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Seasonal development of hypolimnetic ciliate communities in a eutrophic pond

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Abstract: The ciliated protozoan communities in the hypolimnion of a highly productive pond were investigated over two years. Three physiological groups could be distinguished: (a) microaerobic ciliates which tracked the oxic-anoxic boundary within the stratified water column; (b) anaerobic ciliates with endosymbiotic methanogens; and (c) anaerobes without endosymbiotic methanogens. Both groups of anaerobes were confined to the anoxic zone of the hypolimnion. Community biomass was dominated by microaerobic ciliates which had on average 20 times larger cells than anaerobic ciliates. Abundance and biomass of microaerobic ciliates decreased over the summer, while anaerobic ciliates increased. This reflected a spatial shift in the availability of inorganic nutrients and, as a result, of ciliate food from the epi- and metalimnion to the hypolimnion. The low biomass production of anaerobic ciliates was consistent with the low theoretical growth efficiency of anaerobic metabolism. Ciliate species displayed characteristic spatial and seasonal distribution patterns within the water column which were similar in both years investigated. Spatial and temporal distribution was mainly governed by two factors: (1) the distribution of dissolved oxygen; and (2) the availability of food. Distribution patterns were not related to chemical gradients other than the oxygen gradient, but they were correlated with the distribution of major food sources.

Key words: Anaerobic ciliate; Seasonal development; Gross growth efficiency; Anoxic hypolimnion; Predator-prey relationship

Introduction

The hypolimnia of productive lakes harbour diverse protozoan communities with a characteristic species composition [1–4]. If anoxic conditions develop, protozoa become the principal or sole eukaryotes in the plankton [5]. The protozoa are part of the complex microbial communities which differ markedly from those of epilimnia [6]. The structure and function of microbial communities which are composed entirely of anaerobic organisms are still largely unknown. The composition of food sources present in the hypolimnion, i.e. the large amounts of bacterial food, should be reflected in the functional structure of the protozoan community [6]. Additionally it has to be expected that the low growth efficiency of anaer-

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obic metabolism leads to short food chains [5]. Absence or reduction of predation by higher trophic levels should have a major impact on plankton population structure and dynamics.

Anaerobic ciliated protozoa show spatial and temporal non-random population distributions in freshwater [7,8] and marine habitats [9,10]. In contrast to microaerophilic ciliates which migrate to remain in a microoxic environment [11], anaerobic ciliates do not seem to respond to a single chemical gradient [8]. A correlation between ciliate and bacterial biomass distribution, with a time lag of two weeks has been suggested [12]. Guhl and Finlay [13] described a case where an anaerobic ciliate followed the distribution of its major food source. Fenchel et al. [9] could not find a relation between ciliate and bacterial numbers but proposed that bacterial growth would determine ciliate distribution.

The study reported here was carried out to investigate the seasonal development of hypolimnetic ciliate and potential prey populations. The investigations focussed on two areas: (1) the characteristics of the functional structure and production of hypolimnetic ciliate communities and correlations with the aerobic/anaerobic metabolism of the organisms; and (2) temporal and spatial distribution patterns and possible explanations for these.

Materials and Methods

Study site

The sampling programme was carried out between April 1991 and September 1992. The pond investigated, Priest Pot, is situated in the English Lake District. It has an area of 1 ha, a maximum depth of 3.9 m and very high nutrient levels, with, e.g., total phosphorus concentrations up to 3 μmol l^{-1}. The pond stratifies thermally from April to October. The hypolimnion is anoxic from May until the autumn overturn. During this period, dense populations of anaerobic phototrophic bacteria, mainly the purple sulphur bacterium *Thiopedia* sp. and the green sulphur bacterium *Clathrochloris hypolimnica*, develop. The pond has been studied intensively [6,14,15].

Sampling procedure and quantification of organisms

Water column. The water column was investigated during the stratification period of 1991 at weekly sampling intervals. In 1992 sampling was carried out every three weeks. All water samples were taken at the deepest point of the pond using a 1 l Friedinger bottle. The meta- and hypolimnion (i.e. the part of the water column where dissolved oxygen concentrations ≤ 3 mg O_2 l^{-1}) were sampled at 20 to 25 cm intervals. Samples for enumeration of organisms were fixed immediately after collection. Samples were taken and processed as described in Guhl and Finlay [13]. Oxygen, temperature and pH, and in 1992 additionally ammonium and sulphide were determined. Ammonium was measured according to Weatherburn [16]. Oxygen, temperature, pH and sulphide were determined as described in Guhl and Finlay [13].

For enumeration, 10-ml sub-samples were gently centrifuged and reduced to a volume of less than 1 ml. The ciliates were counted in a Sedgewick-Rafter chamber at ×40 magnification. Bacteria were stained with DAPI, filtered onto black membrane filters (Nuclepore, 0.2 μm), and enumerated by epifluorescence microscopy [17]. Bacteria were divided into three size categories by measuring the maximum cell dimensions of the stained cells on the filter with an eyepiece micrometer. The following size categories were distinguished: > 1 μm maximum dimension, 1 μm, and < 0.5 μm.

Biovolume determination of ciliates and bacteria were performed according to Guhl and Finlay [13]. The following biovolume values were used for the different bacterial size categories: < 0.5 $\mu m = 0.004$ μm^3, 1 $\mu m = 0.5$ μm^3, > 1 $\mu m = 0.8$ μm^3. The biovolume of large abundant bacteria of distinct shape, e.g. phototrophic bacteria, was calculated by assuming geometrical shapes and measuring the appropriate cell dimensions.

