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Behavioural and morphological changes in ciliates induced by the predator *Amoeba proteus*

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Abstract. The predator *Amoeba proteus* induced behavioural and morphological changes in ciliates of the genus *Euplotes*. The frequency of avoidance behaviour in *E. octocarinatus* increased from 16 ± 5% to 84 ± 5% (SD) after 14 h of coexistence with the predator. The ciliate's width increased from 59 ± 3 μm to 77 ± 4 μm (SDM) within 48 h. Similar behavioural, but not morphological, change was induced in *E. daidaleos*, but neither morphological nor behavioural responses occurred in *E. aediculatus*. *E. octocarinatus* and *E. daidaleos* populations survived in the presence of *A. proteus*, whereas *E. aediculatus* populations became extinct by predation. Induced behavioural response seemed to be the reason for the low predation risk of *E. octocarinatus* and *E. daidaleos*. The results suggest that *Euplotes* ciliates have evolved specific defence mechanisms to various predators. Defensive changes are induced by a chemical substance released from *A. proteus*. This "kairomone" has a molecular weight between 5000 and 10000 Da. Proteolytic digestion of its activity indicated that the avoidance-inducing substance is a peptide. After the turbellarian *Stenostomum sphagnetorum* had induced a defensive morphology in *E. octocarinatus* or *E. aediculatus*, neither of these ciliates immediately avoided *Amoeba proteus*. Thus, *Euplotes* ciliates with a defensive morphology do not have behavioural defences in reaction to all predators.

Key words: Avoidance behaviour – Defensive morphology – Phenotypic plasticity – Predation – Protozoa

Phenotypic plasticity may be important in reducing the effect of predation in aquatic ecosystems. Potential prey organisms can often detect the presence of predators and alter their own morphology (reviewed by Havel 1987; Appleton and Palmer 1988; Washburn et al. 1988; Wicklow 1988; Dodson 1989; Tollrian 1990; Brönmark and Miner 1992; Kusch 1993a), life history (Lüning 1992; Crowl and Covich 1990; Stibor 1992), or behaviour (e.g. Lampert 1993). Induced behavioural changes are known in cladocerans (Havel and Dodson 1984; Dodson 1988; Loose 1993; Loose et al. 1993), copepods (Neill 1990), and aquatic insects (e.g. Peckarsky 1980; Sih 1982, 1986; Dawidowicz et al. 1990). Predators induce avoidance behaviour in these prey organisms, and in *Daphnia*, *Chaoborus* larvae and in several mayfly nymphs the stimuli are transmitted in the form of chemical substances. Chemical cues ("kairomones", Parejko and Dodson 1990) also are responsible for predator-induced morphological changes in metazoan prey (Gilbert 1966; Halbach 1970; Hebert and Grewe 1985; Parejko and Dodson 1990) and in protozoan prey (Washburn et al. 1988; Wicklow 1988; Kusch 1993a).

Various predaceous ciliates (e.g. *Lembadion bullinum;* Kuhlmann and Heckmann 1985), the turbellarian *Stenostomum sphagnetorum,* and *Amoeba proteus* (Kusch 1993a) induce defensive morphological changes in several ciliates of the genus *Euplotes*. In the presence of one of these predators the prey ciliates develop extended lateral "wings" and dorsal and ventral protuberances. Thereby the prey ciliate shape changes from a typical ovoid form to an enlarged circular form. Morphological changes take place within 2–4 h and they are induced without direct contact between prey ciliates and their predators. Signal substances initiating the changes are transmitted by the surrounding medium. The extent of morphological changes depends on the concentration of the chemical cues (Kusch 1993a). Two of these signal substances have been isolated from the medium of *Lembadion bullinum* (Kusch and Heckmann 1992) and *Stenostomum sphagnetorum* (Kusch 1993b). The signal molecules were proteins with molecular masses of 31.5 kDa and 17.5 kDa, respectively.

Enlargement of potential prey organisms limits the chances of predation by size-selective predators as *Lembadion* or *Stenostomum* (Kuhlmann and Heckmann, in press). Only size-selective predators are known to induce morphological defence in *Euplotes*. Since amoebans do not have well defined mouth openings, food consumption by *Amoeba proteus* is less restricted in terms of particle size. Therefore the effect of predation by *A. proteus* on behaviour of *Euplotes* ciliates was investigated. I here report on behavioural responses of *Euplotes* to the presence of *A. proteus*. Behavioural changes are more significant in reducing the risk of predation than morphological ones. In addition the chemical signal inducing phenotypical changes is described.

