

## The fossil history of sulfur phototrophs in a meromictic lake ecosystem

S. R. Brown &amp; H. J. McIntosh

*Biology Department, Queen's University Kingston, Ontario, Canada. K7L 3N6*

**Abstract.** Changes in two populations of phototrophic bacteria are traced throughout the postglacial history of a lake. Evidence of the changes is derived from a sediment core which provides a fossil record spanning more than 8000 years. Okenone, a carotenoid produced by members of the Chromatiaceae, is used to identify contributions of that group, and both isorenieratene and  $\beta$ -isorenieratene to measure those of Chlorobiaceae.

Substantial populations of both bacterial taxa existed throughout all but the most recent history of the lake. The overall pattern of their productivity shows a somewhat reciprocal relationship in which high levels in one group correlate with depressions in the other. At times both groups were highly successful. The Chlorobiaceae were markedly reduced during an early period in which cyanobacteria (blue-green algae) were prominent in the planktonic assemblage. Under similar circumstances of recent time, both populations of the sulfur phototrophs have crashed.

Our data are compared with those of other workers who studied the fossil record of diatoms and sediment chemistry in cores from the lake. This provides a trophic framework in which to explore the success of the bacteria. We conclude that the underwater light climate has been a major factor in regulating their relative productivity.

**Key words:** Chromatiaceae, Chlorobiaceae, carotenoids, okenone, isorenieratene, lake sediments.

## Introduction

Large populations of phototrophic sulfur bacteria have been observed in many lakes and lagoons where suitable conditions for growth occur (Pfennig, 1978; Biebl and Pfennig, 1979; Schlegel and Jannasch, 1981). Although growth requirements for the organisms have been clearly defined in laboratory cultures, the complex interaction of ecological factors that regulate natural populations is much less well understood (Van Gernerden, 1983; Guerrero et al, 1985; Parkin and Brock, 1980). They may achieve seasonal success in lakes of the temperate latitudes during periods of thermal stratification when the hypolimnion becomes anoxic and a vertical gradient in sulfide is established. Suitable habitat persists more continuously in meromictic lakes provided that sufficient light penetrates to the depth of the chemocline. Complementary gradients of light and sulfide exist in that region, thus the organisms tend to stratify. The upper stratum is composed mainly of populations of purple sulfur bacteria (Chromatiaceae), while brown-colored varieties of the green sulfurs (Chlorobiaceae) occupy the deeper regions.

Bacterial contributions to the total productivity of lake ecosystems appear to be highly variable. In some meromictic lakes 90 % or more may be attributed to sulfur phototrophs, but a much smaller percentage (less than 5 %) is found more frequently

in lakes having holomictic circulation. These observations are based on short-term studies, most often only seasonal or annual in duration. The results are therefore influenced by factors such as local weather conditions which are known to vary considerably from year to year. Very few studies have been continued long enough to smooth out brief perturbations and observe the bacterial response to a broad spectrum of changing environmental conditions. This paper traces the success of two populations of phototrophic bacteria throughout the postglacial history of a lake. Identification of the populations and estimates of their size makes use of fossilized carotenoid pigments from the bacteria and are preserved in the sediments of lakes.

The limnological literature offers relatively few studies of the importance of phototrophic bacteria in aquatic ecosystems apart from those dealing with the cyanobacteria, and these are treated most frequently as part of the algal assemblage (Cyanophyta).

Limnologists tend to ignore the sulfur phototrophs, in part because their populations have been missed in routine water sampling or they have not been identified when standard phycological techniques are employed. This neglect is offset by outstanding work in the traditional field of microbiology where sulfur phototrophs are clearly recognized as important components of the aquatic ecosystem. The gap between disciplines will inevitably narrow as advances are made in knowledge of the microflora of the so-called deep photosynthetic layers in lakes (Craig, 1987).

Fossil records of aquatic ecosystems are scattered through the literature of several disciplines. Marine scientists searching for evidence of change in climate or water chemistry have been interested in diatoms and radiolarians found in sedimentary deposits. Freshwater biologists have made extensive use of structural elements of planktonic organisms in their studies of the ontogeny of lakes. Frustules of diatoms and the chitinous remains of cladocera and insects are preserved in the stratigraphic sequence of lake sediments where they provide valuable records of ecological successions and nature of the environment in which they took place. Bacteria, flagellates and other protists that lack enduring structural parts are not represented in the conventional fossil assemblage. In the case of phototrophic organisms, their chlorophylls and carotenoids may be deposited in quantities sufficient to allow for identification and quantitative measurement (Vallentyne, 1960; Brown, 1969). Early work focused on chlorophylls chiefly as a measure of past productivity. The approach is analogous to estimation of biomass of living phytoplanktonic populations by the chlorophyll method. Lake sediments, however, contain a much greater diversity of chlorophyll derivatives and these complicate analytical procedures and interpretation of results. Preservation of carotenoids is probably better than that of the chlorophylls, and these compounds are of considerable interest because of their taxonomic affinities and the fact that they occur in such widespread distribution. A comprehensive survey of these affinities in living organisms indicates their considerable potential in chemotaxonomic and evolutionary studies (Liaaen-Jensen, 1978). Thus far the approach has not been exploited extensively in examination of the fossil record.



