

# Nutrient and fish effects on the morphology of the dinoflagellate

## *Effets des nutriments et des poissons sur la morphologie des dinoflagellés*

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**Abstract** – The effects of nutrient loading and fish density on *Ceratium hirundinella* morphology were investigated during an experimental mesocosm study in Lake Créteil during the summer of 1990. In the presence of zooplanktivorous fish, more than 80 % of *C. hirundinella* cells had an hypotheca with two horns. In the enclosures without fish, we observed a highly significant increase in the proportion of *C. hirundinella* with three antapical horns. The proportion of *C. hirundinella* cells with three antapical horns tended to increase with nutrient loading, but this effect was not significant and no significant interaction effect between nutrients and fish was observed. Temperature profiles were similar in fish and fishless enclosures and could not explain the morphological variability of *C. hirundinella*. Our results show that biotic factors should be taken into account in polymorphism studies on *Ceratium*. Frequently invoked hypotheses based only on water temperature, nutrient availability or turbulence level, may not be sufficient to explain this phenomenon. (© Académie des sciences / Elsevier, Paris.)

*Ceratium hirundinella* / polymorphism / predation / zooplanktivorous fish / nutrients / mesocosm

**Résumé** – Les effets de la charge en nutriments et de la densité de poissons sur la morphologie de *Ceratium hirundinella* ont été examinés au cours d'une étude expérimentale en mésocosmes, menée pendant l'été 1990 dans le lac de Créteil. En présence de poissons zooplanctonophages, plus de 80 % des cellules de *C. hirundinella* ont une hypothèque à deux cornes. Dans les enceintes sans ces poissons, nous avons observé une augmentation significative de la proportion des cellules de *C. hirundinella* possédant trois cornes postérieures. Nous avons également noté une tendance à l'augmentation de cette même fraction avec le niveau de nutriments sans qu'un effet significatif ne soit détecté. L'interaction nutriments–poissons était également non significative. Les températures de l'eau dans les enceintes étaient identiques et ne peuvent en aucun cas expliquer la variabilité morphologique de *C. hirundinella*. Nos résultats montrent que les facteurs biotiques doivent être pris en compte dans l'étude du polymorphisme chez *Ceratium*. La température de l'eau, les apports en nutriments et le niveau de turbulence semblent insuffisants pour expliquer ce phénomène. (© Académie des sciences / Elsevier, Paris.)

*Ceratium hirundinella* / polymorphisme / prédation / poissons zooplanctonophages / nutriments / mésocosmes

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## Version abrégée

Le polymorphisme saisonnier est souvent évoqué dans la succession des générations de certaines espèces phytoplanctoniques. L'exemple le plus remarquable en eau douce est sans aucun doute celui de la cyclomorphose de *Ceratium hirundinella* (O. F. Müller) Bergh. Ce dinoflagellé, largement répandu dans les lacs tempérés, a la particularité de présenter des variabilités morphologiques spectaculaires qui ont suscité l'intérêt des chercheurs depuis la fin du XIX<sup>e</sup> siècle. Ces variations saisonnières concernent essentiellement le nombre de cornes de l'hypothèque (cornes hypothécales = postérieures = antapicales). Au printemps, la plupart des cellules de *C. hirundinella* possèdent deux cornes postérieures alors que la période estivale est marquée par l'apparition d'une troisième corne. Nous avons étudié cette variabilité de *C. hirundinella* dans le cadre d'une expérience de biomanipulation réalisée en mésocosmes dans le lac de Créteil durant l'été 1990. La charge en nutriments et la densité de poissons zooplanctonophages ont été manipulées. Les effets de ces deux facteurs sur la morphologie de *C. hirundinella* ont été analysés.

