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The meromictic alpine Lake Cadagno: Orographical and biogeochemical description

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ABSTRACT

Lake Cadagno is a 21 m deep alpine meromictic lake situated at an altitude of 1921 m in the Piora valley in the southern part of central Switzerland. The bedrock of the valley containing dolomite and gypsum determines the chemistry of the water. The lake basin was created by glacial erosion and originally dammed by a glacial moraine. The water body is structured in 3 distinct layers, the oxic mixolimnion, the anoxic monimolimnion and a narrow chemocline in between. The water masses of the lake are stabilized by density differences of salt-rich water which is constantly supplied by subaquatic springs to the monimolimnion. In contrast the mixolimnion is fed by electrolyte-poor surface water. Sulfate, hydrogen carbonate, calcium and magnesium are the dominant ionic species. In the monimolimnion sulfide concentrations of more than 1 mM are found. The chemocline at a depth of 10 to 13 m is characterized by steep chemical and physical gradients. It contains dense populations of up to 10^5 cells/mL of phototrophic sulfur bacteria consisting of predominantly *Chromatium okenii*, *C. minus* and *Amoebobacter purpureus*. The lake has proven to be an excellent model system for studies of the role of planktonic bacteria which dominate the sulfur cycle.

Introduction

Lake Cadagno is a small meromictic lake, remote from industrial activities. The specific water chemistry is defined by the geology of the catchment area. High input of sulfate from gypsum coupled with a high productivity in the mixolimnion gives rise to a massive formation of sulfide in the anoxic monimolimnion. In such lakes populations of planktonic phototrophic sulfur bacteria often develop during summer stratification. These bacteria form visible blooms at the interface between the oxic epilimnion and the anoxic hypolimnion, or on sedi-

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ment surfaces, at depths which are still reached by light. In permanently stratified meromictic lakes (Walker and Linkens, 1975; Wetzel, 1983), blooms of phototrophic sulfur bacteria are often present as a layer during the entire year. The ecology of these organisms and their habitats have been recently reviewed (Pedros-Alio and Guerrero, 1993; Van Gemerden and Mas, 1995).

Such a purple-red layer, formed by a bloom of *Chromatium okenii,* was first observed 1913 in lake Ritom and in the nearby lake Cadagno (Düggeli, 1919, 1924), the site of the present observations. At this time various publications on Lake Cadagno had dealt with water chemistry (Bourcart, 1906; Eder-Schweizer, 1924), plankton (Burckhard, 1910; Bachmann, 1924, 1928) and the fauna of the lake bottom (Fuhrmann, 1897; Borner, 1927, 1928). During the past decade a wealth of details of the biology of Lake Cadagno and the organisms present have been reported by Wagener et al. (1990), Peduzzi et al. (1991), Joss et al. (1994), Fischer et al. (1996), Birch et al. (1996), Schanz et al. (1998), Peduzzi et al. (1998), Lehmann and Bachofen, (1999), Tonolla et al. (1999), Wiggli et al. (1999), Bosshard et al. (2000 a, b), Lüthy et al. (2000), Tonolla et al. (2000) and Camacho et al. (this volume).

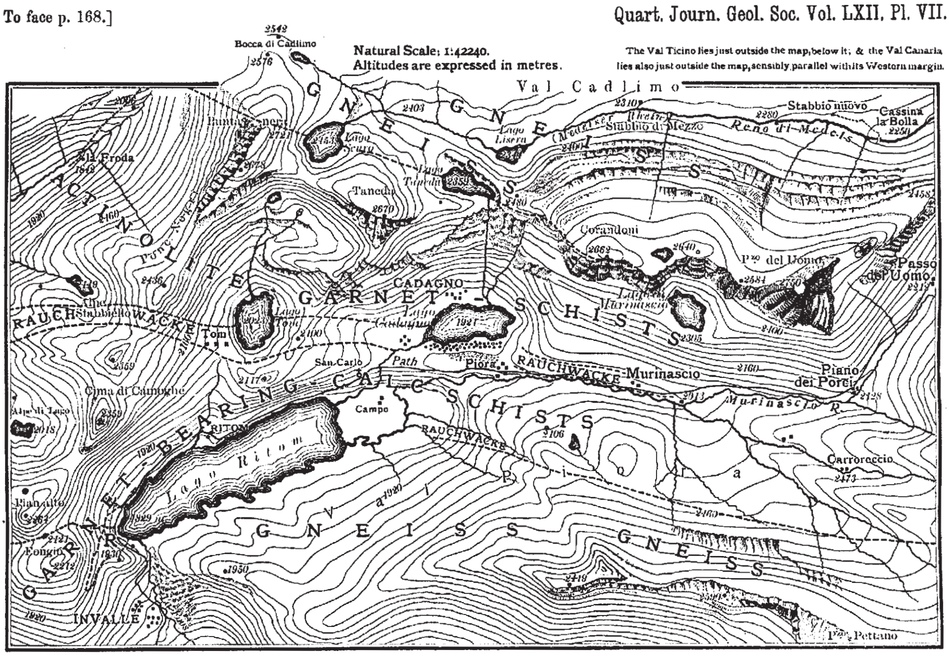
Lake Cadagno proved to be ideally suited for studies in microbial ecology and for investigations on metabolic responses of aquatic bacteria, especially of the phototrophs, to environmental signals such as light and environmental redox conditions. On the other hand, the activities of the dense bacterial population in a narrow layer causes strong gradients in the water chemistry, e.g. in nutrient concentrations as well as in nutrient composition. The dynamics of the water chemistry and the special conditions which follow from it, are consequences of geological features, the lithology in the catchment area and the morphology of the lake basin as well as the metabolism of the bacteria, mainly the phototrophs and the sulfate reducers. As stated by Bourcart, (1906) “*it serait fort intéressant de faire des études approfondies sur ce lac si curieux*”.