Sediment. Sediment samples were taken from May 1991 until April 1992 at weekly (summer) to monthly (winter) intervals. During the stratification period sediment and water samples were taken on the same day. Sediment cores were collected using a Jenkin corer and perspex tubes with an internal diameter of 7 cm. Two cores were taken on each sampling occasion. The samples were immediately transferred to the laboratory where they were stored at 10°C until further examination. All benthos samples were counted on the day of collection.

Two sediment layers were sampled: 0–1.5 cm and 1.5–3.0 cm. Our own preliminary studies as well as earlier investigations by Goulder [18] had shown that ciliates were rare below a depth of 3 cm. The cores were pushed up in the tubes and from each layer, two sub-samples of 2 ml were taken from above with a syringe which had been preflushed with nitrogen. Care was taken to ensure that the sediment remained covered by water to minimise exposure to oxygen. The sub-samples were diluted with filtered (0.2 μm) and N_2-outgassed pond water from the same core to a final dilution of 1:6. The sub-samples were kept in small hypo-vials which were N_2-outgassed periodically during the counting procedure and were closed with a rubber bung. The ciliates were enumerated according to Finlay et al. [19]. At least 150 cells were counted or, at low cell densities, 60 drops were examined. Results were calculated from the means of the four sub-samples taken from each sediment layer.

Results

Seasonal development of ciliate abundances

After stratification of the pond, microaerobic and anaerobic ciliates migrated out of the sediment and developed planktonic populations (Fig. 1). During summer the planktonic ciliate community reached abundances of over 2×10^8 cells m^{-2} lake surface. This corresponds to cell densities of up to 200 ml^{-1}. Pronounced peaks occurred shortly after the migration into the water column in late spring and at the onset of the autumn overturn.

Also the benthic ciliate community of Priest Pot showed a clear seasonal pattern. After a decrease in late spring which was due to the migration of ciliates into the stratifying water column, numbers remained constant during the summer. They increased again after the return of the planktonic ciliates to the sediment during the autumn mixis. During the stratification period benthic ciliates had lower abundances than planktonic ciliates. Maximal cell numbers were found in spring, with 1.3×10^8 ciliates m^{-2}. During this time the surface layer of the sediment contained up to 10000 ciliates ml^{-1}.

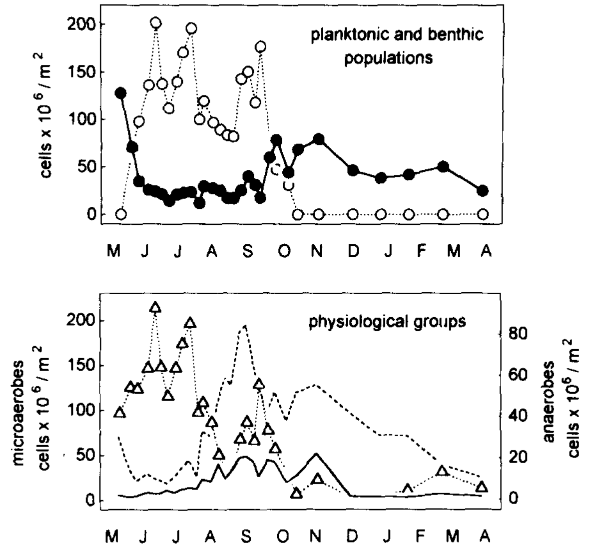


Fig. 1. Ciliate abundances in the hypolimnion of Priest Pot between May 1991 and April 1992. Upper panel: planktonic and benthic abundances, --○-- = planktonic ciliates, -●- = benthic ciliates. Lower panel: abundances of the physiological groups, --△-- = microaerobic ciliates, --- = anaerobic ciliates without methanogens, – = anaerobic ciliates with methanogens. Left y-axis applies to microaerobic ciliates, right y-axis applies to anaerobic ciliates with and without methanogens.

Three physiological groups of ciliates were found in the habitats investigated: (1) microaerobic species with a peak of abundance in microoxic habitats and only low numbers in anoxic environments; (2) ciliates with a clear preference for the anoxic part of the water column but without methanogens. Nearly all of these ciliates belonged to the Scuticociliatida. These species may not have been strict anaerobes with an exclusively fermentative metabolism. None of them could be cultured under oxic or anoxic conditions. However, since no diurnal ciliate migration exists in Priest Pot (unpublished observations) these ciliates must have been capable of growing under anoxic conditions and were classified as 'anaero-

Table 1

Abundant ciliate species in the hypolimnion of Priest Pot [a]

Ciliate taxon	Feeding mechanism	Zoochlorellae present
Microaerobic ciliates		
Loxodes striatus	R	–
Loxodes magnus	R	–
Frontonia vernalis	F/R	+
Euplotes daidaleos	F	+
Lembadion magnum	F/R	–
Spirostomum teres	F	–
Disematostoma bütschlii	F/R	+
Halteria grandinella	F	–
Coleps hirtus	R	+
Strobilidium velox	F	+
Anaerobic ciliates without methanogens		
Dexiotricha plagia	F	–
Dexiotricha sp.	F	–
Cristigera sp.	F	–
Anaerobic ciliates with methanogens		
Caenomorpha medusula	F	–
Prorodon sp.	R	–
Cyclidium porcatum	F	–
Plaguopyla nasuta	F?	–
Saprodinium mimeticum	F	–
Tropidoatractus acuminatus	F	–
Lacrymaria sapropelica	R	–

[a] Feeding mechanisms and presence or absence of zoochlorellae are indicated. F = filter feeder, R = raptorial feeder, F/R = filter feeder with secondarily evolved raptorial feeding. Classification of feeding types modified from [6], for assignment to physiological groups see text.

bic ciliates without methanogens'; and (3) anaerobic ciliates which contained endosymbiotic methanogens and were therefore confined to strictly anoxic habitats.