Les résultats obtenus montrent que l'abondance des *C. hirundinella* ainsi que la proportion des cellules à deux cornes postérieures augmentent dans les enceintes à poissons zooplanctonophages. Les cellules possédant trois cornes hypothécales dominent uniquement en absence de ces poissons. Les facteurs abiotiques tels que la température et les nutriments sont le plus souvent cités comme inducteurs de cette variabilité morphologique. Certains résultats acquis indiquent que la troisième corne postérieure apparaît quand la température dépasse 15 °C et n'est jamais observée entre 21 et 25 °C et qu'une augmentation de la disponibilité des nutriments (azote inorganique dissous) dans l'eau entraîne une dominance de cette forme. Or, la variabilité morphologique de *C. hirundinella* observée au cours de notre expérience ne peut être totalement expliquée par ces deux facteurs. D'une part, la température de l'eau dans l'ensemble des enceintes était similaire et oscillait entre 20 et 25 °C. D'autre part et malgré une tendance à l'augmentation du pourcentage des cellules de *C. hirundinella* à trois cornes postérieures (de 50 % au plus faible niveau de nutriments N<sub>1</sub> à 90 % au plus fort niveau de nutriments N<sub>2</sub> dans les enceintes sans poissons), aucun effet significatif des nutriments sur le polymorphisme n'a été détecté.

À notre connaissance, aucune étude n'a été réalisée sur le polymorphisme de *C. hirundinella* en tenant compte d'une éventuelle influence biotique, bien que l'hypothèse d'un effet de la prédation ait été émise en 1992. L'apparition d'une corne antapicale supplémentaire pourrait avoir une signification adaptative de résistance contre le broutage du zooplancton. En effet, les cellules de *C. hirundinella* possédant une troisième corne postérieure dominent uniquement dans les enceintes sans poissons zooplanctonophages (F<sub>0</sub>). Ces dernières sont caractérisées par une forte pression de broutage due essentiellement au grand cyclopide *Acanthocyclops robustus* (Sars). Nous avons observé l'existence d'une relation positive très significative entre la biomasse d'*A. robustus* et le pourcentage des cellules de *C. hirundinella* à hypothèque à trois cornes. Des expériences de nutrition du zooplancton ont montré que plusieurs espèces de copépodes sont capables d'ingérer *C. hirundinella* et de l'assimiler malgré sa taille et la dureté de sa paroi. *A. robustus* est donc susceptible d'utiliser *C. hirundinella* comme source nutritionnelle. Par ailleurs, il a été démontré récemment que la formation de colonies et l'apparition d'épines chez *Scenedesmus subspicatus* Chod. étaient le résultat d'une induction chimique due au zooplancton.

D'autre part, il existe une relation positive très significative entre la transparence de l'eau et le pourcentage des cellules de *C. hirundinella* à trois cornes postérieures. Les variations de l'intensité et de la nature du spectre lumineux, liées aux modifications de la structure des réseaux trophiques, pourraient avoir un impact sur le polymorphisme de cette espèce. À notre connaissance, la relation entre d'une part la morphologie et d'autre part les variations de la mobilité, du comportement migratoire et de la physiologie de *C. hirundinella* n'a jamais été testée.

De multiples interactions relient les organismes les uns aux autres au sein des réseaux trophiques, et les mécanismes qui gouvernent l'équilibre entre les abondances de *C. hirundinella* à 2 et à 3 cornes pourraient être plus complexes que cela a été souvent suggéré. Quelle que soit la nature de ces mécanismes, nos résultats indiquent clairement que les variations des facteurs biotiques, comme la présence de poissons zooplanctonophages, peuvent avoir d'importants effets sur la morphologie des algues.

## 1. Introduction

In nature, seasonal polymorphism is often observed in successive generations of phytoplankton. This morphological variability has been correlated to buoyancy and cell resistance to sinking. In freshwaters, the most striking example is provided by the dinoflagellate *Ceratium hirundinella* (O. F. Müller) Bergh. This large alga (150–250 µm) is common in mesotrophic lakes and is tolerant to various environmental conditions [1]. A literature survey indicates that *C. hirundinella* populations are always present in

nature in three forms: i) those with two hypothecal horns; ii) those with a third rudimentary posterior horn; and iii) those with a third well-developed antapical horn [1–9]. Abiotic factors such as water temperature, nutrient availability, light and turbulence are often postulated as governing this morphological variability [5, 6, 10–12].

During the summer of 1990, we manipulated nutrient loading and abundance of zooplanktivorous fish within the context of a mesocosm factorial experiment on planktonic communities. In this paper, we present the effects of

these two factors on the morphology of *C. hirundinella* cells.