In this paper we enlarge the data on the bathymetric and orographic characteristics, first presented by Garwood (1906) (Fig. 1), describe the geomorphologic setting of the lake basin and the basic chemistry which are the core for the richness of this microbial habitat. Detailed knowledge about the limnology of the lake will help to better understand the unusual microbiology and form the basis for future investigations on biological aspects of the various microbial populations in the lake.

Materials and methods

Temperature, pH, conductivity, turbidity, oxygen concentration and light

These parameters have been measured in lake profiles simultaneously employing a multisensor unit (HPT c Züllig AG, Rheineck, Switzerland). Vertical transmission and reflection of photosynthetically active radiation (ΣPAR 400-750) have been determined with a cosine corrected Lambda sensor (LI-212 S, Licor, Lincoln, Nebraska, USA). Detailed description of light measurements are given by Fischer et al. (1996).



Map of the Piora Lakes.

[A triangular patch of rauchwacke should have been indicated in the extreme left-hand corner of the map, between Pian alto and Fongio. Also the occurrence of gypsum should have been indicated just above the numerals of altitude 2013, north of the Murinascio stream.]

Figure 1. Map of the Cadagno region as illustrated by Garwood (1906)

Sampling

The multisensor unit and the sampling devices were lowered from a stable working platform above the deepest point of the lake. Fine resolution sampling was achieved with a syringe sampler consisting of 64 plastic syringes (50 mL) mounted on an aluminum frame at distances of 5 or 10 cm. The syringes are opened simultaneously at the desired depth through pressure cylinders driven by compressed air supplied by a cylinder which is attached to the sampler and which can be controlled from the surface. Sample aliquots were divided immediately after retrieval of the syringe sampler into preprepared vials at the sampling site.

Chemical determinations

Carbonate alkalinity was titrated to an endpoint of pH 4.3 in small aliquots with 0.1 normal HCl (Titrisol Merck 9973). Other bases, e.g. HS^-, NH_3, HPO_4^{2-}, $H_2PO_4^-$, normally present in negligible concentrations (in the mixolimnion) were determined by independent analytical procedures and the titrated alkalinity was corrected accordingly (necessary only for samples from the monimolimnion). Ammonia was determined in filtered samples colorimetrically after the methods given by the EDI (1983a). Cations of alkali, earth-alkali and transition metals were determined by ICP-AES at the Federal Institute for Forestry, Snow and Landscape, Birmensdorf (Switzerland). Soluble reactive phosphorous was quantified after filtration of the water through glass fiber filters (Whatman GF/F) by the molybdenum method (EDI, 1983b). Sulfide was determined colorimetrically according to the methylene blue method described by Gilboa-Garber (1971). Sulfate was measured by ion exchange chromatography (precolumn Wescan 269-003, separating column Wescan 269-001) with a conductivity detector (Wescan 213A). Separation was achieved at a flow rate of 1.2 ml min^{-1} with p-hydroxybenzoate (4 mM, pH 8.5) as eluant.

Elemental sulfur was combusted in an oxygen atmosphere and determined as sulfate by titration with barium perchlorate (0.02 M) containing Thorin as the endpoint indicator.

Calculations

Water exchange area, sediment-water exchange area and lake volume were calculated using the appropriate formulas for truncated cones based on a morphometric map with contour lines spaced 1 m apart. The density of the water (ϱ_{eff}) was calculated from the temperature, the conductance and the chemical and particle composition of the water according to

$$\varrho_{\text{eff}} = \varrho_{\text{max}} \cdot h_{(T)} \cdot h_{(\kappa)} \cdot h_{(\mu)}$$