Table 1 lists the most abundant species in Priest Pot. The species are divided into the three physiological groups, based on observed distribution patterns, culture experiments, the presence or absence of methanogens and physiological data compiled by Foissner et al. [20,21] and Berninger et al. [22]. Altogether 67 species were found: 42 microaerobic, 4 anaerobic without endosymbiotic methanogens, and 21 with methanogens. The microaerobic species consisted mainly of raptorial ciliates, such as *Loxodes* spp. and *Coleps hirtus*, or filter feeders with secondarily evolved raptorial feeding, such as *Lembadion magnum* and *Frontonia vernalis*. Many of them contained zoochlorellae. All anaerobic species without methanogens and most of the anaerobes with methanogens were filter feeders specialised on bacterial food.

The lower panel of Fig. 1 presents the seasonal distribution of the three physiological groups. Microaerobic ciliates dominated the ciliate communities of Priest Pot in late spring and then decreased, with a second peak at the onset of the autumn overturn. Anaerobic ciliates without methanogens increased during the summer until they reached a density similar to that of microaerobic ciliates by the end of August. During late summer these physiological groups had abundances of approximately 8×10^7 cells m^{-2}. Anaerobic ciliates with methanogens increased parallel with the other anaerobes, but since the initial population was small, cell numbers of anaerobic ciliates with methanogens stayed well below those of the other groups.

Figure 2 shows the seasonal distribution of the three ciliate groups in the sediment and water column. After stratification of the water column and depletion of oxygen in the hypolimnion the microaerobic ciliates left the sediment and migrated into the water column, leaving only a small resident population behind. In the autumn, at the onset of mixis, they migrated back into the sediment, their overwintering habitat. Anaerobic ciliates migrated into the water column several weeks later than microaerobic ciliates. A considerable proportion of the populations remained in the sediment. Anaerobic ciliates without methanogens had maximal abundances in the plankton by the end of August and largest benthic populations in November after the planktonic community had returned to the sediment. Anaerobes with methanogens were less abundant in the plankton by a factor of 7–8 than the other ciliates. At least half of their population always remained benthic. Abundances in the water column and the sediment showed simultaneous fluctuations which indicate a dynamic equilibrium between planktonic and benthic populations.

Seasonal development of ciliate biomass

The biomass data of the planktonic and benthic ciliate communities generally correspond to the data for abundance (Fig. 3). The three physiological ciliate groups differed with regard to their cell size: microaerobic ciliates had on average 20 times larger cells than the other two groups. Therefore, the total ciliate community biomass was close to that of microaerobic ciliate biomass alone, even at the end of summer when microaerobic ciliate biomass had reached a minimum. Within the physiological groups benthic ciliates were on average larger than planktonic ciliates (Table 2), but the planktonic community had a larger mean cell size than the benthic because it consisted mainly of microaerobes (Table 2, Fig. 2).

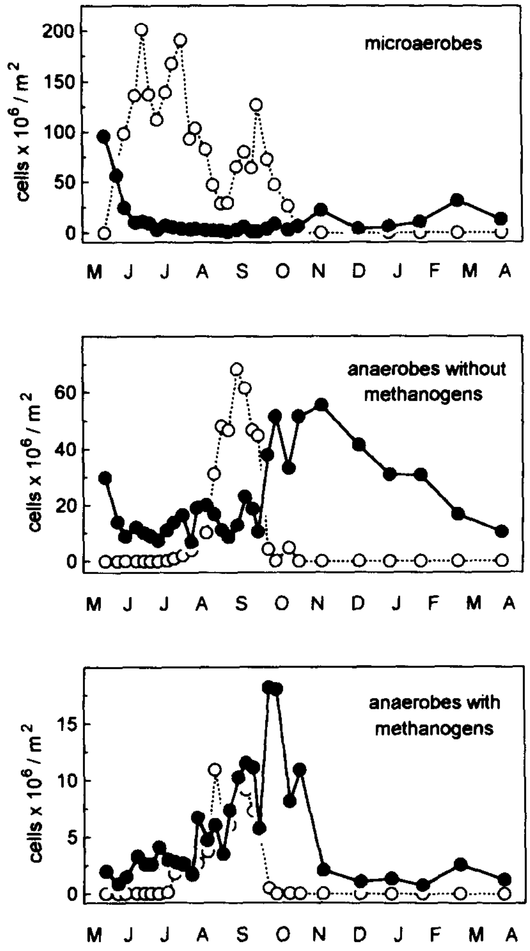


Fig. 2. Planktonic and benthic distribution of microaerobic ciliates (upper panel), anaerobic ciliates without methanogens (middle panel), and anaerobic ciliates with methanogens (lower panel) in the hypolimnion of Priest Pot between May 1991 and April 1992. --○-- = planktonic ciliates, -●- = benthic ciliates.