## 2. Study site, materials and methods

The factorial experiment was conducted in Lake Créteil (suburbs of Paris, France) with the aim of studying top-down and bottom-up interaction effects on the organization of the planktonic community [13]. Lake Créteil is a mesotrophic, polymictic gravel-pit lake, supplied mainly with phreatic waters. It is 42 ha in area, with a mean depth of 4 m, and a maximal depth of 6 m. Further information on the characteristics of the lake can be found elsewhere [14–16].

Experimental enclosures made of translucent polyethylene were placed on 15 June 1990. They were suspended 25 cm above the lake surface, inside a rectangular pontoon, which delimited four blocks of eight enclosures. Twenty-four enclosures are considered in this paper (eight enclosures, which corresponded to other treatments, are not taken into account). Each bag ( $1.5 \times 1.5 \times 4.3$  m deep), open to the atmosphere and completely sealed at the bottom, contained about  $9.5 \text{ m}^3$  of water. The enclosures were filled with lake water, taken at a depth of 1.5 m, with a gasoline-powered pump. In order to minimize plankton heterogeneity, bags were filled randomly and in several steps between 15 and 20 June 1990. Treatments were initiated a fortnight later, to allow the initial development of the planktonic community.

We used a balanced factorial design, which crossed two levels of nutrients and four levels of zooplanktivorous fish density. Each of the eight treatments was run in three replicates. From 27 June, bags were enriched three times a week with soluble phosphorus ( $\text{KH}_2\text{PO}_4$ ) and soluble nitrogen ( $\text{N}_4\text{HNO}_3$ ) at two different concentrations  $\text{N}_1$  and  $\text{N}_2$ , which corresponded, respectively, to phosphorus loading rates of 3.16 and  $31.6 \mu\text{g L}^{-1} \text{d}^{-1}$  (ratio N:P = 20:1). On 29 June, 2-month-old cyprinids [mainly Roach, *Rutilus rutilus* (Linné) and a few bream, *Abramis brama* (Linné)] were introduced in some enclosures to obtain a gradient of four concentrations,  $\text{F}_0$ ,  $\text{F}_1$ ,  $\text{F}_2$  and  $\text{F}_3$  (respectively 0, 10, 20 and 40 individuals by enclosure). On 29 June, mean total length of cyprinids was  $30.0 \pm 0.3$  mm. More details on the experimental design and on the main results can be found elsewhere [13, 17].

Water temperature and dissolved oxygen were measured every 2–3 days at 1 and 4 m deep with a YSI-model 57 meter. At the same time, water transparency was measured with a 25-cm-diameter Secchi disc. The samples used for the analyses of *C. hirundinella* abundance and morphology were taken on 21 July and on 22 August. For each date and in each enclosure, 24 L of water were collected from the surface to the bottom with a 2-L Friedinger bottle. A subsample of 100 mL was immediately taken and preserved in 4% formalin for counts of phytoplankton (type I sample). The remaining water was gently fil-

tered through a nylon screen with a  $36\text{-}\mu\text{m}$  aperture. Due to their large size, most of the *C. hirundinella* cells were retained with zooplanktonic individuals on the screen.

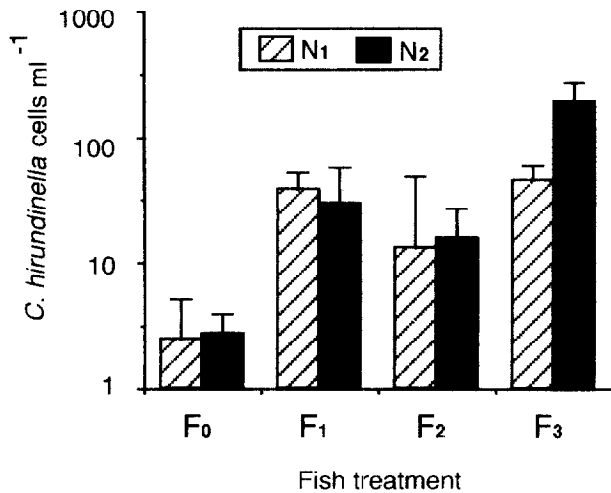
The retained organisms were immediately preserved in a sucrose formalin solution for morphological analyses (type II samples, final concentration of formaldehyde 4 %v/v).

