Hydrobiologia **284**: 219–227, 1994.

Predation risk of typical ovoid and 'winged' morphs of *Euplotes* (Protozoa, Ciliophora)

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Received 14 April 1993; in revised form 31 August 1993; accepted 14 September 1993

Key words: predation risk, predator-induced defense, morphological changes, coexistence, Protozoa, *Euplotes*

Abstract

Freshwater species of the genus *Euplotes* (Protozoa, Ciliophora) change their morphology in the presence of some of their predators. The ciliates develop extended lateral 'wings' as well as dorsal and ventral projections which make engulfment by predators more difficult. In a series of laboratory experiments ingestion rates of four protozoan predators, the ciliates *Lembadion bullinum*, *Dileptus anser*, *Stylonychia mytilus* and *Urostyla grandis*, and one metazoan predator, the turbellarian *Stenostomum sphagnetorum*, on three species of *Euplotes* (*E. octocarinatus*, *E. patella* and *E. aediculatus*) were determined. It was calculated that the probability of rejection by a predator changed from 1:1 for ovoid morphs of *Euplotes* to about 2:1–20:1 for 'winged' morphs of Euplotes, dependent on the prey and predator species that were combined. The nutritional condition of the prey also had some influence. In mixed-species cultures of prey and predators, transformed cells of *E. octocarinatus* survived for several months.

Introduction

Some prey species are capable of developmental polymorphisms in response to signals emitted by predators. Initially described for a rotifer species (de Beauchamp, 1952) inducible defenses have now been reported for more than twenty animals including protozoa (Havel, 1987, for review; Appleton & Palmer, 1988; Washburn *et al.*, 1988; Wicklow, 1988; Stimson & Berman, 1990; Crowl & Covich, 1990; Brönmark & Miner, 1992). The phenomenon has also been reported for about 50 species of terrestrial plants (for references see Havel, 1987). The extensive taxonomic and geographical distribution of prey organisms employing predator-induced defenses suggests that these defenses are a common strategy for prey organisms which encounter fluctuating predation intensity.

The ability of freshwater ciliates of the genus *Euplotes* to respond to predator-produced signals by a defensive change in cell architecture is assumed to provide an effective mechanism for damping population oscillations of both prey and predators, fostering coexistence (Kuhlmann & Heckmann, 1985). The transformation is brought about by a reorganization of the cytoskeleton (Jerka-Dziadosz *et al.*, 1987). That the signal is a protein released into the medium has been demonstrated for at least two predators of *E. octo-*

carinatus (*Lembadion bullinum*, Kusch & Heckmann, 1992; *Stenostomum sphagnetorum*, Kusch, 1993a). The extent of the transformation depends on the concentration of the signal molecule (Kuhlmann & Heckmann, 1985; Kusch, 1993b). Very little has been reported so far on the effectiveness of the induced changes with respect to prey protection (Kuhlmann, 1990, 1992).

The present paper examines the vulnerability of laboratory cultures of three species of *Euplotes* to predatory ciliates and a turbellarian before and after transformation. It also investigates the fate of both prey and predators in mixed-species cultures maintained for a longer period under laboratory conditions. The results clearly show that the induced changes in morphology in *Euplotes* are highly protective.

Materials and methods

Predators (the ciliates *Lembadion bullinum*, *Dileptus anser*, *Stylonychia mytilus*, *Urostyla grandis* and the turbellarian *Stenostomum sphagnetorum*) as well as two of a total of three prey species used in this study (*E. patella* and *E. aediculatus*) were originally collected from freshwater ponds located in the surroundings of Münster, Germany. They were grown and cultivated as clonal cultures. The third prey species, *E. octocarinatus*, strain 1(6)–VI, is a descendant of two interbreeding stocks collected from a freshwater aquarium in Steinfurt/Westf. and one at the Zoological Institute in Münster (see Heckmann & Kuhlmann, 1986).