where ϱ_{max} is the maximal density of pure water at 3.98 °C, $h_{(T)}$ the function to correct the density for temperature deviation (Weast et al., 1986), $h_{(\kappa)}$ the function to correct the density for dissolved materials according to Pytkowicz (1979), and $h_{(\mu)}$ is the function to correct the density for the different suspended particles. Ca^{2+}, Mg^{2+}, Na^+, K^+ and HCO_3^- and SO_4^{2-} accounted for more than 99% of the dissolved compounds in the mixolimnion. For the monimolimnion sulfide, phosphate, iron, manganese and ammonium were included in the calculation (Millero et al., 1977). The influence of the conductivity on ϱ_{eff} can be expressed by the function (Weast et al., 1986)

$$h_{(\kappa)} = 7.7981 \cdot 10^{-7} \cdot \kappa_{25} + 0.9999728 \ (\text{g/cm}^3)$$

where κ_{25} is the conductivity in µS cm^{-1} normalized to 25 °C. The conversion factor $7.7981 \cdot 10^{-7}$ has been derived applying partial molal volume calculations for the chemical entities analyzed.

For the density contribution of the organisms in the bacterial layer a mean density of 1.1 g/cm^{-3} was used for bacterial biomass (Guerrero et al., 1984; Loch, 1989). Based on the turbidity measurements with the HPT-multisensor the following empirical relationship was derived

$$h_{(\mu)} = 1 - 2.9392 \cdot 10^{-14} + 1.0564 \cdot 10^{-13}\ \mu\text{FU} - 2.4238 \cdot 10^{-16}\ \mu^2\text{FU}$$

µFU is the reading of the turbidity in formazan units.

The deviation from 1 is small, in spite of the seemingly high turbidity in the transition layer. For the calculation of the water density changes the correction by $h_{(\mu)}$ had to be included, however, for the pycnocline.

Local water stability was calculated according to Imboden and Wüest (1995).

Cell volumes of the layer of phototrophic bacteria were calculated from microscopical measurements taking cells as spheres at each end or as cylinders with 2 half spheres depending on their growth state. Isopleths were calculated using Systat 5.2.1 (Statistical Production & Service Solutions, Inc., Evanston, USA).

Results

Geographic location and morphology

Lake Cadagno (Lago di Cadagno), situated at 1921 m above sea level, belongs to a group of 9 small lakes in the Piora depression in the central Alps of Switzerland. The Piora valley spans over 8.5 km and is surrounded by a chain of mountains which determine the watershed. The lake serves as one of the reservoirs for the hydroelectric power plant in Piotta. Part of the volume is drained every winter which leads to an annual water level fluctuation of 3 m.

The lake basin was formed during the last glacial period, an estimated 8000 years ago as derived from pollen analyses in peat cores of a nearby swamp (Stapfer, 1991). The west and southwest sides of the basin are filled in by glacial deposits, and moraines build a natural dam. Avalanches, small land slides and accumulations of dolomite “sand” have contributed to the clastic deposits in the lake as determined from seismic profiles along several transects (Kriege, 1918; Dal Vesco et al., 1964).

The north slope of the Piora valley contains metamorphic crystalline rocks, the south is built by the so-called Lukmanier layer, composed of crystalline rock as well. Below the glacial deposits the bottom of the valley consists of a karstic system of Rauwacke and Dolomite which also contain some gypsum. These rocks allowed the carving of a karstic hydrological system from which a portion of the water entering lake Cadagno originates. Water penetrates through the coarse material of the moraines and through the karstic dolomite and reappears as underwater springs in the southern and western part of the lake.

The water from the north is mainly in contact with silicate rocks; it is low in salt content and determines the water composition of the mixolimnion. Many small springs discharge into swamps which overflow into the lake. Water also enters the lake in deeper zones through bottom springs of low or high conductance.

The slope line at the south-west side is flat and the water level low. In contrast, on the north side the mountains rise steeply and the shore drops accordingly (see also Fig. 1). The main parameters describing the lake morphology are summarized in Table 1.

Table 1. Summary of the parameters which describe lake Cadagno

PARAMETER[a]			Summer	Winter[b]
Altitude of water surface		[m]	1921	1918
Maximum depth	Z_{max}	[m]	21	18
Mean depth	Z	[m]	9.27	7.87
Median depth	Z_{50}	[m]	8.5	7.8
Relative depth	Z_r	[%]	3.64	4.43
Maximum effective length (Azimut 45‰)	Le	[m]	842	769
Maximum effective width (Azimut 61.6‰)	Be	[m]	423	380
Shore line length	l_{max}	[m]	2109	1924
Shore line development	l_d	[m]	1164	1168
Surface area	A_{Zmax}	[m^2]	261043	215839
Total volume	V_{Zmax}	[m^3]	2419850	1699600
Benthic contact area	M_{Zmax}	[m^2]	356300	271050
Area error	E	[–]	0.001050	0.000462
Information value of map	I	[–]	0.998721	–

[a] Depth values are calculated in meters above the sediment surface. For the definition of the parameters see Appendix.

[b] The values for the winter situation are based on a water surface level of 1918 m above sea level.