Cells counts were made on type I samples collected on 21 July and on 22 August by the Utermöhl inverted microscope technique at  $40 \times$  magnification [18]. The proportions of *C. hirundinella* cells with two antapical horns, with a third rudimentary antapical horn, or with a third well-developed antapical horn were estimated on 22 August. They were determined with a Zeiss standard microscope at  $60 \times$  magnification on 100 cells, taken randomly from type II samples under a dissecting microscope. Materials for scanning electron microscopy were selected with a micropipette, washed in distilled water, and prepared as described in [19].

In Lake Créteil, the cyclopoids *Acanthocyclops robustus* (Sars) *Thermocyclops oithonoides* (Sars) and *T. crassus* (Fischer), the calanoids *Eudiaptomus gracilis* (Sars) and *Eurytemora velox* (Lilljeborg), and the rotifer *Asplanchna priodonta* Gosse are the only zooplanktonic species able to consume *C. hirundinella* cells during the summer [20–24]. Their abundances in the different enclosures were estimated on 23 July and 22 August in order to analyse their potential impact on *C. hirundinella* cells. Counts were made by sorting out the animals of at least three subsamples, taken with a pipette from the type II samples which had been adjusted to a known volume. Copepods were considered as able to feed on *C. hirundinella* from the fourth copepod instar. Due to the rarity of *E. velox* and *T. oithonoides* in the enclosures, we considered all the calanoids on one hand and all the *Thermocyclops* on the other hand.

In order to obtain more robust estimates of the abundances of *C. hirundinella* and zooplankton in the different enclosures, we considered the averages between the densities observed in July and in August for the statistical analyses. The effects of nutrients and fish on *C. hirundinella* abundance and morphology were assessed using two-way ANOVAs. The logarithmic transformation of cell densities was necessary in order to correct for heteroscedasticity [25]. Severe deviations from the assumption of normality and homoscedasticity were observed on the percentages of the different morphs and could not be corrected by variance stabilizing transformations. Thus, Kruskal-Wallis non-parametric two-factor ANOVAs were performed.

Non-parametric correlation analyses (Spearman rank correlation  $r_s$ ) were performed in order to detect an eventual relationship between the morphology of *C. hirundinella* cells, the mean abundance of their potential predators and Secchi depth during the preceding month. Statistical significance was inferred at  $P \leq 0.05$  for all analyses.



**Figure 1.** Mean abundance (with standard error of the mean cell density) of *Ceratium hirundinella* in the different enclosures for the two levels of nutrient loading (N<sub>1</sub>, N<sub>2</sub>) and the four densities of fish (F<sub>0</sub> = 0, F<sub>1</sub> = 10, F<sub>2</sub> = 20, F<sub>3</sub> = 40 individuals per enclosure).

### 3. Results

A highly significant ( $P = 0.0005$ ) positive effect of roach was observed on the mean abundance of *C. hirundinella* cells (figure 1). No significant effect on nutrient loading and no significant interaction effect were observed. Tukey multiple comparison test on pairs of treatments indicates that the abundance of *C. hirundinella* in fishless enclosures is significantly lower than in F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> enclosures, and that *C. hirundinella* cells are more abundant in the F<sub>3</sub> enclosures than in the F<sub>2</sub> treatments.

The three form types - form type 2, with two posterior horns (figure 2A, B and C); form type 3', with a third rudimentary posterior horn (figure 2D, E and F); form type 3'', with a third well-developed posterior horn (figure 2G, H and I) - occurred simultaneously in the enclosures during our investigation. Their relative distribution differed strongly according to treatments (figure 3A and B). As the intermediate form was never dominant, it was grouped with the form type 3'' for statistical analyses (form type 3).

In the absence of fish and for the N<sub>1</sub> treatment, the population was a mixture of the three forms, with a slight dominance of type 2 (figure 3A). In the F<sub>0</sub>N<sub>2</sub> enriched enclosures, the fraction of *C. hirundinella* cells having a third posterior horn increased from less than 50 to 90 % (figure 3B). The form type 2 was highly dominant in the presence of fish and its proportion represented no less than 80 % of the population over all the enclosures with roach, whatever their densities (figure 3A and B). Kruskal-Wallis non-parametric two-factor ANOVAs showed that the effect of zooplanktivorous fish on *C. hirundinella* morphology is highly significant ( $H = 14.492$ ,  $df = 3$ ,  $P < 0.005$ ). There was a general tendency of the proportion of type 3 to increase with nutrient loading, and espe-

cially so when fish density decreased. However, the effect of fertilization and the interaction effect between fish and nutrient load was not significant (respectively  $H = 1.841$ ,  $df = 1$ ,  $P > 0.1$  and  $H = 1.381$ ,  $df = 3$ ,  $P > 0.5$ ).