All predators were cultivated at 18–22 °C in 100 ml glass bowls in SMB-III-medium (Miyake, 1981), EDTA omitted. The ciliate *Colpidium campylum*, grown on wheat straw infusion at 26 °C and washed in SMB-III, was added to the cultures every other day. The predators were transferred into fresh medium once a week. The prey species were grown as described for the predators, with the exception that they were fed with the photoautotrophic flagellate *Chlorogonium elongatum* (see Kuhlmann & Heckmann, 1989).

Predators and prey organisms were prepared for experiments in the following way: A sufficiently large number of untransformed *Euplotes* cells was provided with a surplus of food several days before the cells were mixed with one of their predators. At the beginning of an experiment the cells were subdivided into two samples. One of the samples was cultivated separately from any predator; the other one was mixed with well-fed predators of the species that was to be used in the experiment. Together with *Euplotes* a surplus of *Colpidium* was added to the predators, so that hardly any cell of *Euplotes* was eaten by the predator before or during the transformation. By this procedure, a size-dependent selection within the prey population was largely excluded. Twenty four hours before the samples of *Euplotes* were mixed with their predators they were either provided with food again, so that they were well-fed during the experiment, or *Chlorogonium* was removed from the two cultures, so that the *Euplotes* population was slightly starved on the day that the experiment was performed. Starved cells of *Euplotes* were prepared in the same way, however, no *Chlorogonium* was added to the cells during a period of seven days.

Vulnerabilities of *Euplotes* were examined by mixing in 1 ml culture medium 100 individuals either of the typical ovoid or of the winged morph, with 25–100 slightly starved predators. The experiments were carried out in 'three-spot-depression-slides'. In the case of the turbellarian *S. sphagnetorum*, 25 slightly starved animals were selected and used in each experiment. The turbellarians were of typical size and had only one mouth (*S. sphagnetorum* multiplies by binary fission; each of two or more 'zooids' that are still connected is able to ingest food). In the cases in which predatory ciliates were employed, 50 slightly starved cells of *U. grandis* or *S. mytilus* and 100 cells of *L. bullinum* or *D. anser* were collected from the culture vessels and mixed with *Euplotes* cells. The predators remained in a slightly starved condition throughout the experiments, although some of the predators ingested a few *Euplotes* cells. The temperature was kept constant at 20 °C in all experiments.

At the beginning of an experiment and then every five minutes, the three-spot-depression-slide

was shaken for a few seconds so that the individuals were more or less equally distributed. Under these conditions the number of the ovally shaped *Euplotes* cells decreased by about 50% within one hour (generally, this was the case already within 20 minutes). The decrease was es-