The number of reports on carotenoids in lacustrine sediments is not great. Most of them relate to algae, and as evidence of changes in overall productivity rather than to assignment of it to specific groups of organisms (e.g. Sanger and Gorham, 1972). It seems that the first one clearly to implicate phototrophic bacteria deals with the occurrence of rhodoviolascins (spirilloxanthin) in sediments of an African lake (Karrer and Koenig, 1940). Later, bacterial pigments were identified in the sediments of a lake in U.S.A. and two lakes in central Canada (Vallentyne, 1956; Brown, 1968; Daley et al, 1977; Brown and Colman, 1963). Analysis of one sediment core showed that bacteriochlorophyll *a* was prominent during the early postglacial history of the lake, then disappeared or fell to insignificant levels before a second modest increase. High concentrations of carotenoids were also found in these cores, but little attention was given to isolating or measuring all but a few members of the complex mixture in which they were found. One of these exceptions was oscillaxanthin, identified for the first time in sediment deposits. Its occurrence together with myxoxanthophyll was given as evidence of *Oscillatoria* spp. in the lake at the time when the sediments were laid down. The pigment has subsequently been used in a number of studies of lacustrine deposits which show trophic and successional changes (Züllig, 1982; Griffiths and Edmondson, 1975; Griffiths, 1978). Three other carotenoids were isolated from the cores at the level where high concentrations of bacteriochlorophyll *a* had been found. Of these only spheroidenone could be isolated in quantities sufficient to crystallize and establish its identity with certainty. Spheroidene and 2-keto-spirilloxanthin were identified by electronic absorption spectra and co-chromatography, but not verified by more rigorous tests. These findings were of interest, but until a larger number of pigments could be identified and measured, little progress was possible in recognizing the bacterial taxa that produced them. The subsequent discovery of sedimentary okenone, isorenieratene,  $\beta$ -isorenieratene, and bacteriochlorophyll *e* provided a basis for distinguishing between purple and green sulfur phototrophs, and tracing these populations in the fossil record. (Brown et al, 1984). Brown-coloured species of the Chlorobiaceae produce bacteriochlorophyll *e* and the isorenieratene carotenoids, whereas okenone is found only in the Chromatiaceae. The latter contain bacteriochlorophyll *a*, but that characteristic is shared by others, including the Rhodospirillaceae. In their use as fossils it is assumed that concentrations of these pigments in the sediment are proportional to those found in the cells of living populations.

There are deficiencies and shortcomings in most fossil records, so it is not surprising to find that they exist among pigmentary fossils as well. As organic entities, they are vulnerable to degradative processes. Photo-oxidation and changes in pH, such as occur in the guts of grazing animals, may be responsible for most of the diagenesis. In this respect the sulfur phototrophs occupy a position in the water column that is especially favourable to preservation of their pigments. Unlike the organisms growing nearer the surface, these bacteria are located in an environment of low light intensity, virtual or total absence of oxygen, and coincidentally, a marked reduction in grazers. This most probably explains why the carotenoids of bacteria tend to dominate the pigment assemblages in

which they occur at all. Those originating much higher in the water column would have been exposed to much harsher environments and relatively greater destruction.

Questions of differential preservation among the carotenoid classes have been raised. There is evidence that fucoxanthin and peridinin are more labile than some others, but no systematic study has yet been undertaken to provide a broad perspective. It may be presumed that loss has occurred, thus it remains to be determined how well the fossil residue represents the living cell populations that produced it. Experimental evidence relating to bacterial carotenoids is lacking, but important insights may be gained from studies of the algae. An outstandingly comprehensive study of the algal carotenoids has been carried out on the sediments of 10 Swiss lakes (Züllig, 1982). The carotenoid studies were supplemented by counts of diatom frustules and cladoceran remains in stratigraphic sequences that span from one to two centuries. Some useful observations relating to the waters of the lakes and human activity in the catchments are found in the written historical record, and these help to explain changes in trophic status of the lakes that are inferred from the sedimentary record. Regions of high concentration of oscillaxanthin and myxoxanthophyll in the sediments correlate with available records of prominence of blue-green algae in the phytoplankton. A much less subjective comparison may be made, however, by using the data available from the diatoms. Highly significant correlations exist between numbers of diatoms and concentrations of fucoxanthin in all of these lakes during eutrophic phases of their history. A similar trend is observable during more oligotrophic periods, but the correlation is much weaker. This evidence relating structural to pigmentary fossils deals with one of the carotenoids presumably most prone to diagenesis, thus offering a yet more favourable outlook relative to more stable ones. It provides the additional information that in reducing sediments, as are formed under highly productive conditions, the pigmentary record is very reliable, but may become much less so in oxidized sediments.