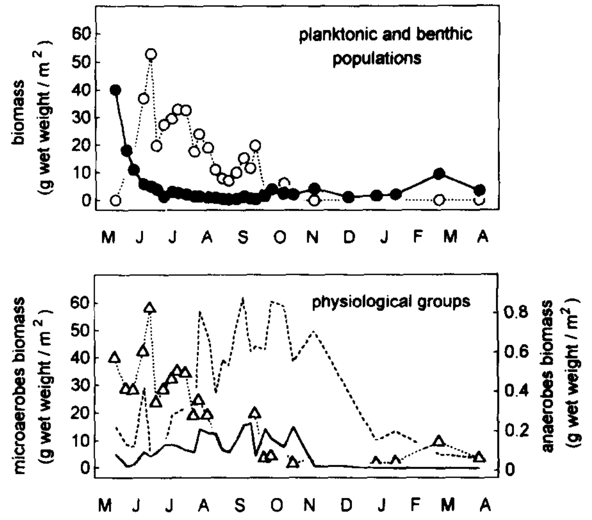


Fig. 3. Ciliate biomass in the hypolimnion of Priest Pot between May 1991 and April 1992. Upper panel: biomass of planktonic and benthic ciliates, --○-- = planktonic ciliates, -●- = benthic ciliates. Lower panel: biomass of the physiological groups, -- △ -- = microaerobic ciliates, --- = anaerobic ciliates without methanogens, – = anaerobic ciliates with methanogens. Left y-axis applies to microaerobic ciliates, right y-axis applies to anaerobic ciliates with and without methanogens. Scales for microaerobes and anaerobes differ by a factor of 70.

Spatial distribution of ciliates and potential food sources within the hypolimnion

Individual ciliate species had a non-random vertical distribution. As an example, the vertical distribution of the four most abundant species on 29 July 1992 is shown (Fig. 4). Each species had maximal cell densities at a different depth. There was no correlation with the distribution of sulphide or ammonium. Instead, ciliate abundances were similar to the distribution of biomass of the corresponding major food source. Potential food sources of ciliates can often be identified by analysis of food vacuole contents. Additional information on the size range of ingested particles is provided by the morphology of the cytostome [23]. Scuticociliates are specialised on filtering small to medium-size bacteria [24]. *Cyclidium porcatum*, a scuticociliate with a cell length of 25 to

Table 2

Mean abundance and cell size of physiological ciliate groups and of the planktonic and benthic communities in Priest Pot in 1991 [a]

Physiological group	Water Column		Sediment	
	mean abundance $\times 10^6$ m^{-2}	mean wet weight per cell (ng)	mean abundance $\times 10^6$ m^{-2}	mean wet weight per cell (ng)
Microaerobes	96.0	192.6	7.9	355.3
Anaerobes – methanogens	17.6	8.9	17.0	14.3
Anaerobes + methanogens	3.1.	9.3	6.2	16.3
Mean cell size of community		159.7		112.4

[a] Abundances are mean values for the stratification period, mean cell weight is calculated from total areal abundance and total biomass in 1991.

30 μm, and *Dexiotricha plagia*, another scuticociliate with cells up to 70 μm long, feed on small bacteria and bacteria ≥ 1 μm respectively. The heterotrich *Caenomorpha medusula* feeds in Priest Pot on large phototrophic bacteria [13]. An unidentified member of the prostomatid genus *Prorodon* was the only abundant raptorial anaerobic ciliate in Priest Pot. It feeds mainly on *Cryptomonas* sp. and sedimenting phytoplankton (this was confirmed by inspecting food vacuole