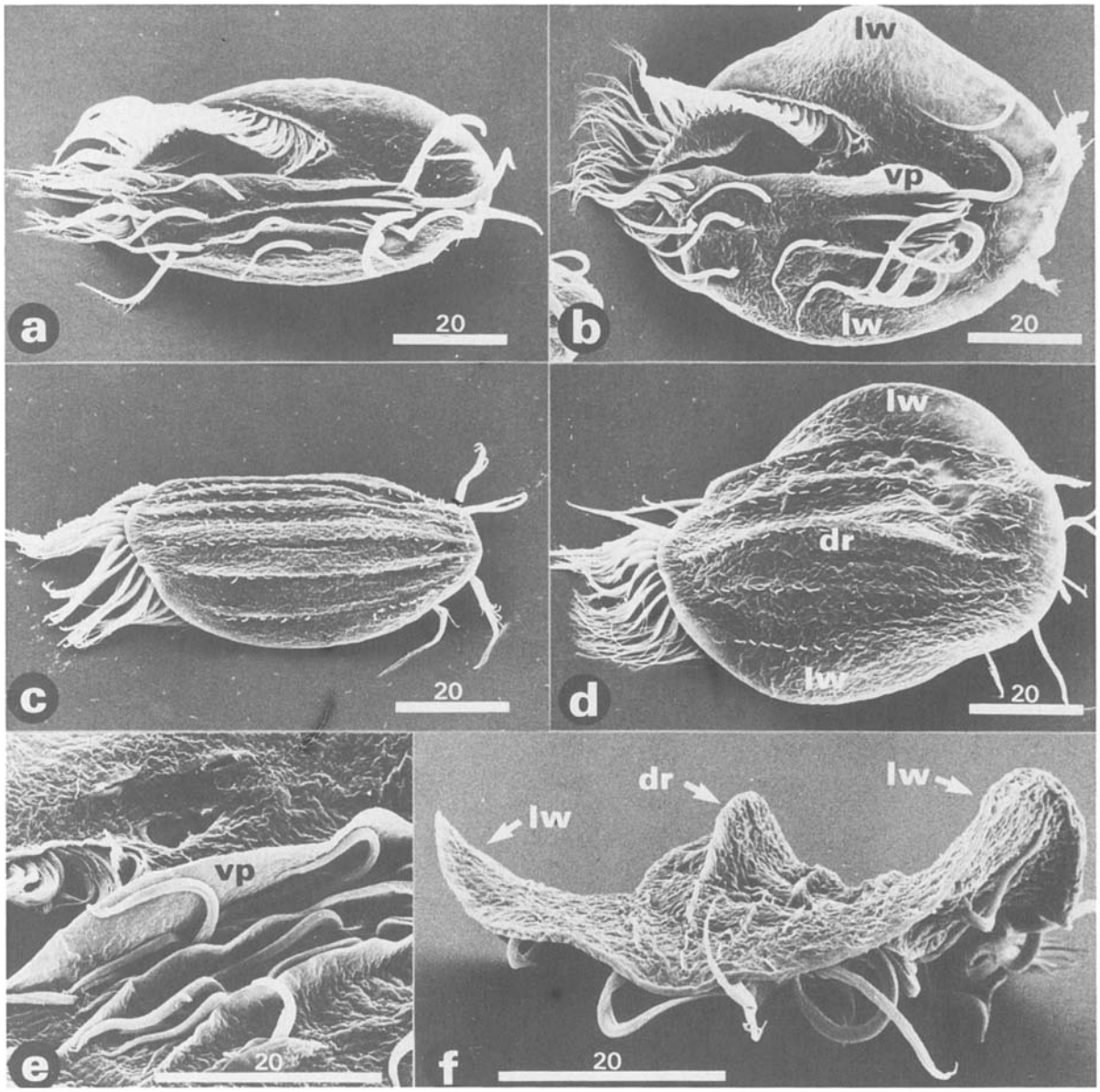

Fig. 1. Scanning electron micrographs of untransformed and transformed morphs of *Euplotes octocarinatus*. a. – Ventral view of an untransformed cell; the triangularly shaped mouth opening as well as numerous cilia are located in the anterior left cell half while cirri (= bundles of cilia) are predominantly positioned on the right ventral cell surface. b. – Ventral view of a transformed cell ('winged morph') of *Euplotes*, 36 hours after co-cultivation with *S. sphagnetorum*; lateral wings (lw) as well as a ventral projection (vp) are visible. c. – In the dorsal view of a non-transformed cell cilia and cirri can be seen at the anterior and posterior cell pole, respectively. d. – Dorsal view of a winged morph with lateral wings (lw) and a protuberant dorsal ridge (dr). e. – Detail of the morphology of the ventral projection (vp) of a transformed cell. f. – Lateral wings (lw) and the dorsal ridge (dr) of a transformed cell as seen from its posterior pole towards the anterior one (scale bars = 20 μm for a–f.).

timated by observation of the cells with a dissecting microscope. An experiment was then stopped by adding 100 µl of a 2% glutaraldehyde solution to each of two parallel mixtures (one with the ovoid and one with the winged circular morphs of *Euplotes*) and the remaining prey individuals were counted by sucking them into a micropipette, so that the number of ingested cells could easily be calculated. At the same time an experiment, which was run in parallel with already transformed *Euplotes* cells, was discontinued and there the number of remaining prey individuals was determined.