A bathymetric map has been constructed based on 210 depth measurements across 16 north-south transects at distances of 50 m resulting in a 1:1000 depth contour map with 1 m depth resolution and a calculated optimal determination information value of 0.9987 (Hakanson, 1981). The lake parameters calculated from the map are given in Table 2. From the hypsographic equations which can be calculated from the data given in Table 2 we determined areas and volumes of specific layers.

Seasonal weather fluctuations and lake dynamics

The large and often rapid changes in atmospheric temperature, wind, radiation and precipitation patterns in the alps govern the physical stability of the water masses and the biological activities in this lake. Temperature extremes in daily and weekly weather patterns during summer and fall are between + 20 °C during the day and near 0 °C at night. The water surface freezes in December and the lake becomes covered with ice- and snow-layers of up to 2 m thickness for 6 months.

Lake compartmentalization and transition zones

The lake can vertically be partitioned into distinct compartments which are defined by the depth profiles of temperature, oxygen concentration and density. Temperature dependent density stratification creates a well defined hypolimnion below about 11 m depth during summer. The size of the epilimnion varies diur-

Table 2. Dimensions describing the morphology of lake Cadagno

Depth above deepest point, Z [m]	Circumference of contour lines [m]	Water exchange area, A_Z [m^2]
21	2110	261000
20	2070	247900
19	2040	234000
18	1920	215800
17	1890	195200
16	1800	175400
15	1720	159400
14	1660	145800
13	1600	134300
12	1540	123400
11	1480	113300
10	1410	103000
9	1340	92100
8	1250	81200
7	1170	70500
6	1050	58100
5	870	45600
4	750	35400
3	650	27500
2	550	20500
1	450	13000
0	110	800

nally at this high alpine location due to large temperature changes at the water surface between day and night. Mixing by convective turbulence can reach as deep as 5 m. In summer, the thermocline is situated between 7 and 8 m (Fig. 2a), while during winter we observe a temperature inversion (Fig. 2b) with a thermocline between 1 and 2 m below the ice. During the winter months, the monimolimnion and the sediment act as heat sources. Geothermal heat from the underwater springs or metabolic heat produced by sedimentary microbial activity might explain the higher temperature near the bottom during the winter months (Fig. 2b).

The density profile in summer shows two zones with water masses which are potentially more stable than those above and below (Fig. 3). Local stability is expressed by the Brunt-Väisälä-Frequency (N) (Imboden and Wüest, 1995). Higher frequencies indicate more stable water masses. In summer, the upper pycnocline (pycnocline 1) situated between 6 m and 7 m depth is due to temperature dependent density stratification while the second one between 8 and 9 m above the sediment (pycnocline 2) originates from the higher salt content in the monimolimnion. During fall, destratification moves the pycnocline 2 to about 6.5 m above the sediment. A rather constant density is characteristic for the homothermal monimolimnion during the summer period. Of special interest is the zone between 11 and 12 m showing almost constant temperature and thus minimal stability (Fig. 3, insert). The irregularity in the profiles suggests that

