SHORT COMMUNICATION

Oxygen Availability and Seasonal Migrations of Ciliated Protozoa in a Freshwater Lake

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Migrations of ciliated protozoa between the benthos and water column of a productive lake are reversible and linked to seasonal changes in oxygen availability. Maximum densities of planktonic populations are maintained for periods of several months at depths where the oxygen concentration is 1 mg l⁻¹ or less. With the possible exception of one genus (Loxodes) there was no evidence for periodic vertical migration within a season. The supposed unconditional requirement for oxygen in large free-living ciliates is questioned.

INTRODUCTION

Soft lacustrine sediments often harbour large numbers of ciliated protozoa (Finlay, 1980; Goulder, 1980). Many species are large (>150 µm) but densities of these are invariably reduced during seasonal deoxygenation of the benthos and overlying water. This is not surprising since the species concerned are commonly assumed to be obligate aerobes. It has been suggested (Goulder, 1980) that ciliate communities displaced from the benthos of a shallow (3 to 4 m) stratified pond might continue to exist in the anoxic water column. There they might indulge in periodic, non-synchronous migrations between their source of oxygen at the oxycline and the lower hypolimnion.

The fate of large ciliates in the anoxic benthos of deeper lakes is less certain. Some species die off or are displaced (Webb, 1961; Goulder, 1974) while others, such as those in the genus Loxodes, appear to have a surprising tolerance of anaerobic conditions (Birge & Juday, 1911; Lindeman, 1942; Webb, 1961; Goulder, 1974).

The study reported here is concerned with the response of a community of benthic ciliates to seasonal deoxygenation of the hypolimnion in a deeper, productive lake. The following possibilities were investigated: (i) benthic-planktonic migrations taking place on a seasonal basis, (ii) oxygen availability having a controlling influence on such migrations, (iii) similar intolerance of anoxia in different species, and (iv) large ciliates migrating periodically within the anoxic hypolimnion.

METHODS

Study site. Esthwaite Water (National Grid Reference SD 360 965) is a productive lake of moderate size (1 km²) in the English Lake District. The essential features are described by Webb (1961) and Goulder (1974). Sediment and water samples were taken at the deepest point (about 15.5 m) in the North Basin.

Sampling for planktonic ciliates. Samples of protozoa were obtained at successive vertical intervals of 20 to 40 cm using the pneumatically operated sampler described by Heaney (1974). Each syringe sample had a volume of 10 ml and all ciliates longer than 150 µm (large ciliates) in the sample were identified and counted with the aid of a low power binocular microscope.
Fig. 1. Migrations of large ciliated protozoa coupled to the availability of dissolved oxygen in Esthwaite Water in 1979 (a) and 1980 (b). The symbols refer to total numbers of ciliates in each sample – see key in (a). Isopleths of dissolved oxygen concentration increase in steps of 1 mg l⁻¹ with the exception of the lowest, thick line representing 0.3 mg l⁻¹.
**Sampling for benthic ciliates.** Ciliates in the top 1 cm of Jenkin core samples were enumerated using the method of Finlay *et al.* (1979). Alternatively, at least 30 samples (5 μl each) were removed using an automatic pipette from the surface sediment of six cores. These samples were diluted on a slide with membrane-filtered water and all ciliates present were recorded. The latter method provided more accurate estimates of ciliate numbers when densities were low.

**Dissolved oxygen.** The level of dissolved oxygen in the water column was recorded at 0.5 m depth intervals at least once a week. The limit of detection for the membrane-covered galvanic electrode used was approximately 0.3 mg 1\(^{-1}\). This concentration was assumed to be a marker for the oxic–anoxic boundary. Polarographic measurements (Davison, 1977) have confirmed that water below this boundary is anoxic.

**RESULTS AND DISCUSSION**

A community of large ciliates thrives in the top 1 cm of soft, oxidized sediments in Esthwaite Water. High densities (3633 ± 974 cm\(^{-2}\), mean of all sampling occasions with 95% confidence limits) are typical between October and May when the community is dominated by two genera, *Loxodes* and *Spirostomum*. Goulder (1974) obtained similar data from the south basin of Esthwaite. During the summer, the lake becomes thermally stratified, benthic and hypolimnetic demand for oxygen exceeds supply from atmospheric and photosynthetic sources, and the volume of the anoxic hypolimnion increases (Heaney & Talling, 1980). As the last traces of detectable oxygen are removed at the sediment surface, the community of large ciliates undergoes several changes (Fig. 1). Most representatives moved into the overlying water, a few (87 ± 54 cm\(^{-2}\)) remained active in the sediment and some, like *Paramecium*, disappeared. Thereafter, ciliates were always found in the water column with peak numbers at an oxygen concentration of 1 mg 1\(^{-1}\) or less. The coincidence of ciliates and available oxygen was maintained through periods of temporary destratification (September 1979) and persisted until the autumn overturn when both oxygen and ciliates returned to the benthos. During the winter of 1979–1980 the water column was checked twice (12 December and 27 March) for the presence of large ciliates. None were recorded on either occasion.