Mixed-species cultures of predators and prey organisms were established during a period of three months by mixing in 25 ml culture medium 100 turbellarians with about 10000 cells of *E. octocarinatus*. Once a week, the old medium was partially withdrawn and the culture bowls were replaced by cleaned ones. The cultures were kept at 18–22 °C.

For scanning electron microscopy, cells of *E. octocarinatus* were fixed with 3% glutaraldehyde and 2% OsO_4 ($\pm$ 30 and $\pm$ 45 min, respectively). The cells were then dehydrated, critical point dried, sputter-coated with gold/palladium following a routine procedure according to Bardele (see, e. g., Hiller & Bardele, 1988), and observed in a Cambridge Stereoscan 250 MK 2.

Results

Slightly starved cells of the oval and of the circular 'winged' morph of *E. octocarinatus*, at this nutritional condition most strikingly differing from each other, are shown in Fig. 1. While unexposed cells of this prey species have an ovoid form that is slightly dorso-ventrally flattened, the transformed cells obtained by co-cultivation with a predator have an almost circular shape when viewed from above. In addition they show distinct projections on their dorsal and ventral surfaces. Cell sizes of unexposed and transformed cells of *E. octocarinatus* are given in Table 1.

The other two prey species, *E. patella* and *E. aediculatus*, also enlarged considerably under the influence of the predators used in this study. Generally, the transformation was completed after 24–36 hours. Slightly starved cells of unexposed *E. patella* had an average width of 65 ± 6 µm compared to 100 ± 7 µm after transformation, while cells of *E. aediculatus* increased from 71 ± 6 µm to 114 ± 8 µm in cell width after co-cultivation with *Stenostomum*. In both species the morphological changes were rather similar to those described for *E. octocarinatus*, with the exceptions that *E. patella* generally developed two protuberant dorsal ridges instead of only one and that transformed cells of *E. aediculatus* had a more or less rhombic instead of a circular shape. Only a few individuals of *E. aediculatus* developed protuberant dorsal ridges or ventral projections (further data on the cell shape of *E. aediculatus* are given in Kusch, 1993b).

The predators that induced morphological changes in the three *Euplotes* species are shown in Fig. 2. The mouth opening of each of these predators (pre-adapted to the prey *Colpidium campylum*) had an average length of less than 100 µm in the slightly starved individuals that were used for the experiments. However, the mouth openings of four of these predators were

Table 1. Cell size of *Euplotes octocarinatus* before and after transformation.

Nutritional condition	Width (µm) $\pm \sigma$	Length (µm) $\pm \sigma$	Height (µm) $\pm \sigma$
Well-fed cells			
– typical ovoid form:	71 ± 6	88 ± 7	31 ± 7
– 'winged' form:	105 ± 8	111 ± 10	39 ± 8
Slightly starved cells			
– typical ovoid form:	61 ± 5	82 ± 6	20 ± 4
– 'winged' form:	99 ± 7	103 ± 7	36 ± 6
Starved cells			
– typical ovoid form:	55 ± 5	70 ± 7	15 ± 4
– 'winged' form:	86 ± 8	83 ± 9	22 ± 5

The size of *Euplotes* was determined as described by Kuhlmann & Heckmann, 1985, and by Kusch & Heckmann, 1992. Sample size: $n = 25$. The 'winged morph' was obtained by co-cultivation with *S. sphagnetorum* for 36 h. Nutritional conditions are defined in the Material and Methods section.