The Spearman rank correlation test between the proportions of form types and the densities of the potential consumers of *C. hirundinella* indicates a very significant ( $r_s = 0.637$ ,  $P = 0.0023$ ) positive relationship between the percentage of type 3 and the biomass of *A. robustus* individuals. These cyclopoids were negatively associated with fish density ( $P < 0.0001$ ) and positively associated with nutrient loading ( $P < 0.001$ ). On the other hand, we found no significant correlation between *C. hirundinella* morphology and the biomass of the small *Thermocyclops* spp., the calanoids, or the rotifer *A. priodonta*.

The temperature of water was always higher than 18 °C during the experiment and exceeded 20 °C on 22 August [13]. The temperature profiles were very similar in all the enclosures and no significant effects of treatments, neither on the mean temperature nor on the vertical gradient (two-way ANOVAs) were observed.

A very significant ( $r_s = 0.585$ ,  $P = 0.0051$ ) positive correlation was observed between the transparency of water and the proportion of *C. hirundinella* cells with a third antapical horn.

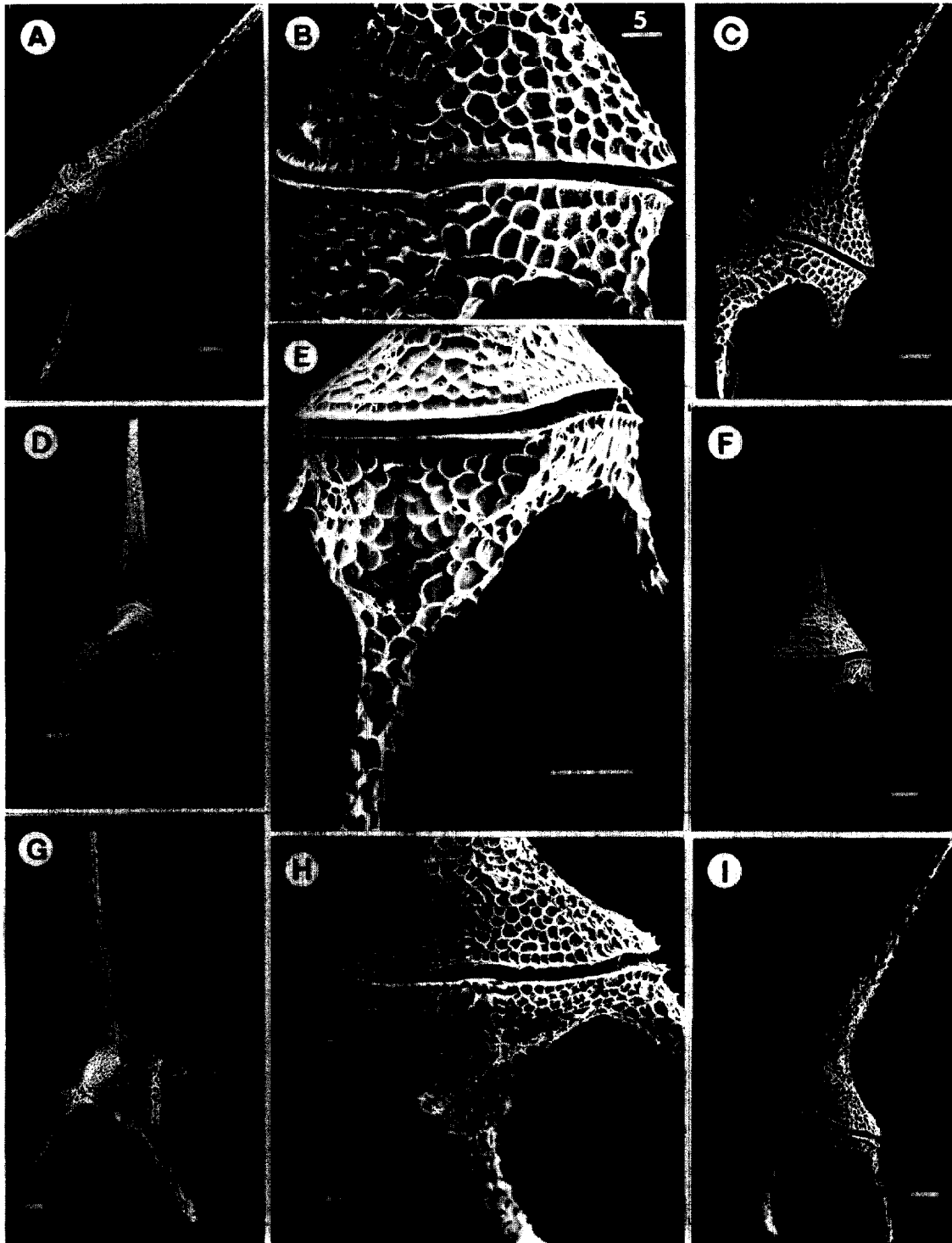
### 4. Discussion

*C. hirundinella* polymorphism is often considered to be due to a cyclomorphosis. Pearsall [4] described three periods in the annual cycle of *C. hirundinella*: i) in winter the population is entirely encysted; ii) in spring it is dominated by a large type with two posterior horns; iii) in summer it is dominated by a smaller form with the appearance of a third posterior horn. But Dottne-Lindgren and Ekbohm [5] reported that the simultaneous occurrence of all forms at the same time do not support the cyclomorphosis hypothesis.