#### Materials and methods

Sunfish Lake (43°27'N, 75°40'W) is located in southern Ontario. Its surface area is 8.3 ha, maximum depth is 20 m. and area of its catchment is 2.25 km<sup>2</sup>. A detailed description of the lake is given in previous work (Sreenivasa and Duthie, 1973; Adams and Duthie, 1976; Sreenivasa, 1973). The lake becomes strongly thermally stratified during summer, hypolimnetic anoxia develops, and oxygen and conductivity measurements indicate that a chemocline of rather low stability exists. Some entrainment of monimolimnetic water occurs during autumn overturn, but the layer is never obliterated. Enrichment cultures of water taken at and beneath the chemocline during summer developed populations of sulfur phototrophs, although there was no visible coloration in the original water samples. Sediment cores were taken in the deepest plateau of the lake basin, at positions within a few metres of the core sites of earlier studies. The present report deals with only the uppermost 340 cm out of the 485 cm recovered. Cores were



split on the vertical axis, photographed, and sectioned at 1 cm intervals. These sections were placed in vials and stored under nitrogen atmosphere at 5° until analysed. A 1-cm section of sediment was analysed at 5 cm intervals throughout the core unless otherwise stated. Pigments were extracted with acetone:methanol (16:3 v/v), using sonication, and separated by thin-layer reversed-phase chromatography (Daley et al, 1973). The system was slightly modified so as to achieve a clear separation of the selected carotenoids from all other pigments. They were measured in situ on the chromatograms by densitometry, using values established with known concentrations of each carotenoid.

## Results and discussion

Sunfish Lake is located in a region of southern Ontario that was deglaciated early in the retreat of the Wisconsin continental ice sheet. Radiocarbon dating of its basal organic sediments places the occurrence at about 12,000 BP recognizing uncertainty introduced by the "hardwater effect" (Terasmae, 1981; Olsson, 1979). The catchment is characterized by the presence of sandy kames, and is underlain by bedrock of gypsum, shale, and salt. Pollen stratigraphy shows changes in terrestrial vegetation typical of much of Ontario. These changes are relevant to the present study in that they have provided a partial basis for correlating our sediment stratigraphy with that of previous studies, and also identify two events which relate to profound trophic changes within the lake.

Early postglacial forests of spruce *Picea* were replaced by a few deciduous trees and pine *Pinus* which was the dominant species at the 300-cm level in the sediment cores. Pine then declined sharply, and hemlock *Tsuga* became the increasingly important conifer in association with beech *Fagus* and oak *Quercus*, prominent in the deciduous vegetation. The importance of hemlock dropped suddenly to low levels at about 230 cm. Deciduous trees characterized the forest vegetation until about 160 cm where hemlock began to show small but growing proportions which continue throughout the upper part of the core. From 40-0 cm an increase in pine is also seen, but more importantly this is the zone in which *Ambrosia* and the gramineae first appear as evidence of beginning human activity in the locality through forest clearance, agriculture, and residential development.

Prior to our study the trophic history of Sunfish Lake was explored by other workers who concentrated on fossil diatoms and sediment chemistry in relation to phases of succession in the terrestrial vegetation (Sreenivasa and Duthie, 1973; Adams and Duthie, 1976; Sreenivasa, 1973). Fig 1 provides some excerpts from their data. A remarkable reciprocity can be observed in the success of the diatom taxa shown here, but the original paper should be consulted for comprehensive analysis of the complete profiles. The authors state that the number of individuals and their diversity both increase throughout postglacial time. *Cyclotella bodanica* dominates the diatom flora throughout much of the core except possibly for periods of co-dominance with *Fragilaria construens* at about 300 cm, and a similar but more clear-cut relation with *C. kuetz-*