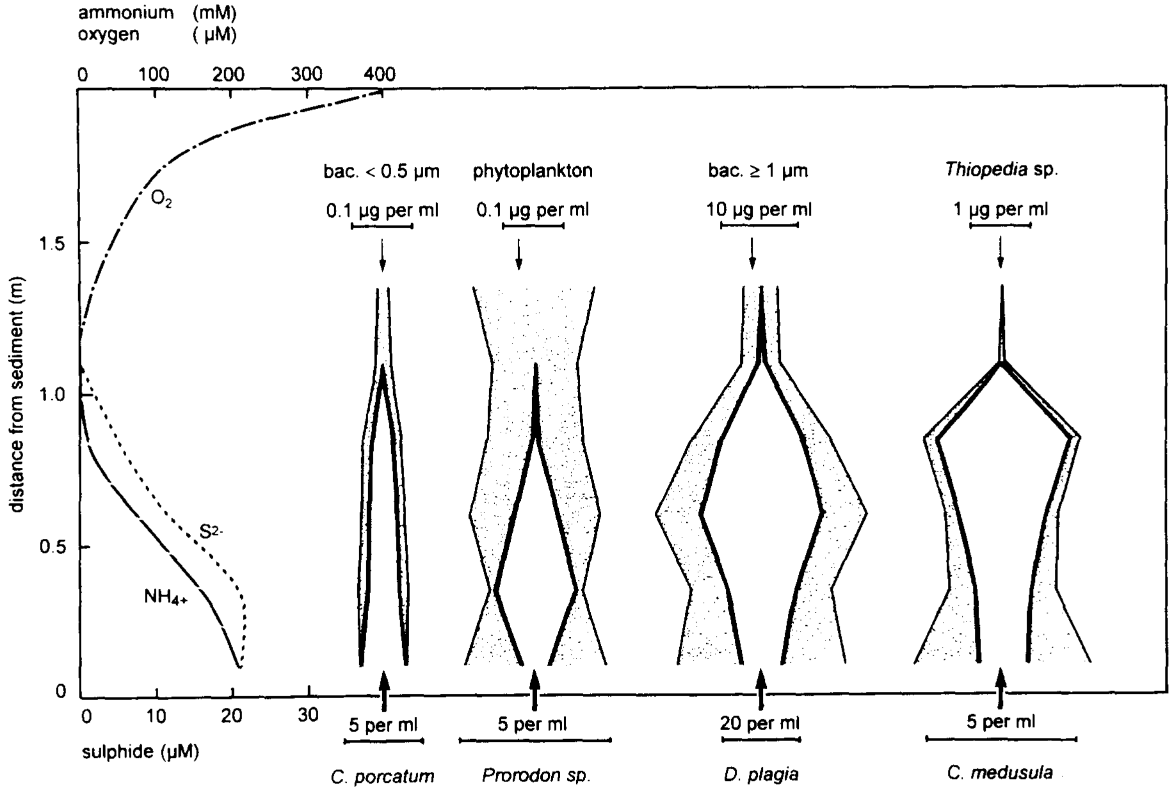


Fig. 4. Vertical distribution of the anaerobic ciliates *Cyclidium porcatum*, *Prorodon* sp., *Dexiotricha plagia*, and *Caenomorpha medusula*, their corresponding major food sources, and some chemical parameters within the water column of Priest Pot on 29 July 1992. The clear areas correspond to abundance of ciliates, the dotted areas correspond to food biomass. Bars below graph indicate abundance of ciliates in cells per ml, bars above graph indicate food biomass as wet weight per ml.

contents using epifluorescence microscopy). On the sampling occasion illustrated, the correlation between the *Prorodon* and phytoplankton distribution was least pronounced but the correspondence between the two distribution patterns was evident when the data for the entire stratification period were pooled (see below).

On 12 September 1991 three hypolimnetic depth profiles with 20 cm sampling intervals were taken with a horizontal distance of 2 m between each other, to monitor horizontal patchiness within the hypolimnion. Figure 5 presents the vertical distribution of the different physiological groups. Each had a characteristic distribution pattern. Microaerobic ciliates had highest cell numbers at 1.7 m above the sediment, and decreased rapidly with increasing depth. Anaerobic ciliates without methanogens peaked at 1.3 m, ciliates with methanogens at 1.1 m, and their populations stretched over greater depth ranges than the microaerobes. The three depth profiles demonstrate a relatively uniform horizontal distribution of ciliates in the hypolimnion: maximal cell numbers for the three ciliate groups occurred at the same depth in each profile. Horizontal patchiness was more pronounced in the metalimnion. Maximal cell numbers of microaerobic ciliates varied by a factor of two whereas variability of the other ciliate populations was smaller.

Seasonal development of individual species

Abundant species developed characteristic seasonal patterns which were similar in the two years of investigation. As examples the hypolimnetic distribution of *Caenomorpha medusula*, *Prorodon* sp., and *Dexiotricha plagia* are presented for 1991 and 1992 (Fig. 6). For 1991 the sediment data are included.

Like all species of the hypolimnetic ciliate community, *C. medusula* developed a benthic population before it started to migrate into the water column (Fig. 6a). In 1991 it was most abun-