There are at least two alternative explanations for ciliate migrations into the water column. The first is that the ciliates concerned are following the upwards migration of living, aerobic food sources. Although bacteria, and especially iron bacteria, do appear in large numbers in the hypolimnion following deoxygenation of the benthos (Jones, 1978), they do not appear to be a food source. The only items identified in the food vacuoles of ciliates were small green algae, diatoms or fragments thereof, all of which sediment from their sites of production in the upper water column.

Secondly, ciliate migrations may be described as a retreat from increasing concentrations of reduced compounds in the hypolimnion rather than movement towards a source of oxygen. Although high concentrations of H\(_2\)S, NH\(_3\) and CO\(_2\) are probably toxic to many protozoa (Bick, 1972), it is likely that toxic concentrations cannot be produced until some time after oxygen has been removed. The pattern observed in the hypolimnion of Esthwaite over several years (Mortimer, 1941; Goulder, 1974; Jones, 1978; Davison, 1980) has been for concentrations of reduced compounds to increase gradually over several months following the establishment of deep-water anoxia. Maximum concentrations, and those likely to be toxic to protozoa (Bick, 1972), are not produced until shortly before the overturn.

The benthic habitat vacated by large ciliates during the summer was exploited by a community of anaerobic 'sulfide ciliates' similar to marine communities already described (Fenchel *et al.*, 1977). These remained in the surface sediment and lower hypolimnion while anaerobic conditions persisted, but declined in numbers when oxygen and the associated community of large ciliates returned.

Thus, the total ciliate community can be divided into two groups on the basis of oxygen requirements. The first, a group of large ciliates, needs access to a source of oxygen presumably for aerobic respiration, while the second group, of small (<150 μm) sulfide
ciliates, has no requirement for oxygen. Closer examination of Fig. 1 casts some doubt on that generalization. Although peak numbers of large ciliates were usually found close to the oxic–anoxic boundary, individuals could usually be recorded throughout the anoxic hypolimnion (Fig. 2) and some large ciliates were invariably found in the benthos; indeed, *Loxodes magnus* was often the only species recorded from the bottom water and benthos. Apparently healthy, reproducing cells of this species have been recorded from both the oxycline and the benthos on the same day. Regular sampling of the complete community over several 24 h periods has not revealed synchronized vertical migration of this or any other large ciliate species. One possible explanation is that *Loxodes* migrates periodically between the sediment and the upper hypolimnion. This presumably would involve such protozoa spending long periods in anoxic water (cf. Goulder, 1980).

Preliminary cytochemical analyses of the ciliates involved indicated that they may be capable of responding in different ways to the absence of oxygen. Unlike *Spirostomum*, *Loxodes magnus* shows a negative response to tests for cytochrome oxidase (Fenchel et al., 1977) and the formazan dye 2-(4-iodophenyl)-3-(4-nitrophenyl)-5-phenyltetrazolium chloride (INT). Preliminary investigations using light microscopy and staining with Janus Green B indicated that mitochondria may be lacking, at least in the population inhabiting anoxic sediment (cf. *L. striatus*; de Puytorac & Njiné, 1970). However, the cytoplasm of *L. magnus* does contain a diversity of granules of various sizes. Some, like Müllers vesicles, are easily identified and others may be glycogen granules, fat inclusions or mucocysts (Corliss, 1979), but it is possible that other spherical, microbody-like structures in the size range 0.5 to 2.0 μm are redox organelles such as hydrogenosomes (Müller, 1980). Similar spherical organelles have been observed in the anaerobic ciliate *Caenomorpha* from the same habitat.

The nature and function of organellar inclusions in *Loxodes* is being investigated further.

Even with maximum numbers occurring in the vicinity of the oxic–anoxic boundary, protozoa are still the dominant eukaryotic organisms in the anoxic hypolimnion of Esthwaite Water. Thus in some years, a water column almost 10 m deep (Heaney & Talling, 1980) could be devoid of other meiofaunal grazers during the summer. A motile organism the size of *Loxodes* with the ability to switch periodically between aerobic and anaerobic metabolic pathways would be ideally equipped to graze the suspended microalgae and fine detritus of the entire hypolimnion. It is clear, however, that large ciliates in general will have no part to play as grazers in the plankton unless deep-water anoxia first forces them out of their preferred habitat – the benthos.

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**Fig. 2.** Vertical distribution of *Loxodes magnus* (●) and all other large ciliates (○) in the water column (lower 11 m) on 10 September 1980. Substantial numbers of *Loxodes magnus* were recorded in all samples down to the sediment where the density was about 70 cm⁻². All ciliates peaked strongly in the vicinity of the oxic–anoxic boundary (---, 0.3 mg l⁻¹).
Short communication

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REFERENCES