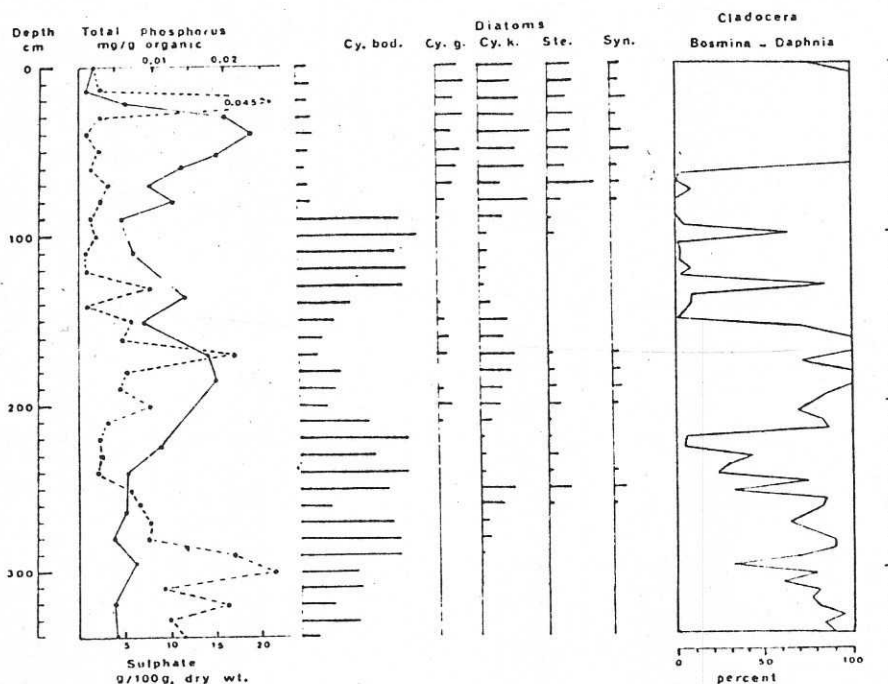


Fig. 1. Selected data, redrawn from previously published studies. Sediment analyses of total phosphorus (---) mg/g organic material; sulphate, g/100 g dry weight (Adams and Duthie, 1976). Selected diatom profiles, *Cyclotella bodanica* Cy. bod., *Cyclotella glomerata* Cy. g., *Cyclotella kuetzingiana* Cy. k., *Stephanodiscus hantzschii* Ste., *Synedra* Syn. (Sreenivasa and Duthie, 1973). Ratio of *Bosmina* to *Daphnia* calculated from data on cladocera (Sreenivasa, 1973).

*ingiana* in the region between 200-150 cm. The uppermost 70 cm shows a striking decrease in *C. bodanica* which is replaced by an assemblage in which *C. glomerata*, *C. kuetzingiana* and *Stephanodiscus hantzschii* are the most prominent members. *Synedra delicatissima* which appeared twice in earlier sections of the core now appears again, and as previously, as only a small percentage of the diatom population. The profiles were interpreted as reflecting changes in climate and the nutrient regimen of the lake. *C. bodanica* is characteristic of oligotrophic waters and *C. glomerata*, *C. kuetzingiana* and *S. hantzschii* are typical of more nutrient rich conditions such as might be associated with high rates of soil erosion. We have included the profile of *Synedra delicatissima* in Fig. 1 although the relative importance of this diatom is small, and the original studies