Materials and methods

Organisms and culture conditions

Amoeba proteus was cultivated at 20° C in SMB medium (synthetic medium for *Blepharisma;* 1.5 mM NaCl, 0.05 mM KCl, 0.4 mM $CaCl_2$, 0.05 mM $MgCl_2$, 0.05 mM $MgSO_4$, 2.0 mM sodium phosphate buffer, pH 6.8). The ciliate *Colpidium campylum* was used as food. *Euplotes* ciliates were also grown in SMB medium, and they were offered the photosynthetic flagellate *Chlorogonium elongatum* as food.

Evaluation of morphological and behavioural changes

The experiments were set up by adding approximately 1000 well-fed *Euplotes* individuals ml^{-1} to a culture of *Amoeba proteus* or to *Amoeba*-conditioned medium. The mixtures were incubated for certain periods at 20–22° C, and then *Euplotes* ciliates were examined for induced morphological or behavioural changes. The diameter of the *Euplotes* cells was measured to determine morphological effects (Kusch 1993a, b). For this purpose cells were fixed by adding a 2.5% solution of glutaraldehyde to a sample (1:10, v/v). For each sample, the diameter of 40 *Euplotes* cells was measured in a Fuchs-Rosenthal-counting chamber with an ocular micrometer at a 400-fold magnification. Controls were carried out for each test series. For this purpose *Euplotes* cells were incubated in SMB medium without adding predators or predator-conditioned medium.

The behaviour of *Euplotes* was observed directly in mixed cultures. One hundred contacts between prey ciliates and *Amoeba* predators were observed in each of five identical experiments to describe the kind and frequency of behavioural response. At each contact, I noted whether *Euplotes* ciliates moved straight ahead across *A. proteus* cells, or whether the ciliates changed their direction away from the predator (avoidance behaviour).

To investigate the effect of chemical cues with respect to induction of defensive changes in *Euplotes*, 1000 ciliates in 250 µl SMB medium were added to 1 ml sterile filtered medium previously inhabited by amoebae. To compensate for bacterial or thermic degradation of signal substances during the time of incubation with *Euplotes*, 1 ml predator-conditioned medium was also added after 4, 14, 24, and 34 h, respectively. *Euplotes* cells that had been incubated in *Amoeba*-conditioned culture medium were added to *A. proteus* after the incubation periods (4, 14, 24, 34 and 48 h) and the behaviour of *Euplotes* ciliates was observed immediately.

Characterization of the signal substance(s)

Ultrafiltration experiments were done with Ultrafree-MC filter units (no. UFC3 LGC; and no. UFC3 LCC; Millipore, Eschborn, Germany) as described in the directions for use. Effects of the enzyme proteinase K on the signal substance were measured by determining changes of its defence inducing activity after incubation with this reagent. Twenty milligrams of lyophilized proteinase K-agarose (185 units/g agarose; Sigma, Deisenhofen, Germany) were suspended and washed three times in SMB and incubated with 1 ml conditioned medium at 37° C for 1 h. Following the incubation, the immobilized enzyme was removed from the samples by centrifugation (350 *g*, 2000 rpm, 1 min, Biofuge A, Heraeus, Osterode, Germany), and the supernatant was studied for its effect on the behaviour and morphology of *E. octocarinatus*. To examine a possible binding of the signal substance to the agarose of the immobilized enzyme, samples were incubated with agarose (Serva No. 11401 and No. 11397) alone, and the activity of the samples was subsequently measured.

Results

Predation risk

Amoeba proteus is able to prey on cells of *Euplotes aediculatus* that do not have any induced defence properties. In the presence of 10 *A. proteus* ml^{-1} the coexisting *E. aediculatus* population (160 ciliates ml^{-1}) was exterminated by predation in 10 days (Fig. 1). *E. octocarinatus* (Fig. 1), and *E. daidaleos* (data not shown), on the other hand, survived coexistence with *A. proteus* for 10 days. *E. aediculatus* populations cultivated without predators did not decrease (Fig. 1). During 10 days of cultivation predator populations increased their densities from 10 to 15 ± 2 (SD) amoebae ml^{-1} in the presence of *E. octocarinatus*, or to 29 ± 1 amoebae ml^{-1} in the presence of *E. aediculatus*.

