Dynamics of pelagic ciliates in eutrophic estuarine waters: importance of functional groups among ciliates and responses to bacterial and phytoplankton production

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Abstract

The planktonic ciliate community was investigated during field studies and enclosure experiments in the shallow eutrophic Darss-Zingst estuary (southern Baltic). The functional groups of ciliates were separated according to their main food items known from literature and from a few observations of our own. In response to temporal changes in the production of bacteria and phytoplankton changes in the composition of the ciliate community appeared. Algivores dominated during the spring bloom and in early summer and early autumn corresponding to the pulses of small phytoflagellates and green algae, respectively. Bactivorous ciliates were of the highest importance during summer and autumn. Estimates of the feeding rates of functional groups revealed no significant impact of algivores but bactivores should be able to consume one third of annual bacterial production and can control bacterial production during certain periods. At high concentrations of ciliates their density seemed to be regulated within the pelagic ciliate community itself by the impact of omnivores. Nutrient loading into enclosures during summer did not lead to considerable changes in ciliate community. The most important function of pelagic ciliates within the matter flux of this estuarine community seems to be the mineralization of bacterial production.

Introduction

Studies regarding the microbial loop received great attention among marine biologists during the last decade showing that microbes (esp. bacteria, heterotrophic flagellates, ciliates) significantly contribute to the functioning of pelagic marine ecosystems (e.g. WILLIAMS 1981). In contrast with it the microbial web in limnetic and estuarine ecosystems, were only seldom under study up to now, but all the published studies point to the quantitative importance of microbes within these pelagic ecosystems (e.g. PACE & ORCUTT 1981, PORTER et al. 1985).

The results presented here were part of a complex ecosystem analysis performed in the estuarine waters south of the Darss-Zingst peninsula, southern Baltic (cf. VIETINGHOFF 1984, SCHIEWER et al. 1986, ARNDT 1986 a). Preliminary studies regarding the structure of the microzooplankton community (ARNDT et al. 1989 b and unpubl.) indicated a very diverse group of organisms. All animals illustrated in Fig. 1 are representatives of taxonomic groups which are at least during certain periods of massive importance in the pelagic region of the shallow eutrophic estuary. Animals graphed on one horizontal line should represent a similar trophic level. Clearly comes out that microzooplankters (within the triangle) can occupy the same trophic levels like mesozooplankters. The protozoans are

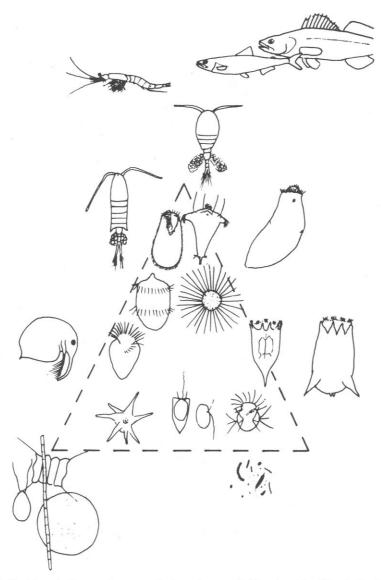


Fig. 1. Position of micro- and nanozooplankters (surrounded by triangle) within the food web of the pelagic community of the brackish waters south of the Darss-Zingst peninsula.

included in the pelagic food web and serve as a food source for upper trophic levels including the "herbivorous" copepod *Eurytemora*, even mysids feed on protozoans. Therefore, the terms "microbial web" or "microbes in the food web" (e.g. PORTER et al. 1985) seem to be much more suitable terms to describe the dense integration of microbes within the traditionally investigated pelagic food webs rather than the term "microbial loop" which suggests something apart from the former knowledge of pelagic interactions.

As a by-product of our studies in protozooplankton we found that small rotifers ($< 100 \, \mu m$ body length) like small species of *Synchaeta* and *Trichocerca* nearly completely pass the common used plankton nets ($60 \, \mu m$ mesh size) and are thus underestimated though they can form up to 50% of the total metazooplankton biomass in estuarine and limnetic waters during early summer (ARNDT et al. 1989 b and unpubl.).

