceptibility is defined as the ratio between the corresponding values (either concentrations, ingestion or clearance rates) for *Metacylis* sp*.* versus *Strobilidium spiralis*. (a) Nominal prey concentration, assuming an equal value of 100. (b) Effective prey concentration (i.e. encountered), considering that the dispersal of *S. spiralis* is 1.5 · that of *Metacylis* sp. (c) Attack success (as % of prey ingested after attack, see Table 2). (d) Expected ingestion rate calculated as the effective prey concentration times the attack success. (e, f) Clearance rates on both ciliates from experiments with mixtures (see Table 3)

	Parameters	*S. spiralis*	*Metacylis* sp.	Ratio
From behavioral observation				
a	Nominal prey concentration	100	100	1
b	Effective prey concentration	150	100	0.7
c	Attack success (%)	32	64	–
d	Expected ingestion rate	48	64	1.3
From feeding experiments				
e	Clearances rates from Expt 1	12	40	3.3
f	Clearances rates from Expt 2	7	74	11

predators to complete ingestion (Capriulo et al. 1981). However, tintinnids have been found in the gut contents and fecal pellets of copepods, and many others mesozooplankters (Gilmer & Harbison 1991), indicating that a lorica does not protect against many predators.

Interestingly, the differences in encounter probability and escape ability between *Strobilidium spiralis* and *Metacylis* sp. do not explain the ca 7-fold difference in clearance rate found in the feeding experiments. First of all, our behavioral results could have underestimated the advantage of the escape response since the analysis did not include events where *S. spiralis* detects the approaching copepod first and escapes without triggering a copepod attack. Secondly, our prey-predator behavioral interaction was analyzed following the predator with a single prey at a time while feeding experiments were made in mixture of both ciliates.

A prey switching behavior might be an explanation of the high predation pressure on *Metacylis* sp. and it can be supposed that the more easily caught *Metacylis* sp. may have induced a switch to selective feeding by *Acartia clausi* on the tintinnid. There is previous evidence of prey switching in copepods in relation to prey size and velocity and also to turbulence (Landry & Fagerness 1988, Kiørboe et al. 1996). In natural systems, predators encounter a diversity of prey types, differing not only in abundance but also in size, motility, taste and nutritional quality. In this diverse prey environment, switching should represent a strategy to optimize the predator intake of energy in presence of an alternative prey (Pyke 1984). In effect, switching strategies may have a considerable effect on prey composition in pelagic systems with copepods controlling ciliate abundance due to higher selectivity for ciliates over algae (Gismervik & Andersen 1997).

In conclusion, we would like to emphasize the importance of small-scale processes in predator-prey interactions. Not only swimming speed but also the shape of swimming paths can affect dispersal rates and consequently encounter rates. Moreover, we have shown that post-encounter processes, like the ability to escape, can significantly change the outcome of the encounter. Further research should focus on other mechanisms, like switching behavior, which might greatly outweigh escape behavior and predator perceptive abilities considered in isolation.

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