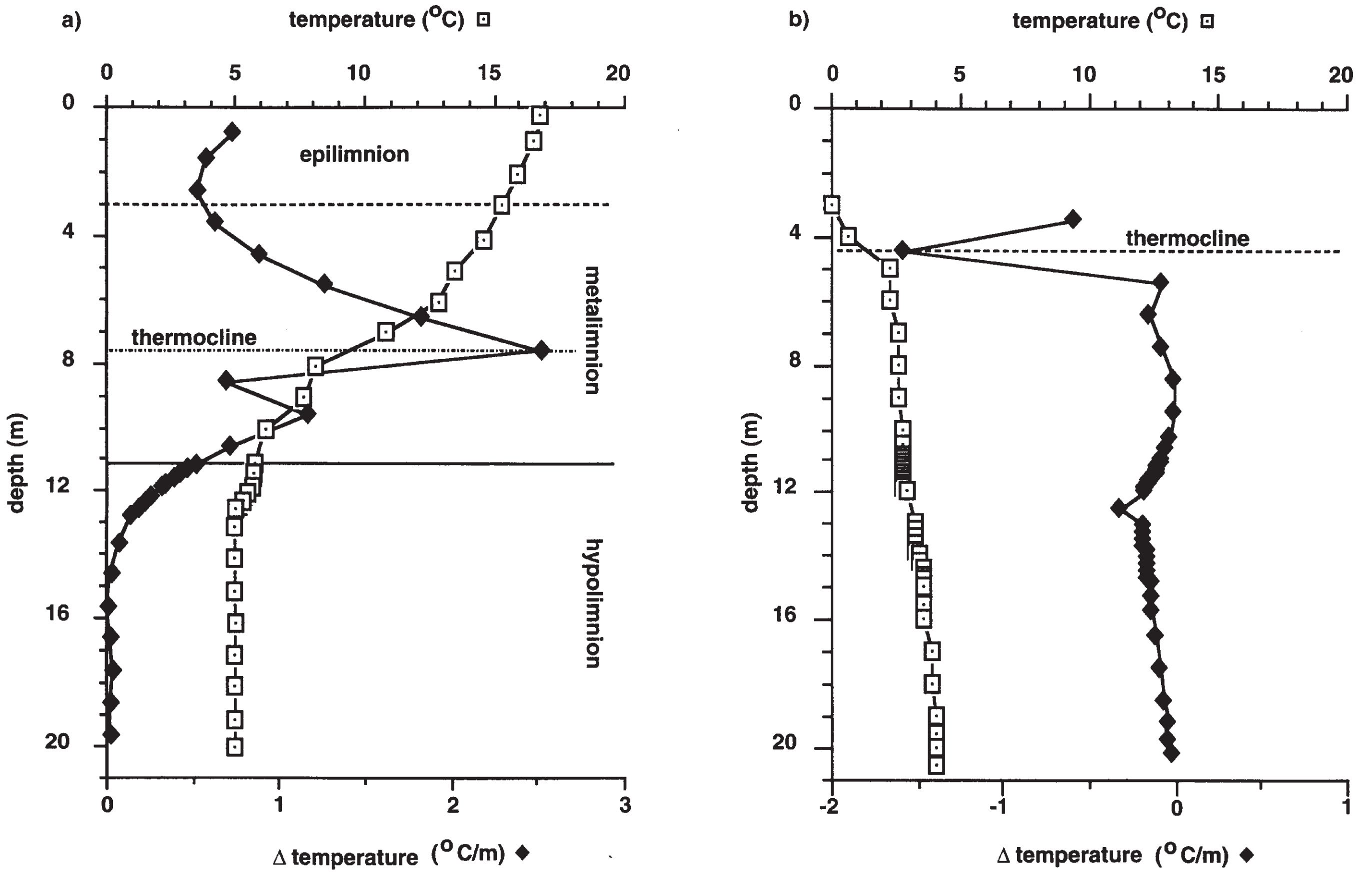


Figure 2. Depth profiles of temperature □ and the temperature gradient $\delta T/\delta z$ ♦ (a: summer, b: winter). Summer values were taken on August 18, 1987, winter values on March 31, 1985