Morphological changes

Differences in the size of the *Euplotes* species could be the reason for the observed differences in their vulnerability to predation. *Amoeba proteus* induced significant morphological changes in *E. octocarinatus* during 24 h of coexistence. At a density of 10 predators ml^{-1} the width of this ciliate increased from 59 ± 5 µm to 72 ± 8 µm (SD) (Student's *t*-test, $P \ll 0.01$). At 100 predators ml^{-1} the cells were 77 ± 7 µm wide after 48 h (Fig. 2), and their length was 94 ± 8 µm. Medium conditioned by *A. proteus*

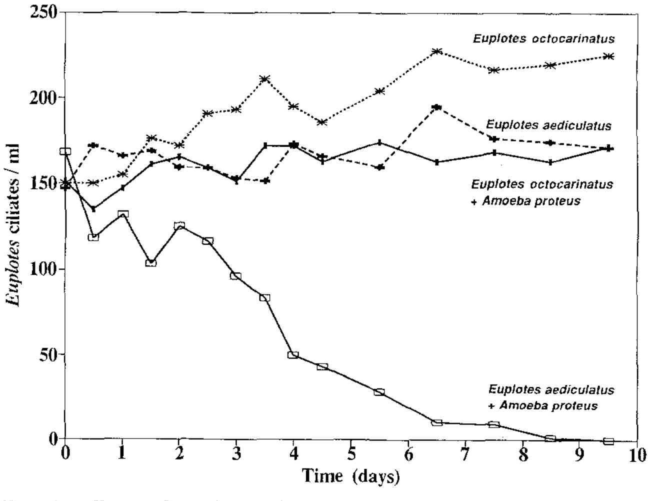

Fig. 1. Effects of predation by *Amoeba proteus* on the ciliates *Euplotes octocarinatus* and *E. aediculatus*. Densities of the prey ciliates were counted in four cultures after various periods of incubation with 10 *A. proteus* ml^{-1}, and in control cultures without predators

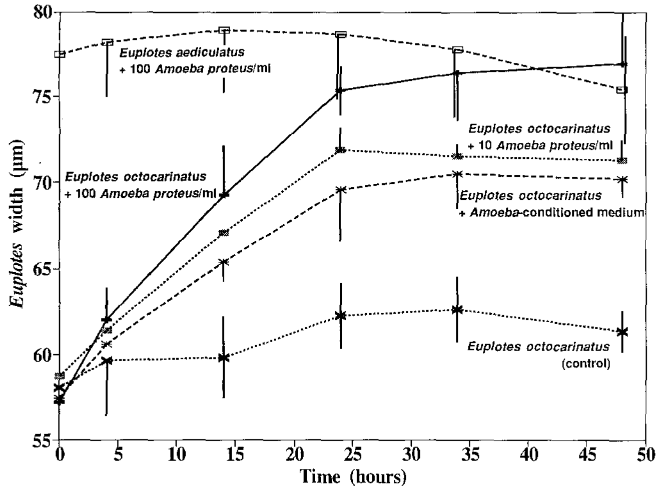

Fig. 2. Morphological change of the ciliates *Euplotes octocarinatus* and *E. aediculatus* as a function of incubation time and of amoeban predator density. 1000 well-fed *Euplotes* ciliates ml^{-1} were incubated either without predators or with 10 or 100 *Amoeba proteus* ml^{-1}, or with medium that had been conditioned by 100 predators ml^{-1}. The *vertical lines* represent SDM

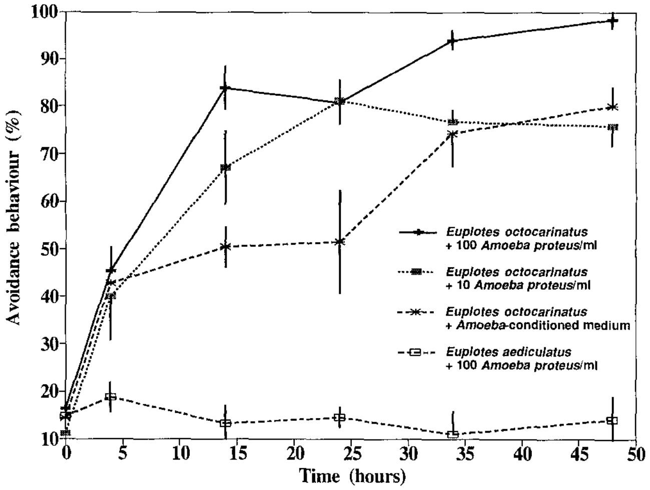

Fig. 3. Behavioural changes in *Euplotes octocarinatus* and in *E. aediculatus* as a function of incubation time and predator density. *Euplotes* ciliates were incubated with 10, or 100 *Amoeba proteus* predators ml^{-1}, or with medium that had been conditioned by 100 predators ml^{-1}. After various incubation periods the frequency of avoidance behaviour of the ciliates in relation to a total number of 100 prey-predator *(A. proteus)* contacts was counted from microscopical observations. The *vertical lines* represent SD