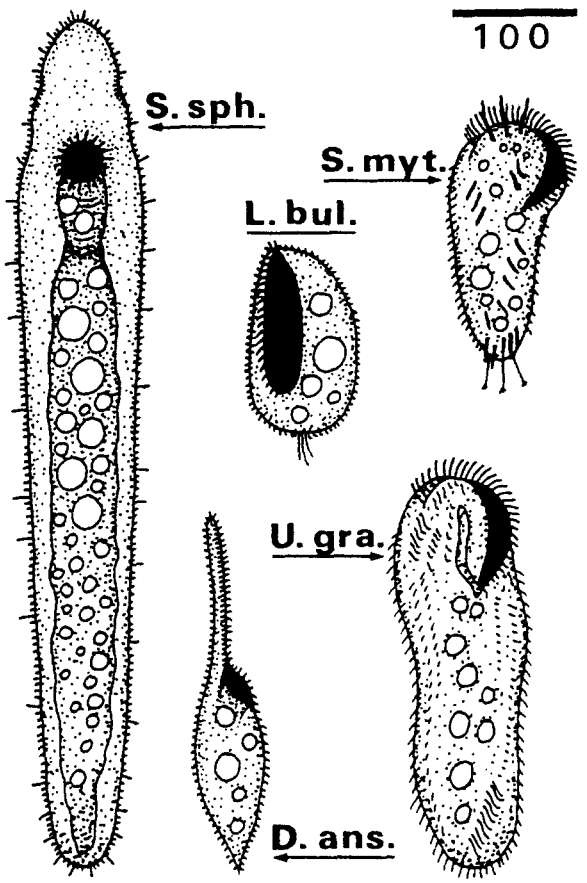

Fig. 2. The predators of freshwater *Euplotes* species used in this study. S. sph. = *Stenostomum sphagnetorum*, S. myt. = *Stylonychia mytilus*, L. bul. = *Lembadion bullinum*, U. gra. = *Urostyla grandis*, D. ans. = *Dileptus anser*. Dark areas show the mouth openings of the predators, which are well expandable in *S. spagnetorum* and *D. anser*, to a lesser extent also in *S. mytilus* and *U. grandis*, while the mouth of *L. bullinum* is inflexible (scale bar = 100 μm).

observed to be expandable, most of all in the turbellarian *S. sphagnetorum* and the ciliate *D. anser*, and to a lesser extent also in *S. mytilus* and *U. grandis*. It was impossible to measure the diameters of the predators' mouths at their maximum expansion. Only in *L. bullinum* was the mouth opening not flexible. The length and width of the mouth ('buccal cavity') was 85 ± 8 μm and 35 ± 5 μm, respectively, measured on slightly starved cells (for a detailed biometrical characterization of *L. bullinum*, see Kuhlmann, 1993).

To test the predation risk of unexposed and winged morphs of the three *Euplotes* species, cells of one prey species were combined with individuals of one of the five predatory species. In a few combinations of prey and predators, individual cells of the prey organism, either untransformed or transformed, were added *successively* to a certain number of predators. The time that elapsed until a cell was ingested by one of the predators was recorded. The results are shown in Fig. 3. Within 15 min after mixing prey and predators, the majority of *Euplotes* cells of the unexposed morph were ingested by their predators. However, only 5–15% of the transformed *Euplotes* cells were ingested.

In similar experiments prey and predator species were combined in nine different combinations: *E. octocarinatus* was mixed with four protozoan predators and with the turbellarian *S. sphagnetorum*. *E. patella* as well as *E. aediculatus* were tested against *U. grandis* and *S. sphagnetorum*. In each one of the nine combinations, either well-fed, slightly underfed, or starved *Euplotes* cells were used. This time one hundred prey individuals were simultaneously added to the predators (for numbers of predators, nutri-