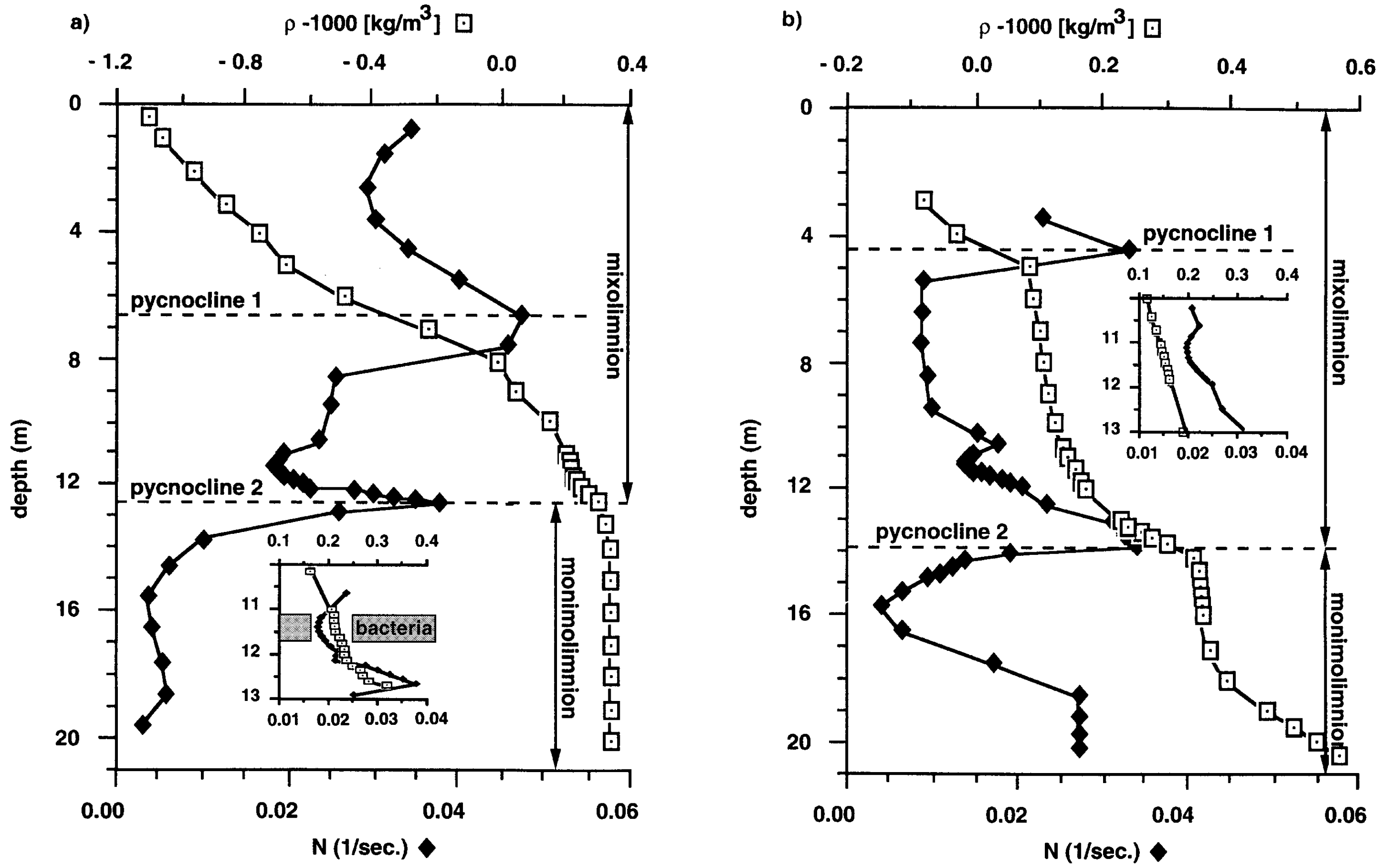


Figure 3. Depth profiles of the water density ☐ and the Brunt-Vaisälä-Frequency (N) ◆ as indicators for the stability of the water masses (a: summer, b: winter). Sampling dates as in Fig. 1. Insert: Magnification of zone of bacterial layer