also induced morphological changes in *E. octocarinatus*; the ciliates' width increased from 57 ± 6 µm to 70 ± 8 µm (SD) (Student's *t*-test, $P \ll 0.01$). The morphology of *E. aediculatus* (width 75–78 ± 6 µm, length 125–128 ± 9 µm) (Fig. 2) and of *E. daidaleos* (width 70 ± 5 µm, length 102 ± 5 µm) was not influenced by the presence of 100 amoebae ml^{-1} for 48 h. Thus, the largest width of *E. octocarinatus* was approximately the same as that of *E. aediculatus*, while the length was always shorter. Therefore it seemed unlikely that the size of the *Euplotes* cells was the reason for the observed differences in vulnerability to *Amoeba* predators. This was confirmed by experiments with *E. octocarinatus* and *E. aediculatus* cells that had a *Stenostomum*-induced defensive morphology (95 ± 8 µm or 182 ± 15 µm cell width, respectively). The enlarged ciliates of both species were consumed by *Amoeba proteus* a short time after they were added to this predator.

Behavioural changes

Ciliates of the genus *Euplotes* tend to "walk" with their cirri on the bottom or the walls of the culture vessel and on any particles. *Euplotes* cells that were added to cultures of *Amoeba proteus* "walked" across these predators as they did on other particles. The predators then often caught the ciliates. Some hours or a day later, *E. octocarinatus* ciliates were very seldom observed to move across the amoebae. Instead, when they came into contact with amoebae (either with their fronto-ventral cirri or with their adoral membranelles) they immediately moved backwards, turned around and withdrew.

Avoidance behaviour upon contact with *A. proteus* was quantified by counting the frequency of backward movements in relation to the total number of predator-prey contacts (Fig. 3). Over 24 h the frequency of avoidance behaviour increased in *E. octocarinatus* from 11 ± 3% (SD) to 81 ± 5% in the presence of 10 *A. proteus* ml^{-1}. At a higher predator density (100 amoebae ml^{-1}) avoidance frequencies reached 84 ± 5% in 14 h and 98 ± 2% in 48 h. Significant behavioural changes were already induced after 4 h of coexistence with 10 or 100 *A. proteus* ml^{-1} (to 40 ± 11% or 45 ± 6%, respectively) (χ^2-test, $P \ll 0.001$). Several days after removal of predators *Euplotes* ciliates did not immediately avoid newly introduced amoebae. Medium that was conditioned by 100 *A. proteus* ml^{-1} also induced behavioural changes in *E. octocarinatus*. The frequency of avoidance behaviour increased to 80 ± 4% after 48 h of incubation (χ^2-test, $P \ll 0.001$) (Fig. 3). Ciliates that avoided *A. proteus* did not avoid other particles such as detritus, glass or agarose beads.

A. proteus also induced behavioural changes in *E. daidaleos*. In 24 h after addition of predators avoidance frequency increased from 14 ± 3% to 64 ± 6%. *E. aediculatus* cells that coexisted with *A. proteus* did not change their behaviour during two days although predator density was very high (100 *A. proteus*/ml). The frequency of avoidance behaviour remained at 14 ± 4% (χ^2-test, $P > 0.7$) (Fig. 3). These behavioural differences between *Euplotes* species may be crucial for the differences in the predation risk by *Amoeba proteus*.