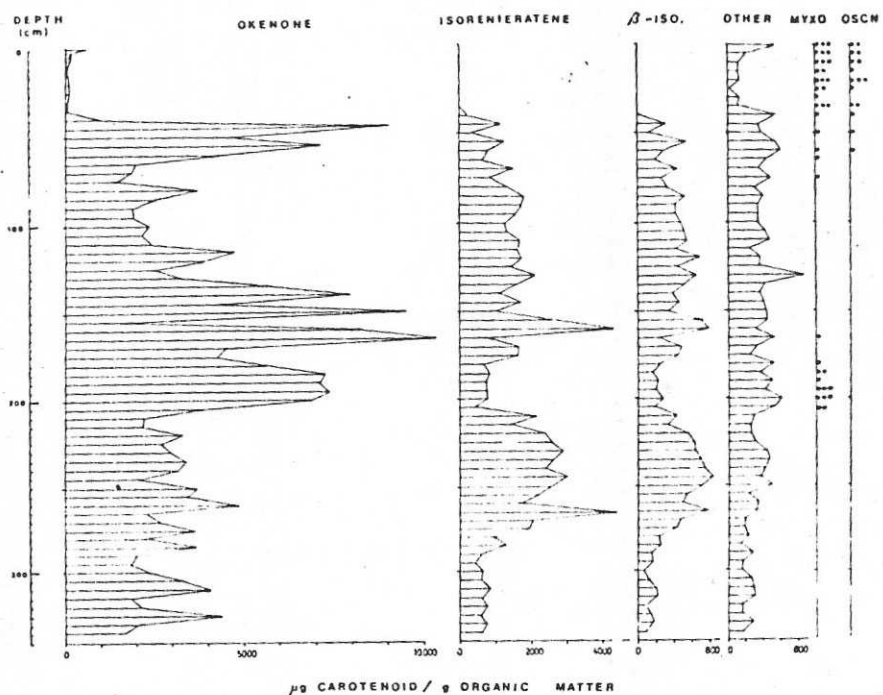


Fig. 2. Profiles of carotenoids extracted from the sedimentary core. Okenone from Chromatiaceae. Isorenieratene and  $\beta$ -isorenieratene [ $\beta$ -iso.] from Chlorobiaceae; other carotenoids (other); myxoxanthophyll (myxo) and oscillaxanthin (oscn) from cyanobacteria. Carotenoids of cyanobacteria are relative quantities, rather than absolute weights.

did not emphasize its significance as a trophic indicator. It has been suggested (Smol et al, 1984) that thinly silicified species such as this may have a competitive advantage during initial stages of cultural eutrophication. The relative success of these species is attributed to diminished sinking rates which allow the organisms to remain longer in the euphotic zone than contemporary species that are more heavily silicified. The reasoning follows that their presence in the fossil planktonic assemblage indicates compression of the zone when light penetration is reduced by turbidity or light shading by other photosynthetic organisms.

Sedimentary profiles of sulfate and total phosphorus are included in Fig. 1 to provide some insight into the chemical nature of the environment through the history of the lake. It is also felt that changes in the cladoceran populations are important to an understanding of trophic dynamics of the system. These zooplankters are the major



herbivores of the system, and although they may be responding mainly to changes in food availability, they also reflect grazing pressures and selective removal of primary production from the water column. Unfortunately rotifers are not preserved in lake sediments, so we have no knowledge of how they may have affected populations of the phototrophic bacteria or algae that belong to that size category.

The data from our pigment analyses are given in Fig. 2. The pigments are taxon-specific, but their concentrations per cell may not be identical between taxa. Although these differences are probably not great, their existence should be recognized. Equal quantities of okenone should measure equivalent populations of Chromatiaceae at different stratigraphic levels, but it cannot be presumed that equal weights of okenone and isorenieratene represent equal numbers of Chromatiaceae and Chlorobiaceae. A proportional relationship does exist, however.

It is seen immediately from the pigment profiles that sizeable populations of both of these sulfur phototrophs were present throughout all but the most recent time represented in this sediment core. It is also obvious that the success of these populations was differentially affected by conditions prevailing at various times in the 8,000-yr record, and only in the last 150 years did these conditions become so unfavourable that both populations were virtually eliminated. Some significant changes may have been missed because of sampling only roughly 50-yr segments from each 250-yr interval. It is possible nevertheless to explore trends in population structure and to relate them to highlights of the environmental conditions.

In the stratigraphic depths of 340-290 cm the Chlorobiaceae were only modestly successful. There was greater variability in the Chromatiaceae, but they managed to maintain substantial populations. Conditions were probably oligotrophic, judging by the complete dominance of *Cyclotella bodanica* in the diatom assemblage and the absence of any eutrophic indicators. It may be significant also that the sediment content of organic matter was lower in this section than in any other region of the core.

The next obvious change took place in the region from 290 to about 205 cm. In that period the green sulfurs achieved their greatest sustained success in the entire history of the lake, and only once in succeeding years did a population peak reach the height recorded here. Nutrient conditions and availability of light must have been highly favourable. There was little change in the purple sulfurs within that period however, and very minimal increase relative to previous time. There is scant information that explains the differential success between the two groups. The small planktivorous *Bosmina* was replaced gradually and almost totally by larger *Daphnia* species and thus may have increased grazing pressure on the Chromatiaceae. Nutrient supplies appear to have increased slightly, then fallen again, as may be inferred by the appearance and subsequent decline of eutrophic indicators among the diatoms. The sediment chemistry shows a marked trend in reduction of phosphorus content and the reverse trend in sulfate. There was a steady increase in percentage of organic material in the sediment throughout this period. Terrestrial vegetation also experienced extensive changes, notably the precipitous decline in pine and gradual replacement of it by hemlock while deciduous trees



dominated the forest. Then, toward the end of the period the hemlock vanished. It is probable that these vegetational changes influenced soil erosion, nutrient export, and seasonal patterns in run-off, but we cannot relate them directly to success of the phototrophic bacteria.