The data presented here clearly show that the occurrence of zooplanktivorous fish in the enclosures greatly increased *C. hirundinella* abundance and the proportion of *C. hirundinella* with two posterior horns. Individuals with three posterior horns were dominant only in the absence of fish.

Many authors have related the morphological variability of *C. hirundinella* to seasonal changes in water temperature [5, 10–12]. Pearsall [4] indicated that the third posterior horn appears when the temperature exceeds 15 °C. Bruno [6] demonstrated experimentally that this additional horn appears in cultures at 15 °C and never at 21 or 25 °C. However, the morphological variability observed in our experiment cannot be explained by temperature, since it was the same in all the enclosures and nearly always between 20 and 25 °C.

Nutrients are also considered as an important environmental factor influencing this polymorphism. An experi-

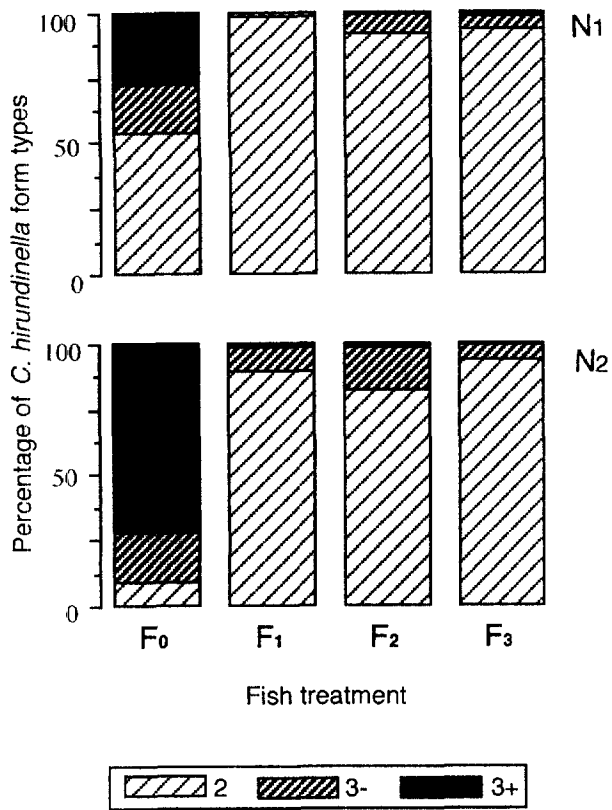


**Figure 2.** *C. hirundinella* morphology.

**A–C.** form type 2: ventral side (**A**); detail of cingular gutter (**B**); dorsal side (**C**). **D–F.** form type 3<sup>+</sup>: ventral side (**D**); detail of antapical horns (**E**); dorsal side (**F**). **G–I.** form type 3<sup>+</sup>: ventral side (**G**); detail of antapical horns (**H**); dorsal side (**I**). [SEM], scale bar = 10  $\mu$ m, except figure **B**