Since preliminary studies on microzooplankton of the Darss-Zingst estuary (ARNDT 1986b) showed that ciliates are an important component within the pelagic community, we present here more detailed studies regarding their functional importance. Preliminary studies using live counts of size classes revealed overestimations of ciliate biomass but even our present studies discriminating among individual species (or at least genus) showed that the total ciliate biomass was in the same range as the total metazooplankton biomass. To get an impression of their functional importance we separated ciliates according to their main food items.

Material and methods

Plankton samples for studies of seasonal changes in the ciliate community were collected in a depth of 0.5 m at station Zingster Strom, Darss-Zingst estuary (S: 3–7%; winter T_w : 0–3°C; summer T_w : 16–24°C; mean depth 1.7 m) at intervals of 1 to 3 weeks in 1986. The Darss-Zingst estuary is situated between the towns Rostock and Stralsund (G.D.R.). For the description of the study area see Schiewer et al. (1986). Enclosure experiments (3.14 m²) were carried out in the shallow bay Kirr-Bight near Zingster Strom at a depth of 0.7 m. Three enclosures (A: control, B: stepwise addition of 5.5 g N/m³ and 2.6 g P/m³, C: addition of 23.0 g N/m³ and 2.9 g P/m³) and the surrounding water (K) were investigated twice a week in the course of an 8-week experimental period (June/July 1986). For a description of experiments and other results see Schiewer et al. (1989) and Arnot et al. (1989 b). Ciliates were investigated by the live-counting method (Dale & Burkill 1982) and the additionally counting of HgCl₂-fixed and stained samples (Bereczky 1985). Ciliate biovolumes were estimated using approximations to simple geometrical forms. Functional groups (herbivores, bactivores, omnivores) were established according to Kahl (1930–35), Pratt & Cairns (1985) and some own observations of food vacuole content. In addition primary production (14C-method) and bacterial production (3H-thymidine incorporation method) were determined (Jost 1983, Borner 1984).

Results and discussion

Studies in the seasonal changes of ciliate biomass in 1986 revealed the typical pattern with a peak in spring and high biomasses during summer and autumn (Fig. 2). The low ciliate biomass during winter corresponds to the low standing stock of bacteria and phytoplankton. In addition, metazooplankters like *Synchaeta* spp. and *Eurytemora affinis* were able to consume nearly the whole ciliate production (BURCKHARDT & ARNDT 1987, ARNDT et al. 1989a). Strong predation pressure also explains the low biomass during late April and May when *Eurytemora* reaches its population maximum. Another but not so pronounced decline in August may be caused by the predation pressure of omnivorous ciliates (see below) and competition with nanophagous rotifers. Herbivorous ciliates responded to high abundances of nanophytoplankters (in March: small (< 10 µm) cryptophyceans; in June and early autumn: small chlorophyceans like *Scenedesmus*, *Crucigenia*, *Kirchneriella*, which were also observed in food vacuoles). The biomass of bactivorous species corresponded very well to changes in bacterial production. The group of omnivorous species which includes especially predacious species occurred only at high

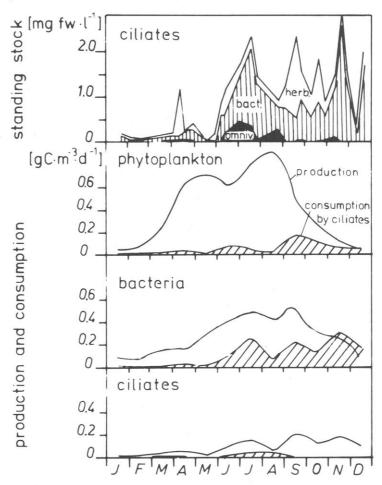


Fig. 2. Seasonal changes in the standing stock of pelagic ciliates including different functional groups (upper graph) and the production of food organisms in relation to the estimated consumption rate by ciliates (primary production vs. consumption by herbivorous ciliates; bacterial production vs. consumption by bactivorous ciliates; production by herbivorous and bactivorous ciliates vs. consumption by omnivorous ciliates).