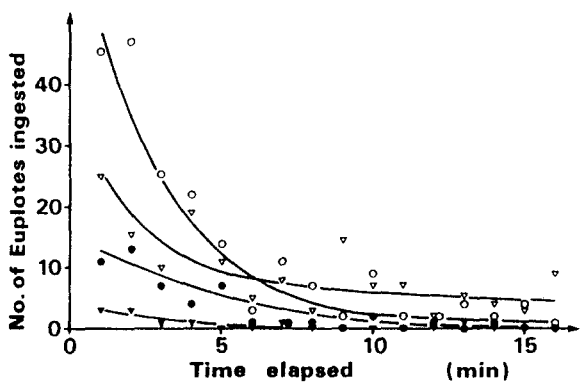

Fig. 3. Time that elapsed until individual slightly starved cells of *Euplotes* that were successively added to a predator population were ingested. Open circles: typical morphs of *E. octocarinatus* were mixed with 25 animals of their predator *S. sphagnetorum* in 1 ml culture fluid; closed circles: winged morphs of *E. octocarinatus* were mixed with the same number of *S. sphagnetorum*. Open triangles: typical morphs of *E. octocarinatus* were mixed with 100 cells of their predator *L. bullinum* in 1 ml culture fluid; closed triangles: winged morphs of *E. octocarinatus* were mixed with the same number of *L. bullinum*. The total number of *Euplotes* cells added to their predators was 300 for each of the four different combinations.

tional conditions, volumes, etc., see Material and methods). The results (numbers of *Euplotes* cells ingested by their predators) are summarized in Fig. 4.

In all nine prey-predator-combinations the population of ovoid morphs of *Euplotes* decreased more rapidly compared to the population of transformed cells, irrespectively of whether the prey was well-fed, slightly underfed, or starved. Cell transformation was most effective in slightly starved cells of *Euplotes* (transformed cells of *E. octocarinatus* were, on the average, 12 times more likely to be rejected by their predators than typical cells). The transformation was less effective in well-fed and starved cells of the same species (probabilities of rejection: 8:1 and 3:1, respectively, compared to 1:1 for typical cells). With regard to the predators *U. grandis* and *S. sphagnetorum*, the prey *E. aediculatus* appears to be better protected than *E. octocarinatus* and *E. patella* (average rejection rates were calculated to be 5–16 times higher for transformed *E. aediculatus* in contrast to 3–15 and 3–8 times for *E. octocarinatus* and for *E. patella*, respectively).

In addition to the experiments so far reported, one combination of prey and predator was followed over a period of three months. In this case, cells of *E. octocarinatus* were mixed with their predator *S. sphagnetorum* in mixed-species cultures. A surplus of *Euplotes* cells was added to *Stenostomum* so that the cells of the prey organism that were not ingested could transform into