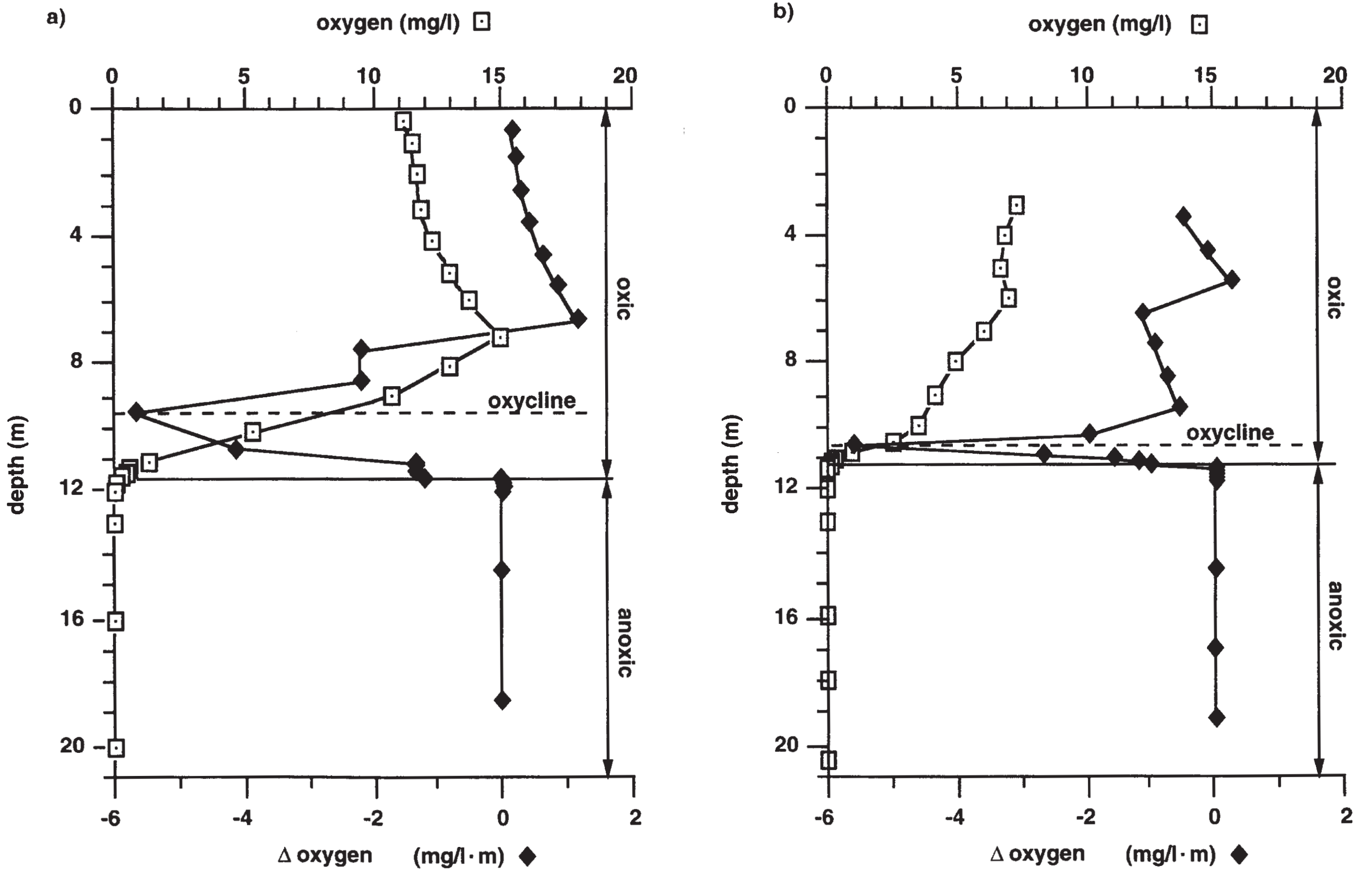


Figure 4. Depth profiles of oxygen concentration ⊡ and the oxygen gradient $\delta[O_2]\delta z$ ◆ (a: summer, b: winter). Sampling dates as in Fig. 1

mixing by convection, probably induced by the active movement of the large motile bacteria, *Chromatium okenii*, destabilizes the density gradient. Maximal densities observed in the monimolimnion are 1.00025 g/cm^{-3} and 1.00060 g/cm^{-3} for summer and winter situations, respectively.

The permanently anoxic monimolimnion has a volume of 201800 m^3, the mixolimnion is more than ten times larger (2318000 m^3). The redox-transition zone located between 10 m and 12 m depth is a few m in size and contains the greatest part of the active population of the phototrophic sulfur bacteria, it measures up to 100000 m^3. The exchange area between the oxic and anoxic water bodies varies between 81000 m^2 in 13 m depth towards the end of the summer, and 113000 m^2 measured 10 m below the surface just after the ice has melted. If the bacteria contained in a 1 m thick layer at 10 m depth would all sink to 13 m their packing density would thus increase by a factor of 1.4.

The litoriprofundal which extends between 8 m depth and 12.5 m depth and which is partially covered with bacterial mats comprises a sediment-water exchange area of 474000 m^2. The sediment area through which hydrogen sulfide and methane exchange in the profundal benthos measures 114800 m^2 equivalent to 17.4% of the total sediment surface. Since 30% of the total lake volume are drained in late fall, 70% of the littoral remains uncovered for six winter months.

Typical for a meromictic lake, the monimolimnion remains constantly anoxic. During summer the midpoint of the oxygen gradient (the oxycline) is located between 11 and 12 m above the sediment (Fig. 4). It is lowered to 7 m above the sediment during the fall overturn (Fig. 5). During the period of ice cover oxygen consumption in the mixolimnion lifts the oxycline again to about 15 m above sediment. The habitats in which fish can survive are thus further reduced by this upward movement of the anoxic-oxic transition zone.

Stratification in the water column

Lake Cadagno is clearly a meromictic lake. Complete mixing of the water body is prevented by the salt dependent density increase in the monimolimnion which stabilizes the water masses even under homothermal conditions. The profiles of temperature, conductivity and of the calculated density, typical for summer and winter situations (Figs. 2 and 3), illustrate the dependence of the pycnocline on temperature and dissolved solutes during the annual cycle. The separation into monimolimnion and mixolimnion, whose upper limit is established after the fall overturn, is maintained during the winter season below the massive ice cover. The increase in salt concentration in the deep water is seen in the conductance increases during winter from 400 µS/cm^{-1} to about 800 µS/cm^{-1} near the sediment-water interface. This leads to an upward movement of the pycnocline in spring.

Light penetration

Light intensity determines colonization of pelagic and benthic habitats by phototrophic organisms. Planktonic, oxigenic eucaryotes are preferentially found at depths down to 8 m. Furthermore, the development of a dense population of phytoflagellates has often been observed especially in the microoxic region of the metalimnion at a depth of 10 to 11 m. Mass developments of phototrophic purple sulfur bacteria occur at depths between 11.5 and 13.5 m just below the oxycline where the light intensity is still a few percent of the surface radiation (Fig. 6). The light climate typical for summer situations has been described in more detail by Fischer et al. (1996).

The transition zone of the litoriprofundal is covered with compact bacterial mats composed of cyanobacteria, *Beggiatoa* spp. and large areas of purple pigmented sulfur bacteria. In winter, below a thick layer of snow and ice, only a fraction of a percent of the surface radiation is measured at the water-ice interface. Turbidity indicating microorganisms is less pronounced at depths between 8 and 12 m as indicated by increased light penetration.