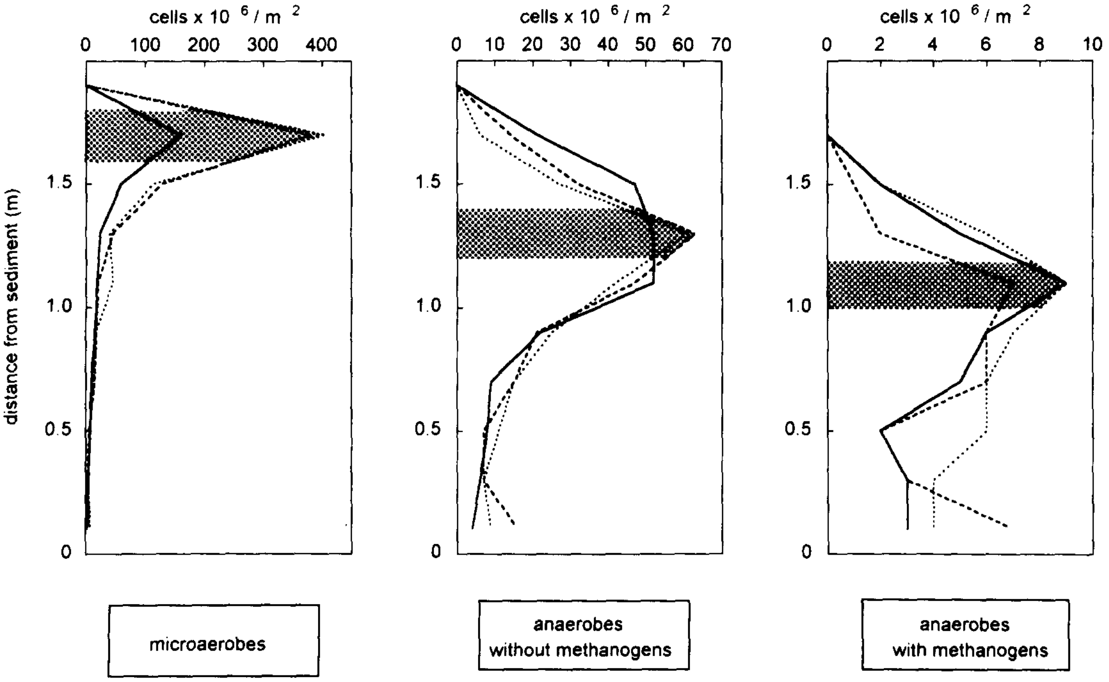
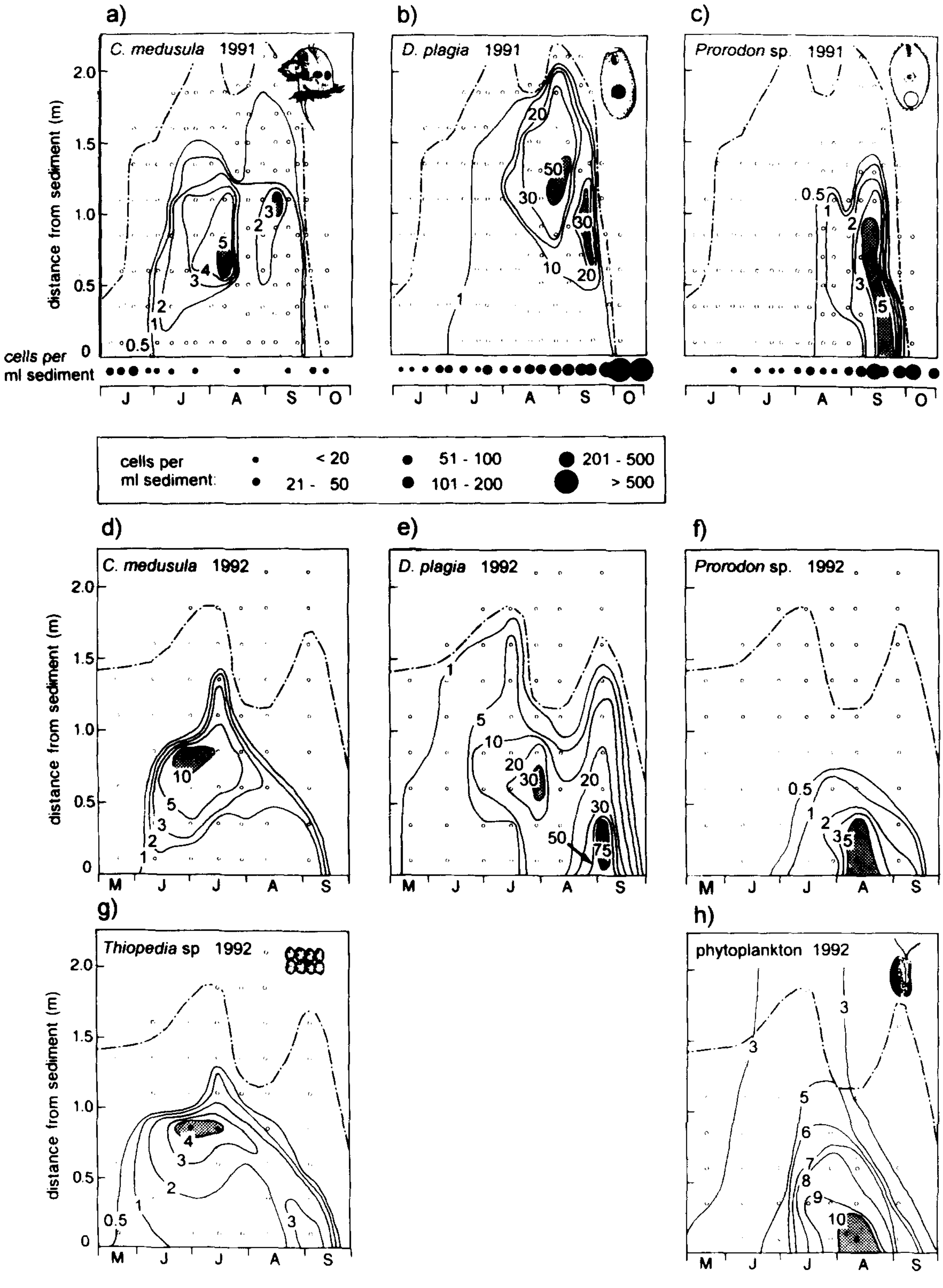


Fig. 5. Vertical distribution of microaerobic ciliates, anaerobic ciliates with methanogens, and anaerobic ciliates without methanogens in three parallel profiles in the water column of Priest Pot on 12 September 1991 – = profile 1, --- = profile 2, ... = profile 3. Shaded areas indicate the depth of abundance maximum for each physiological group.


a)
C. medusula 1991
b)
D. plagia 1991
c)
Prorodon sp. 1991
distance from sediment (m)
0
0.5
1.0
1.5
2.0
cells per ml sediment
J J A S O
cells per ml sediment:
< 20
21 - 50
51 - 100
101 - 200
201 - 500
> 500
d)
C. medusula 1992
e)
D. plagia 1992
f)
Prorodon sp. 1992
M J J A S
g)
Thiopedia sp 1992
h)
phytoplankton 1992
0.5
1
2
3
4
5
10
20
30
50
75
6
7
8
9

dant in the water column at the end of July/ beginning of August. A smaller peak of abundance occurred after a short period of bad weather and the following re-establishment of the planktonic community. Maximal cell densities were always well above the sediment. *Dexiotricha plagia* left the sediment later than *C. medusula* (Fig. 6b). Part of its population remained benthic. In 1991 maximal cell numbers were found in the middle of August, just between the two *C. medusula* peaks, and at the onset of the autumn overturn. Also this species had maximal cell densities around 1 m above the sediment. In 1991 *Prorodon* started to develop a benthic population from July onwards and a planktonic population towards the end of August (Fig. 6c). This species had highest cell numbers in the water column around the middle of September, with the peak of abundance stretching down to the sediment surface. Half of its population remained in the sediment.