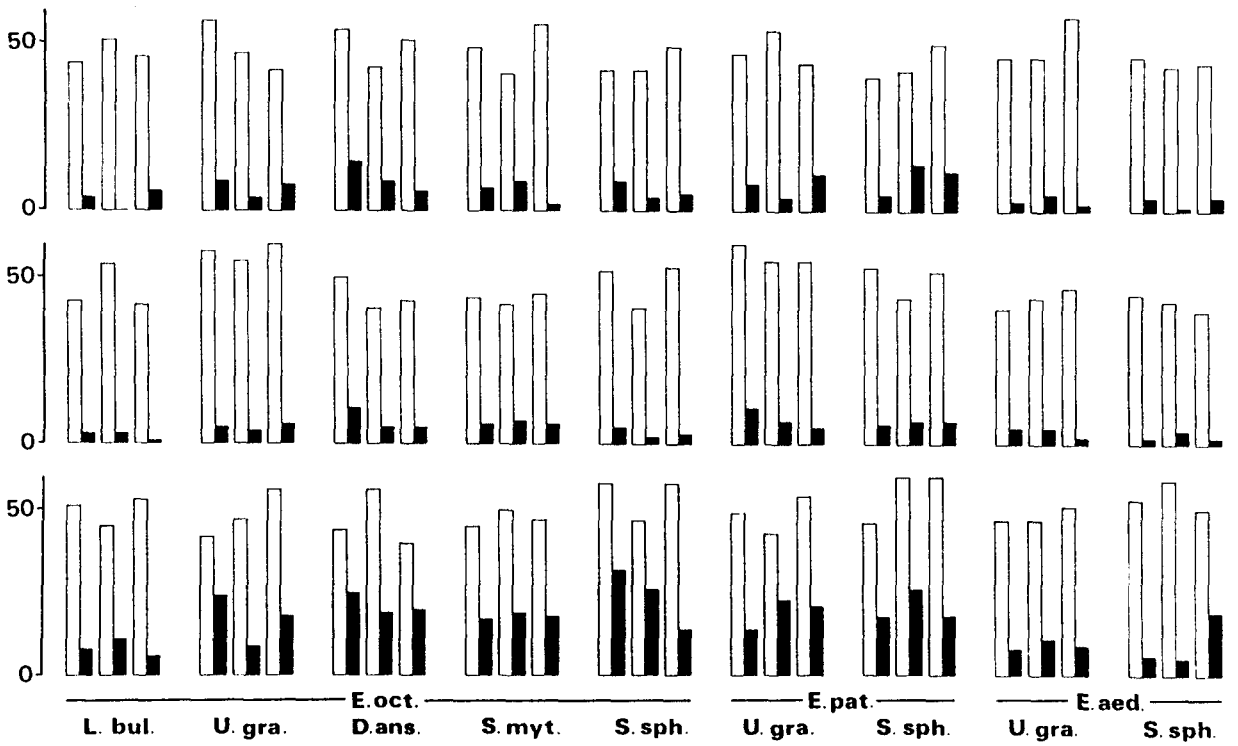

Fig. 4. Absolute numbers of ovoid (open columns) and winged (closed columns) morphs of *Euplotes* (see ordinates) that – in parallel experiments done at same time – were ingested by their predators within a certain time. The length of an experiment depended on the time the predator needed to ingest about one half of the cells out of a total of 100 ovoid *Euplotes* cells added at time 0. At the time when half of the cells had been captured the two parallel experiments were stopped, and the number of ingested ovoid morphs and winged morphs was determined. For each of the different combinations of prey and predators (indicated beneath the columns), nine parallel experiments were performed. Well-fed *Euplotes* cells were used in three of the nine parallel experiments (first row of columns, from above); slightly underfed and starved *Euplotes* cells were used in another three parallel experiments, respectively (second and third rows of columns, from above). E. oct. = *Euplotes octocarinatus*, E. pat. = *E. patella*, E. aed. = *E. aediculatus*. (For abbreviations of predators, see Fig. 2).

the protective winged morph. The transformation of *Euplotes* was completed on the second day of the experiment and was maintained during the following weeks. The time until either the prey or the predator population died out was recorded. It was found that 16 (out of a total of 16) prey and predator populations could coexist if the prey population was occasionally (about every other week) fed with a small amount of *Chlorogonium elongatum*. If no food was provided, in 9 (again out of a total of 16) combinations either the prey, the predator population, or both died out after about 6 to 10 weeks of starvation. In 7 combinations a very few predator and prey organisms coexisted for three months.

Discussion

Anti-predator phenotypic plasticities are predicted to evolve when the defense is beneficial in the presence of the predator, but lowers fitness compared to non-defended forms when the predator is absent (Lively, 1986; Harvell, 1984; Black & Dodson, 1990). The results of this study clearly demonstrate that there are considerable benefits associated with predator-induced plasticities in *Euplotes*. The fact that cells tend to return to their ovoid form as soon as the concentration of the predator released substance allows this (Kuhlmann & Heckmann, 1985), on the other hand, makes it likely that cell transformation in *Euplotes* has demographic costs. The costs have not been investigated in detail. However, it was found that the winged morph of *E. octocarinatus* has a longer generation time than the ovoid form (Kuhlmann & Kusch, unpublished results).