Whether ciliates with a defensive morphology avoid amoebae on principle was investigated using cells of *E. octocarinatus* that had a *Stenostomum*-induced enlargement (95 ± 8 µm cell width). Those ciliates did not avoid amoebae (12 ± 4% frequency) immediately upon exposure to the predator (but avoidance behaviour increased with increasing time of coexistence similarly to

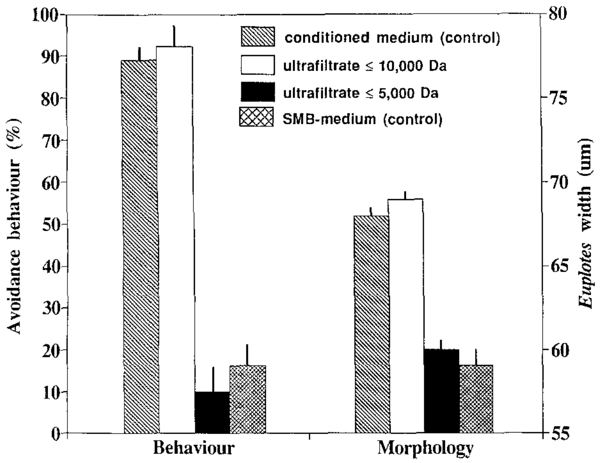

Fig. 4. Induction of behavioural and morphological changes in *Euplotes octocarinatus* by ultrafiltrate of *Amoeba*-conditioned medium. For the determination of the molecular mass of the signal substance(s) the ciliates were incubated with ultrafiltrate or with control samples for 24 h and the frequency of avoidance of *Amoeba proteus*, or the width of *Euplotes octocarinatus* was measured. The *vertical lines* on each bar represent SD (behaviour), or SDM (morphology)

that described in Fig. 3). *E. aediculatus* that had a *Stenostomum*-induced defensive morphology (182 ± 15 µm cell width) dit not increase avoidance of *Amoeba* at all (8 ± 2% frequency). Thus the behavioural response of *Euplotes* ciliates was not linked to morphological changes, and was specific to the defence-inducing predators.

The signal substance(s)

Culture medium conditioned by *A. proteus* induced morphological and behavioural changes in *E. octocarinatus* (Figs. 2, 3). This indicates that a defence-inducing substance is released by the predator. Ultrafiltration experiments showed that this substance has a molecular weight between 5000 and 10000 Da. A filter that excluded molecules heavier than 10 kDa did not retain the defence-inducing substance. When exposed to an ultrafiltrate ≤10000 Da, 95 ± 1% (SD) of the predator-prey contacts resulted in avoidance behaviour, and the width of the ciliates reached 69 ± 1 µm (SDM) after 24 h of incubation. In comparison, only 10 ± 6% of the contacts resulted in avoidance behaviour, and a width of 60 ± 1 µm was measured after 24 h of incubation with an ultrafiltrate ≤5000 Da (Fig. 4).

The released defence-inducing signal substance was further analysed by enzymatic degradation of its biological activity. The proteolytic enzyme proteinase K inactivated the signal substance. To investigate whether proteinase K inactivated the signal substance or whether it interfered with structures on the target cells necessary for signal recognition, conditioned medium was incubated with proteinase K that was immobilized on agarose. Induction of avoidance behaviour in *E. octocarinatus* by signal substance treated with proteinase K-agarose was significantly lower (21 ± 9% avoidance) than by signal substance incubated with agarose (59 ± 6% avoidance) (χ^2-test, $P \ll 0.001$). This indicates that the avoidance-inducing signal substance of *Amoeba proteus* is a peptide. Induction of morphological changes was as low in experiments with proteinase K (62 ± 3 µm *Euplotes* width) as in the controls with agarose (65 ± 3 µm) (χ^2-test, $P \geq 0.5$).

Discussion

Predation risk

Two different defensive responses seem to occur in *Euplotes* prey ciliates. Whereas morphological defence may be important in determining the risk of predation by size-selective predators like the ciliate *Lembadion bullinum* or the turbellarian *Stenostomum sphagnetorum* (Kuhlmann and Heckmann 1985; Kusch 1993a; Kuhlmann and Heckmann, in press), behavioural changes considerably lower the vulnerability to the less size-selective predator *Amoeba proteus*. *E. octocarinatus* and *E. daidaleos* showed a significant increase of avoidance behaviour to *A. proteus* after only 4 h of coexistence. *E. aediculatus* did not avoid this predator. Risk of predation by *A. proteus* was found to vary considerably in these three prey species.

Avoidance behaviour and defensive morphology

Avoidance behaviour occurs before a predator initiates an attack, whereas escape behaviour occurs after the attack begins (Sih 1986). By this definition *Euplotes* ciliates respond to *Amoeba* predators by avoidance. Kuhlmann (in press) described in detail the behavioural response of *E. octocarinatus* to *Stenostomum sphagnetorum*. Avoidance of *Amoeba proteus* by *E. octocarinatus* mainly shows the same pattern, i.e. the ciliates change their direction of movement immediately upon contact with the predator. *E. aediculatus* did not avoid *Stenostomum* (Kusch, unpubl.), nor dit it avoid *Amoeba* predators. However, behavioural response to quickly moving predators like *Stenostomum* is more difficult to quantify than that to slow-moving amoebae.