mental nutrient enrichment of a lagoon was conducted by Kimmel and Holt [8]. They observed a rapid increase in the fraction of the population having three antapical horns and recorded that morphological changes were correlated with increasing dissolved inorganic nitrogen in the

water. Although we observed a tendency of the proportion of three-horned cells to be larger at the higher nutrient level, this effect was not significant. Moreover, preliminary results obtained on additional fertilization experiments with a very large range of nutrient loading in



**Figure 3.** Percentage composition of *C. hirundinella* form types for the two levels of nutrient loading ( $N_1$ ,  $N_2$ ) and for the four fish densities.

2 = cell with two posterior horns, 3<sup>-</sup> = cell with a third rudimentary posterior horn, 3<sup>+</sup> = cell with three posterior horns.  $F_0 = 0$ ,  $F_1 = 10$ ,  $F_2 = 20$ ,  $F_3 = 40$  individuals per enclosure.

fishless enclosures did not reveal any significant nutrient effect on cell morphology (unpublished data). Analyses are under way in order to verify whether modifications of food web structure could modify nutrient recycling.

Results of optical experiments [10] on post-cyst stages of *C. hirundinella* indicate that red light can produce a reduction of the third posterior horn. In our experiments, we found a very strong negative effect of fish on water transparency [13], and a very significant positive association between Secchi depth and the proportion of *C. hirundinella* cells with three antapical horns. Thus, we cannot eliminate a possible effect of a modification of light spectrum due to changes in particulate suspensoids or dissolved organic matter with modifications of food web structure. To our knowledge, the possibility of mod-

ifications of the motility and migration pattern of *C. hirundinella* or changes in photosynthetic activity (for example autotrophy versus heterotrophy) with morphology have never been tested.

To our knowledge, biotic pressures have not been taken into account as potential proximate or ultimate factors influencing the morphology of *C. hirundinella*. Lindström [9] proposed for the first time that the appearance of the third posterior horn might be the result of adaptations to predation, but he did not present data supporting this view. Few studies give information regarding the ability of freshwater zooplankton to consume dinoflagellates. Karabin [20] indicated that the cyclopoid *Mesocyclops leuckarti* Claus can consume *C. hirundinella* at low rates when phytoplankton contains 90 % of *C. hirundinella*. Moreover, some recent studies indicate that, under natural conditions, *C. hirundinella* can serve as an additional food source for copepods when soft-bodied flagellates, rotifers, calanoid and cyclopoid nauplii are deficient [21–24]. Santer [24] reported also that cyclopoids were able not only to ingest but also to metabolize *C. hirundinella*.

In our field study, the enclosures without zooplanktivorous fish were characterized by the dominance of large crustacean species and by the rarity of rotifers [17]. According to Santer's results [24], *C. hirundinella* might have been an alternative food resource for copepods, especially for *A. robustus*. We found a very significant positive relationship between the biomass of the cyclopoid *A. robustus* and the percentage of cells with three posterior horns. We have no indication of the role of *C. hirundinella* morphology on attack efficiency by cyclopoids. Recently, it was demonstrated that colony and spine formation in *Scenedesmus subspicatus* are induced by a chemical factor released by *Daphnia magna* Straus [26]. Laboratory experiments are necessary to test the possibility of a predator-mediated induction of an additional horn in *C. hirundinella*.

Multiple pathways link the different organisms and the abiotic factors in food webs, and the mechanisms governing the balance between two- and three-horned forms could be more complex than usually suggested. Whatever these mechanisms, our results clearly indicate that variations in biotic factors, such as the occurrence of zooplanktivorous fish, can induce a strong morphological response of *C. hirundinella*. Further experiments should be conducted in order to distinguish between the different 'bottom-up' and 'top-down' effects, which could interact in the control of algal polymorphisms and to evaluate the cost of such adaptive responses.

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