Compared to other model systems for predator-induced defenses, changes in morphology appear to be highly protective in *Euplotes*. The probability of rejection by a predator changed in the experiments from 1:1 for ovoid morphs to at least 2:1, generally to 5:1–20:1 for the circular morph of *Euplotes* (see Fig. 4). In rotifers, where predator-induced defense has been studied to some extent (Stemberger & Gilbert, 1987, for review; Roche, 1987, 1990), rejection rates of well-defended 'spined morphs' are about 3–4 times as high as rejection rates of non-defended forms (Gilbert & Williamson, 1978; Gilbert, 1980; Williamson & Gilbert, 1980; Stemberger & Gilbert, 1984b, 1987, and references therein; Williamson & Stoeckel, 1990). In the case of *Keratella slacki* those forms with long predator (*Asplanchna*)-induced spines are even about 10 times less vulnerable to *Asplanchna* than short spined forms (Gilbert & Stemberger, 1984). Generally, spines (as wings and ridges in *Euplotes*) interfere with a predator's ability to capture or manipulate prey for ingestion (Stemberger & Gilbert, 1984a). However, longitudinal spine growth cannot be an optimal protection if the transformed prey exceeds the width of the mouth opening of a predator in only one dimension: A potential prey which is attacked via its fronto-ventral axis often fits into the pharyngeal cavity of the predator. Spine formation as a defensive adaptation in direct response to predation pressure has also been described for several cladocerans (Havel & Dodson, 1984; Havel, 1985, 1987, for review) and for the ciliated protozoan, *Onychodromus quadricornutus* (Wicklow, 1988). Whether spine growth occurring on the dorsal cell side of *Onychodromus* has a comparable effect as the induced defense in *Euplotes* is unexplored.

It appears likely that the protection of *Euplotes* against some of its predators is so efficient because under the influence of the predator-released factor a cell increases in length, width, and height (Kuhlmann & Heckmann, 1985). Body size in comparison to that of the predator is an important variable affecting a species' vulnerability to predation (Lynch *et al.*, 1981; Stemberger & Gilbert, 1987). Ovoid morphs of *Euplotes* have a length that is similar to or slightly larger than the diameter of the mouth openings of the predators used in this study. The width and height of typical cells, however, are generally smaller compared to the length and width of the mouth openings of the predators. In transformed *Euplotes* cells both the cell's width and, to a lesser extent, its height are greatly enlarged so that both come into the range of the predators' mouth opening diameters or even exceed them. Thereby, capture of *Euplotes*

usually is prevented independently of whether a predator tries to engulf its potential prey from its anterior, posterior, or lateral side. It is a surprising fact that five different predators of *Euplotes* have mouth openings that are of similar size (at least if greatly expanded). The protection that is conferred by the lateral 'wings' and the dorsal and ventral ridges may be reduced or lost if the predator's body size is relatively large in comparison with prey body size, as it is the case in starved cells of *Euplotes*.

In contrast to predator-induced defenses reported for rotifers, cladocerans, bryozoans, barnacles (Havel, 1987, for review), or crucian carp (Brönmark & Miner, 1992), where morphological defenses occur after a few days, weeks, or even months, the transformation of *Euplotes* sets in within a few hours after exposure to signals released by a predator and is completed within 24–36 h. Reproduction is not required; on the contrary, it is postponed until the cells have completed transformation. The rapid transformation is the reason why under laboratory conditions *Euplotes* mixed with predators usually was not completely extinguished. In a natural habitat where, on the one hand, the number of predators is expected to increase successively over a period of at least a few days and, on the other hand, *Euplotes* is expected to have less frequently physical contact to a predator than under the laboratory conditions selected here, *Euplotes* should be able to survive periods of predation pressure.

In addition to the morphological transformation at least one of the prey species, *E. octocarinatus*, has evolved a defensive behavioural adaptation against the turbellarian *S. sphagnetorum*. Physical contact with this predator initiates an 'escape response' by which the cells rapidly move away from their predators (Kuhlmann, 1991). Winged morphs of *Euplotes* show this effect much more frequently than ovoid morphs (Kuhlmann, in press). The behavioural response must be taken into account when the data presented on prey-predator combinations with *Stenostomum* are interpreted. Starved cells gradually lose the ability for the behavioural response; this could be the reason for the remarkable reduction in the protection of starved cells in the presence of *Stenostomum*.

Acknowledgements

The authors are grateful to Drs C. F. Bardele for helpful advice and to J. Kusch for valuable comments on the manuscript. The technical assistance of H. Schoppmann with the REM preparations and help with the language by L. Platt is acknowledged.

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