Dramatic changes occurred at 205 cm, and continued to ripple through much of the succeeding metre of sediment. There was a sharp and sudden increase in the purple sulfurs and a reciprocal decrease in the green sulfur populations. Other environmental changes also can be observed throughout the lake ecosystem. Eutrophic indicators among the diatoms are seen to replace the species that compete best under more oligotrophic conditions, and much importance is attached to the appearance of cyanobacteria (myxoxanthophyll and oscillaxanthin) in the planktonic assemblage. Although diatoms are important components of freshwater phytoplankton and various species are adapted to a broad range in trophic conditions, their productivity may be greatly overshadowed by other elements of the photosynthetic community. Thus, despite their usefulness as fossils, there is considerable danger in treating them in isolation when primary productivity is a major consideration in the dynamics of an ecosystem. Increased production may have impinged on the sulfur phototrophs in several ways. Filamentous cyanobacteria are thought to be a poor food resource for *Daphnia* and may have contributed to the virtual elimination of these grazers during this time frame. The resulting ungrazed production could have at least two important effects in the water column. It could be responsible for considerable light shading as well as providing an increased carbon source for the phototrophs and sulfate-reducing bacteria (Van Gernerden, 1983; Orr and Gaines, 1974). The possibility of induction of biogenic meromixis is yet a third factor worth considering. Light shading and an increase in reduced sulfur compound would be more favourable to the purple than the green sulfur phototrophs because of their position in the water column. Their success, in turn, would further reduce light availability to those organisms in the lower stratum.

Although there is no direct evidence of the occurrence, the postulated meromixis would have functioned as a nutrient trap gradually withdrawing these resources from circulation in the water column. Alternatively, reduced nutrient input may have accounted for the changes seen to begin at about 170 cm in the stratigraphy. The Chlorobiaceae began to recover and reached maximum productivity at 160 cm. The highest production of purple sulfurs also took place at about the same time. Also, in the period from 205-150 cm oligotrophic species of diatoms decreased and then increased, accompanied by the reverse trend in eutrophic species. The cyanobacteria were outstandingly successful for a time, then fell to undetectable levels. Throughout this time *Bosmina* dominated the cladocera. These changes accord with the hypothesis that the underwater light climate improved as light-shading diminished and an adequate nutrient supply was maintained for the sulfur phototrophs.

There can be little doubt about the reality of the dramatic fall and then recovery of purple sulfurs seen between 165-150 cm. It is mirrored in the Chlorobiaceae, as well. This section of the core was not analysed at close stratigraphic intervals as was done in

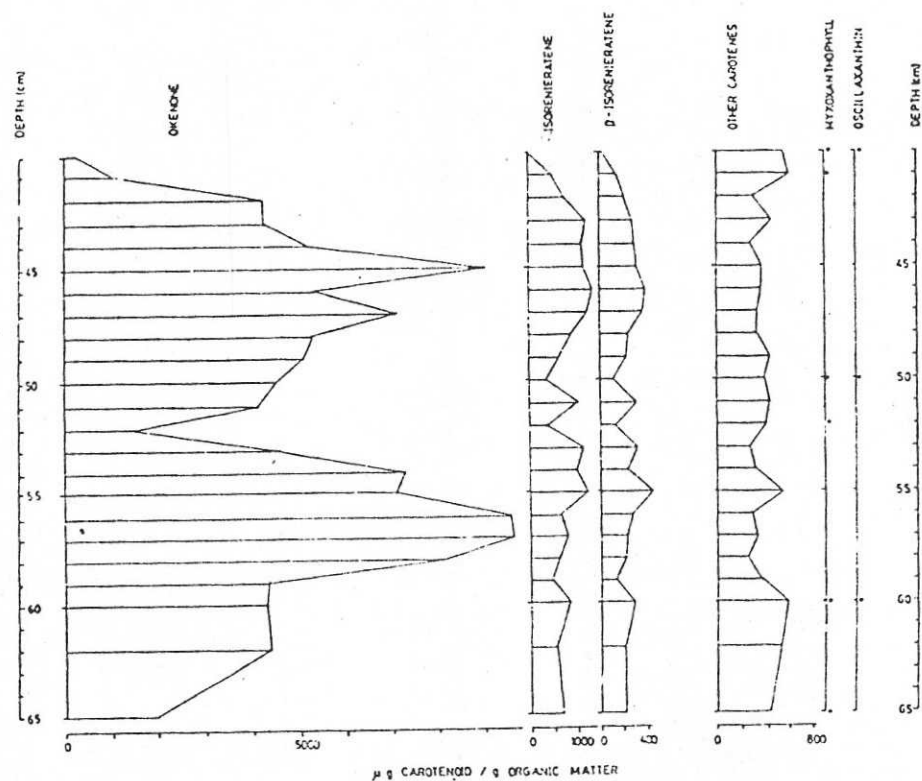


Fig. 3. Analysis of section 65-40 cm of sediment core, done in sequential 1-cm intervals.

the section from 60-45 cm (Fig. 3). A similar sudden change occurred at that depth, where analysis of sequential 1-cm sections verified the event and amplified the detail. We cannot offer a plausible explanation other than to note changes in the cladocera and suggest that episodes of change in light climate may have been involved in both instances.