In 1992, spring was warmer and the benthic ciliates migrated earlier into the water column (Fig. 6d–f). But due to a colder summer the upward extension of the anoxic hypolimnion was curtailed and the ciliates stayed closer to the sediment. *C. medusula* developed only one hypolimnetic maximum. Apart from these differences, the spatial distribution and the seasonal succession of the three species was similar to that in 1991. In particular, the sequence of population maxima was the same in both years and maximal abundances did not overlap.

For *C. medusula* and *Prorodon* sp. there was a clear correlation between ciliate abundance and availability of the major food source (Fig. 6 g,h). The distribution of *C. medusula* followed that of purple sulphur bacteria, especially *Thiopedia* sp., which are a potential food source of *C. medusula* [13]. The distribution of *Prorodon* was related to total biomass of phytoplankton. For *D. plagia* the major food source could not be identified beyond a certain size class of bacteria, i.e. bacteria 1 μm; and ciliate and bacterial biomass distribution only partly corresponded.

Discussion

Spatial and temporal distribution patterns of ciliate communities

The spatial and temporal distribution of hypolimnetic ciliates was mainly governed by two factors: (1) the distribution of dissolved oxygen; and (2) the availability of food.

Apart from oxygen, no other chemical parameter was found to directly influence ciliate distribution. This also holds true for sulphide: in Priest Pot, sulphide concentrations up to 25 μmol l^{-1} did not lead to any apparent effect on ciliate distribution. It is known from other lakes that anaerobic ciliates can tolerate sulphide concentrations of more than 1 mmol l^{-1} [8].

There was no significant grazing pressure on hypolimnetic ciliates. Priest Pot does not support planktonic crustaceans [6], and rotifers, which are extremely abundant in this pond, were never found in the oxygen-free part of the water column (unpublished observations, [15]). The only potential predators in Priest Pot were the diurnally migrating larvae of the midge *Chaoborus flavicans*. The first two instars of *Chaoborus* are known to feed on protozoa [25,26]. These two instars were absent from the water column of Priest Pot from July onwards (unpublished observations).

Once anoxic conditions were established in the hypolimnion the major factor affecting ciliate distribution was the availability of food. In contrast to microaerobic ciliates, anaerobic ciliates were

Fig. 6. Spatial and temporal distribution of *Caenomorpha medusula*, *Dexiotricha plagia*, and *Prorodon* sp. and their food sources in the hypolimnion of Priest Pot in 1991 and 1992. Isopleths for ciliate distributions indicate cells per ml, for food distribution biomass as wet weight per ml (*Thiopedia* sp. g wet weight $\times 10^{-6}$ per ml, phytoplankton g wet weight x 10^{-7} per ml). The filled circles represent ciliate abundance in the sediment. Isopleths shown as dotted lines indicate the depth of detectable dissolved oxygen (5 μM). The small, empty circles show the depth-time coordinates of all water samples that were taken.

not forced out of the sediment by a chemical gradient, and many anaerobic ciliates remained benthic during the summer. The ciliates which left the sediment took advantage of the populations of anaerobic bacteria which developed in the water column. Anaerobic ciliates which contained endosymbiotic methanogens and were therefore strictly confined to anoxic environments were probably better adapted to benthic food sources and, with the exception of *C. medusula*, did not develop extensive planktonic populations. In contrast, the anaerobic ciliates without methanogens, i.e. the scuticociliates, fed predominantly on the large populations of bacteria developing in the water column.

In the hypolimnion there was a clear food niche separation. Anaerobic ciliates were mainly bacteria feeders with a preference for a certain particle size range. The correlation between predator and prey distribution was particularly evident when one species was specialised on a clearly discernible food source, such as *C. medusula* on large phototrophic bacteria, or *Prorodon* sp. on phytoplankton. In these cases the seasonal development of the ciliate population and that of its food were nearly identical. For the scuticociliates which fed on bacteria with only slightly differing size ranges there was no simple correlation with bacteria abundance of a certain size. The bacteria species present may have had different food values for each ciliate species as was shown for laboratory cultures of anaerobic ciliates [27]. For the scuticociliates, the corresponding food source could not be precisely identified, so no unambiguous correlation could be demonstrated. But also for scuticociliates, cell numbers were regularly highest at the depth of maximal bacteria biomass. From productive lakes, high numbers of scuticociliates at the oxycline, together with a peak of bacterial abundance, are often reported [28].