ciliate biomasses (0.5 mm³/l seems to be the lower limit). In order to estimate the role of the different functional groups we calculated feeding rates by assuming a specific feeding rate of 200% body weight/d for ciliates in the size class 5–50 x 10³ µm³. This value is in accordance with our determinations of growth rates which were even in winter around 1d⁻¹ in enclosures excluding predators (additional assumptions: production efficiency 50%; C-content 10% wet weight). The specific consumption rate was assumed to be 300%/d for smaller individuals, for larger ones 150%/d. Feeding rates were compared with the long term monthly mean values of primary and bacterial production (BÖRNER 1984, JOST 1983). These estimates (Fig. 2, lower graph) revealed that herbivores had a very low impact on primary production. Only in autumn they were able to consume a significant part of

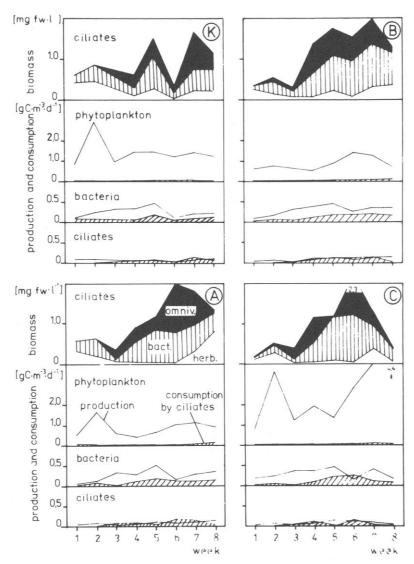


Fig. 3. Weekly changes during June and July 1986 in the standing stock of pelagic ciliates and the production of food organisms in relation to the estimated consumption by ciliates in three enclosures (A: control; B: low nutrient loading; C: high nutrient loading) and in the surrounding water (K).

primary production. But at this time also heterotrophic flagellates served probably as an additional food source and some oligotrichs seemed to contain autotrophic symbionts (cf. Stoecker et al. 1987). On the other hand bactivores were able to consume about one third of the annual bacterial production and should be considered important mineralizers of bacterial production. Feeding rates in late autumn were probably overestimated since some species (e. g. *Mesodinium* sp.) made use of autotrophic symbionts (LINDHOLM 1981).

To have a more precise view on the interactions between ciliates and bacterial and phytoplankton production in this estuarine ecosystem simultaneous measurements were carried out in enclosures with different nutrient supply. The observations summarized in Fig. 3 were similar to those regarding the annual cycle. Herbivores responded to temporal changes in primary production but their impact was negligible. Bactivore abundances increased with increasing bacterial production. During the sixth week they were able to control bacterial biomass. From the third till the seventh week omnivorous ciliates should be important regulators of ciliate density but they probably did not consume only ciliates. Ciliate community within the three enclosures and the surrounding water behaved in a very similar way except for the sixth week when bad weather conditions lead to water exchange processes in surrounding waters. Noteworthy, ciliates in enclosure C with high nutrient supply also did not respond significantly to the high primary production. This observations point to the stability of the ciliate community caused probably by high species diversity and occupation of several trophic levels by ciliates (see Fig. 1). A report on the interactions between the pelagic and benthic microfauna during these experiments and the short term fluctuations of ciliates is given in ARNDT et al. (1989b).

Concluding remarks

Ciliate biomass at station Zingster Strom was in the upper range of values reported for estuarine waters and seemed to be a response to the eutrophic conditions (PORTER et al. 1985). The separation of individual species according to functional groups showed that all groups were influenced by the abundance of their food items. Only bactivores, which reached the highest standing stocks among the pelagic ciliate community, and omnivores seemed to be able to control the dynamics of their food organisms. Bactivorous ciliates are important mineralizers of bacterial biomass and contribute significantly to the high degradation rate of organic matter in the estuarine waters south of the Darss-Zingst peninsula. This is in accordance with findings from limnetic as well as marine ecosystems. Detailed determinations of in situ feeding rates and food selectivity should be necessary in future for a more precise analysis of the grazing impact by ciliates.

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