In the period for 140-70 cm the green sulfurs were quite successful, but the purples were adversely affected. It is possible that grazing by *Daphnia* was a factor, as was suggested relative to an earlier period. These zooplankters dominated the cladoceran population, and only twice and for short times were the *Bosmina* an important component. Productivity undoubtedly declined, as evidenced by absence of cyanobacteria and eutrophic diatoms, thus the light climate would have been favourable.



The topmost 50 cm of the core shows virtual annihilation of the sulfur phototrophs. The Chlorobiaceae were first to go, and only a remnant of the purple sulfur bacteria remained. In this period the oligotrophic diatoms all but disappeared, whereas all of the eutrophic forms were able to flourish. The cyanobacteria became the dominant primary producers, as is shown by a decline in all carotenoids except those produced by this taxon. The daphnids disappeared as *Bosmina* took over again. Sediment chemistry reflects a rich nutrient regime which probably had its origins in processes of soil erosion and input, especially of phosphorus, through human activity in the drainage area of the lake. Inorganic soil particles may have contributed turbidity in addition to light attenuation by the planktonic community, but there can be little doubt that the demise of the sulfur phototrophs was brought about by deterioration of the underwater light climate. This is underscored by the fact that the green sulfurs, the element most vulnerable to light shading, were the first to disappear.

In this study we have explored a long history of the performance of two groups of sulfur phototrophs within an environmental framework that has been inferred to a considerable extent from evidence derived from fossil diatoms. These diatoms are widely held to be reliable trophic indicators, but in addition we have provided evidence of marked variations in cyanobacterial populations, cladocerans, sediment chemistry, and changes in terrestrial vegetation that may have had profound effects on the lake ecosystem. It has not been possible to explain some very remarkable episodes of change in the sulfur phototrophs. It may be speculated however, that grazing zooplankters played a part both in removing a portion of the purple sulfur population and in clearing the water column, thus allowing increased light penetration to greater depths. The possibility exists, although to our knowledge it has not been demonstrated, that suppression of sulfur phototrophs may result from allelopathic interaction with cyanobacteria or some other organisms. It seems reasonably clear that the nutrient base has been adequate for maintenance of these bacteria throughout most of the history of Sunfish Lake. Our evidence lends support to previous contentions that light may be a critical factor in the development of natural populations. Certainly the underwater light climate has regulated these populations through part of the time traced in this study, and it may have had a significant influence throughout the entire history of the lake.

## ACKNOWLEDGEMENTS

We thank the Natural Sciences and Engineering Research Council of Canada for complete financial support for this study in a grant to S. R. B. We also acknowledge our indebtedness to earlier studies on Sunfish Lake in providing much of the trophic framework.