It may be argued that the similarity between distribution patterns of ciliates and bacteria or phytoplankton indicate the influence of another factor on both populations, rather than a predator-prey relationship. *C. medusula* could, for example, feed on heterotrophic bacteria which use *Thiopedia* exudates as substrate. This can be ruled out on theoretical considerations. The biovolume ratio between *C. medusula* and *Thiopedia* at the time and depth of their maximum population development was approximately 5% [13]. Due to its anaerobic metabolism the upper limit of gross growth efficiency of *C. medusula* is 15% [5]. No information exists on the rate of dissolved organic matter (DOM) released by anaerobic phototrophs. Assuming similar rates as for aerobic phytoplankton, *Thiopedia* would not release more than 50% of the fixed carbon [29], often values are much lower [30]. Even if the heterotrophic bacteria took up all DOM released by *Thiopedia* they would have had to grow with a gross growth efficiency of about 70% to support the observed *C. medusula* population. This is unreasonably high for anaerobic bacteria [31]. *C. medusula* had in situ doubling times of about 14 days. Data on in situ growth of anaerobic phototrophic bacteria is sparse. Mas et al. [32] reported summer doubling times for *Chromatium minus* in the same range, i.e. 11 to 13 days. It is therefore possible that *C. medusula* and *Thiopedia* populations grew with similar growth rates. Since planktonic prey populations started to develop 2 to 3 weeks before ciliate populations, this lead, once established, may have lasted for a considerable part of the stratification period.

The tight coupling of ciliate and prey distribution led to a seasonal succession of ciliates parallel with that of the hypolimnetic bacterial community. When, for example, the purple sulphur bacterium *Thiopedia* was replaced by the green sulphur bacterium *Clathrochloris hypolimnica* the population of *C. medusula* decreased markedly. In the autumn, large amounts of phytoplankton sedimented into the hypolimnion where they served as food for an increasing *Prorodon* population. Since environmental conditions were more stable in the hypolimnion than in epilimnetic habitats, seasonal fluctuations were less pronounced. Notably, horizontal patchiness was reduced.

Psenner and Schlott-Idl [12] investigated the hypolimnetic ciliate community of mesotrophic Lake Piburg and found a correlation between ciliate and bacterial biomass with a time lag (between peaks) of two weeks. Lake Piburg is larger

(13 ha), deeper (max. depth 25 m) and located at an altitude of 900 m. Water temperatures of the hypolimnion are lower than in Priest Pot and there are no anaerobic phototrophic bacteria. Nutrient fluxes and bacterial and ciliate growth rates are probably considerably higher in the shallow hypolimnion of Priest Pot, and ciliates are able to quickly track their food over the short distances within the water column. As a result, no time lag between predator and prey maxima was observed. But as mentioned above, often there was a time lag of two to three weeks between the initial build up of a food population and the migration of ciliate predators into the water column.

It should be mentioned that ciliate as well as bacteria abundance might have been influenced by the presence and activity of viruses and bacteriophages. Investigations on virus abundance and activity are scarce and the results are conflicting [33,34]. Our findings did not provide any quantitative information on viral infections. But we investigated ciliates from Priest Pot using transmission electron microscopy. During these studies no indication for viral infections of ciliates was found (in contrast virus-like particles were present in an anaerobic amoeba isolated from Priest Pot sediment, unpublished observations). It therefore seems to be unlikely that significant numbers of ciliates were virus-infected. Although bacterial abundances in Priest Pot were high infection by bacteriophages might have had an impact on absolute bacterial numbers and consequently on biovolume ratios between bacteria and ciliates. Nevertheless, the biovolume ratios between anaerobic ciliates and their major food source were about a quarter of those between aerobes and their food [5]. This difference is almost certainly due to differing efficiencies of aerobic and anaerobic metabolism rather than differences in bacteriophage infections.

Production of hypolimnetic ciliate populations

The hypolimnion of Priest Pot had an abundant ciliate community. This community was supported by high bacterial numbers which reflected the high inorganic nutrient level of this pond [28,35]. The reported numbers are in the upper range of data previously published for this habitat [3,4,36,37].

During the stratification period the thermocline formed a physical barrier. Inorganic nutrients bound in organic matter sedimented into the hypolimnion and became available again only at the autumn mixis. While during the summer the epilimnion became depleted of inorganic nutrients, in the hypolimnion anaerobic degradation of organic matter and nutrient release from the anoxic sediment led to inorganic nutrient enrichment. This was, for example, demonstrated by an increase in ammonium above the sediment, from less than 10 to more than 200 μmol l^{-1} during the stratification period. These processes were reflected in the decrease of metalimnetic microaerobes and the simultaneous increase of hypolimnetic ciliates over the summer. For the metalimnetic microaerobes, predation cannot be ruled out completely. Due to the absence of any significant predation in the anoxic part of the water column, the numbers of anaerobic ciliates probably reflected the carrying capacity of their environment.

Ciliate community biomass was dominated by microaerobic ciliates. Anaerobes, regardless of whether they contained methanogens, were on average much smaller than their microaerobic counterparts. There was a nutrient shift from the epi- to the hypolimnion over the summer, but ciliate production in the anoxic hypolimnion remained comparatively low. These findings are consistent with the low growth efficiency of anaerobic ciliate metabolism known from laboratory cultures. Cultures of aerobic ciliates produce approximately four times higher cell yields than those of anaerobes [27,38].

Although there was a considerable diversity of species, at any time there were only one or two species present in the water column in large numbers (i.e. > 5 ml^{-1}) which shared the same size range of food. Due to the low growth efficiency of the anaerobic metabolism the available food sustained only a limited ciliate biomass. The observed seasonal succession of ciliates can therefore also be partly attributed to the physiological properties of the anaerobic microbial community.

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