Predators also induce avoidance behaviour in other zooplankton organisms (Lampert 1993). Seven *Daphnia* species, *Diaptomus kenai* (Copepoda), and *Chaoborus flavicans* larvae (Insecta) showed vertical migration in response to the presence of fish or invertebrate predators (Dodson 1988; Dawidowicz et al. 1990; Neill 1990; Loose 1993). Additionally, *Daphnia pulex* with a defensive "spined" morphology has a higher escape efficiency to *Chaoborus* predators (Havel and Dodson 1984).

Morphological changes were induced by *A. proteus* only in *E. octocarinatus*. The changes were less extensive than those induced by other predators (Kusch 1993a). The reason why *E. aediculatus* shows defensive morphology in the presence of predaceous *Lembadion* ciliates and *Stenostomum* turbellarians but not in that of *Amoeba* *proteus* is unclear. Possibly *A. proteus* and *E. aediculatus* inhabit different microhabitats of natural ponds.

Specificity of induced defence

Different predators may induce the two types of defensive responses simultaneously or separately in different *Euplotes* species. *E. octocarinatus* showed a behavioural response to amoebae only after exposure to this predator. The ciliates did not avoid amoebae after exposure to *Stenostomum* turbellarian predators, which also induced morphological (Kusch 1993a) and behavioural defence (Kuhlmann, in press). Thus *Euplotes* ciliates must be able to distinguish between various predator species, possibly by different substances on the predators' surfaces, which may be identical with the released signal substances (since avoidance behaviour occurs after contact with the predator's surface, whereas "avoidance readiness" is induced by a predator-released signal substance). *Daphnia* species also showed prey-specific and predator-specific behaviours. These zooplankton species can distinguish between three different predators (Dodson 1988). Lively (1986a) predicted that induced morphological defences should develop in response to specific predators.

Signal substances

Differences between the defence-inducing signal substances from various predators seem to be responsible for the species-specific reactions. The avoidance-inducing signal substance of *Amoeba proteus* is a peptide of a molecular weight between 5000 and 10000 Da. Whether both the morphological and the behavioural responses of *Euplotes octocarinatus* are induced by the same signal substance from *A. proteus*, or by two diverse kairomones of similar molecular weight, is still unclear. Morphological-defence-inducing signal substances from *Lembadion bullinum* and from *Stenostomum sphagnetorum* have been isolated and identified as polypeptides with molecular weights of 31500 and 17500 Da, respectively (Kusch and Heckmann 1992; Kusch 1993b). Thus, the known signal substances that induce defensive responses in *Euplotes* are polypeptides, but they differ considerably in molecular weight. Their amino acid sequences need to be analysed to learn more about the differences and the evolution of induced defence mechanisms in ciliates. The substance released by the carnivorous rotifer *Asplanchna brightwelli* that causes a defensive morphology in offspring of the rotifer *Brachionus calyciflorus* is also a polypeptide (Gilbert 1966). The kairomones released by larvae of the dipteran *Chaoborus americanus* (Hebert and Grewe 1985; Parejko and Dodson 1990), which induce morphological changes in *Daphnia*, and by fish (Loose et al. 1993), which induce vertical migration in this prey, are low-molecular-weight molecules (≤ 500 Da).

Cost of induced defence

Anti-predator phenotypic plasticities are predicted to evolve if they are beneficial when predators are present. However, fitness costs are incurred when predators are absent (Lively 1986a). A cost of induced defences has been shown in several prey organisms (Yoshioka 1982; Dodson 1984; Lively 1986b; Black and Dodson 1990; Riessen and Sprules 1990). Thus a decrease in reproductive rate or growth of the defended prey was measurable as a result of e.g. the synthesis of extra tissue, lower feeding rate or stronger swimming effort (Tollrian 1991). Specific defence mechanisms to various predators, like behavioural and morphological changes in *Euplotes*, could lower the cost for the prey by avoiding unnecessary changes. However, the cost in terms of reduced fitness because of avoidance behaviour in *Euplotes* is still unknown. Some energy expenditure is necessary for avoidance, but the magnitude of this cost relative to other metabolic costs is hard to evaluate. Feeding rates should be largely unaffected by the presence of predators since avoidance takes place only upon contact with a predator.

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