## REFERENCES

- ADAMS, R.W. & DUTHIE, H.C. 1976: Relationship between sediment chemistry and postglacial production rates in a small Canadian lake. — *Int. Revue ges. Hydrobiol.* 61:21-36.
- BIEBL, H. & PFENNIG, N. 1979: Anaerobic CO<sub>2</sub> uptake by phototrophic bacteria. A review. — *Arch. Hydrobiol. Beih.* 12:48-58.
- BROWN, S.R. & COLMAN, B. 1963: Oscillaxanthin in lake sediments. — *Limnol. Oceanogr.* 8:352-353.
- BROWN, S.R., MCINTOSH, H.J. & SMOL, J.P. 1984: Recent paleolimnology of a meromictic lake: Fossil pigments of photosynthetic bacteria. — *Verh. Internat. Verein. Limnol.* 22:1357-1360.
- BROWN, S.R., 1968: Bacterial carotenoids from freshwater sediments. — *Limnol. Oceanogr.* 13: 233-241.
- BROWN, S.R., 1969: Paleolimnological evidence from fossil pigments. — *Mitt. Internat. Verein. Limnol.* 17:95-103.
- CRAIG, S.R. 1987: The distribution and contribution of picoplankton to deep photosynthetic layers in some meromictic lakes. — *Acta. Acad. Aboensis. Ser. B*, 47(2):55-81.
- DALEY R.J., GRAY, C.B.J. & BROWN, S.R. 1973: Reversed-phase thin-layer chromatography of chlorophyll derivatives. — *J. Chromatography* 76:175-183.
- DALEY, R.J., BROWN, S.R. & MCNEELY, R.N. 1977: Chromatographic and SCDP measurements of fossil phorbins nad the postglacial history of Little Round Lake, Ontario. — *Limnol. Oceanogr.* 22:349-360.
- GRIFFITHS, M. & EDMONDSON, W.T. 1975: Burial of oscillaxanthin in the sediment of Lake Washington. — *Limnol. Oceanogr.* 20:945-952.
- GRIFFITHS, M. 1978: Specific blue-green algal carotenoids in sediments of Esthwaite Water. — *Limnol. Oceogr.* 23:777-784.
- GUERRERO, R., MONTESINOS, E., PEDRÓS-ALÍO, C., ESTEVE, I., MAS, J., van GEMERDEN, H., HOFMAN, P.A.G. & BAKKER, J.F., 1985: Phototrophic sulphur bacteria in two Spanish lakes: Vertical distribution and limiting factors. — *Limnol. Oceanogr.* 30:919-931.
- KARRER, P. & KOENIG, H., 1940: Carotinoide der Purpurbakterien v. Über Rhodoviolascin. — *Helv. Chim. Acta* 23:460-463.
- LIAAEN-JENSEN, S. 1978: Marine carotenoids. — In SCHEUER, P.J. (ed) *Marine natural products. Chemical and biological perspectives Vol 2.* pp. 1-73. Academic Press, New York.
- OLSSON, I.U. 1979: A warning against radiocarbon dating of samples containing little carbon. — *Boreas* 8:203-207.
- ORR, W.L. & GAINES, A.G. 1974: Observations on rate of sulfate reduction and organic matter oxidation in the bottom waters of an estuarine basin. — In TISSOTT, B. & BIENNER, F. (eds) *Advances in organic geochemistry 1973.* pp. 791-812. Editions Technip.



- PARKIN, T.B. & BROCK, T.D. 1980: Photosynthetic bacterial production in lakes: the effects of light intensity. — *Limnol. Oceanogr.* 25:711-718.
- PFENNIG, N. 1978: General physiology and ecology of photosynthetic bacteria. — In CLAYTON, R.K. & SISTROM, W.R. (eds) *The photosynthetic bacteria*. pp. 3-18. Plenum Press, New York.
- SANGER, J.E. & GORHAM, E. 1972: Stratigraphy of fossil pigments as a guide to the postglacial history of Kirchner Marsh, Minnesota. — *Limnol. Oceanogr.* 17:840-854.
- SCHLEGEL, H.G. & JANNASCH, H.W. 1981: Prokaryotes and their habitats. — In STARR, M.P. et al (eds) *The Prokaryotes Vol 1*. pp. 43-82. Springer-Verlag, Berlin.
- SMOL, J.P., BROWN, S.R. & MCINTOSH, H.J. 1984: A hypothetical relationship between differential algal sedimentation and diatom succession. — *Verh. Internat. Verein. Limnol.* 22:1361-1365.
- SREENIVASA, M.R. & DUTHIE, H.C. 1973: The postglacial diatom history of Sunfish Lake, southwestern Ontario. — *Can. J. Bot.* 51:1599-1609.
- SREENIVASA, B.A. 1973: Paleolimnological studies of Sunfish Lake and its environs. — Ph D Thesis. University of Waterloo, Waterloo, Canada.
- TERASMAE, J. 1981: Late-Wisconsin deglaciation and migration of spruce into southern Ontario, Canada. — In ROMANS, R.C. (ed) *Geobotany I*. pp. 75-90. Plenum, New York.
- VALLENTYNE, J.R. 1956: Epiphase carotenoids in post-glacial lake sediments. — *Limnol. Oceanogr.* 1:252-262.
- VALLENTYNE, J.R. 1960: Fossil pigments. — In ALLEN, M.B. (ed.) *Comparative biochemistry of photoreactive systems*. pp. 83-105. Academic Press, New York.
- VAN GEMERDEN, H. 1983: Physiological ecology of purple and green bacteria. — *Ann. Microbiol. (Inst. Pasteur)* 134 B:73-92.
- ZÜLLIG, H. 1982: Untersuchungen über die Stratigraphie von Carotinoiden im geschichteten Sediment von 10 Schweizer Seen zur Erkundung früherer Phytoplankton-Entfaltungen. — *Schweiz. Z. Hydrobiol.* 44:1-98.

*Accepted: March 1986.*