Dynamics of the lake chemistry

Over the seasons, the chemical as well as the biological parameters change in the lake concomitantly with the physical parameters temperature and density. Large variations in the chemical composition are typical for the mixolimnion during the annual cycle. As is seen from the oxygen concentration during the

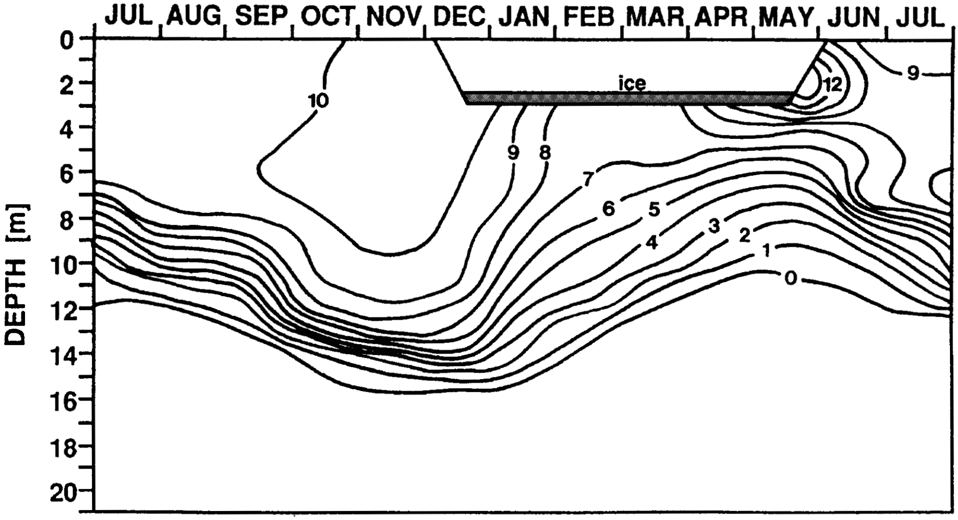


Figure 5. Oxygen concentration isopleths during an annual cycle. From November to the end of May the lake surface was 3 m lower than during the summer. Numbers are in mg O_2/L

Table 3. The ionic composition of subaquatic spring water[a]

Depth of springs [m]	Conductivity [µS/cm] 20 °C measured	Conductivity [µS/cm] 20 °C calculated	Density[f] [g/cm⁻³]	Calcium [mM]	Magnesium [mM]	Σ Cations [meq/L][e]	Sulfate [mM]	Σ Carbonate[d] [mM]	Σ Anions [meq/L][e]
12.5		1509	1.08570	4.94	3.48	16.84	7.40	0.71	16.22
12.5		1376	0.89928	4.55	3.27	15.64	6.50	0.73	14.47
9		331	0.18770	0.96	0.85	3.53	1.15	0.60	3.50
9	1485	1513	0.63996	4.47	3.46	15.86	7.55	1.44	17.98
9[b]	1322	1310	0.91363	4.03	2.91	13.88	6.17	1.57	15.48
8.5		498	0.26802	1.95	1.03	4.96	1.66	0.79	4.71
8[c]		1402	0.94705	4.55	3.27	15.64	6.50	1.47	> 14.47
8	1130	1313	0.91856	4.15	2.76	13.82	6.27	1.40	15.34
8[b]	1097	1087	0.75502	3.19	2.36	11.10	5.00	1.48	12.80
5.5		559	0.31153	1.50	1.10	5.20	1.60	1.60	6.40
5.0[c]	447	476	0.31123	1.45	1.03	4.96	1.60	1.58	> 4.70
2.5	230	332	0.20022	0.92	0.79	3.43	1.22	0.63	3.71

[a] Values from 3 different campaigns during August and September 1990.

[b] From Uhde (1992), campaigns 1991.

[c] Campaigns 1989.

[d] Σ carbonate = $[HCO_3^-] + [CO_3^{2-}]$.

[e] meq = milliequivalents = $c_i \cdot |z_i|$ = concentration of ion i in millimole/l · absolute value of charge of ion i.

[f] Density calculated according to Wüest (1987) for 20 °C.

– = Not determined.

fall overturn (October–November) the mixolimnion is uniformly mixed and saturated with more than 8 mg/L^{-1} of oxygen as deep as 14 m (Fig. 5). After freezing, when photosynthetic oxygen production is almost abolished, the various chemical and biological oxygen consuming activities persist and the oxic/anoxic interface moves upward. The 1 mg L^{-1} boundary reaches a depth of about 8 m below the ice cover in late spring. During the melting period the mixolimnion fills up with oxygen- and nutrient-rich water and oxygenic photosynthesis starts immediately (Bertoni et al., 1998; Schanz and Stalder, 1998). The boundary between oxic and anoxic conditions drops to a depth below 10 m (end of June).

During summer when light penetrates into the zones which lack oxygen but are rich in hydrogen sulfide (Figs. 4, 5 and 8), a dense population of phototrophic sulfur bacteria develops. Their activity and position in the water column is regulated by the intensity and quality of the radiant flux which reaches the depth of the oxycline and by the availability of reduced sulfur species as electron donors (Fig. 8). Due to the presence of sulfate reducing bacteria in the layer and the ability of the phototrophic sulfur bacteria to utilize hydrogen sulfide in the light and to produce it in the darkness (Lüthy et al., 2000; Tonolla et al., 2000), the sulfidocline shows diurnal fluctuations between 11 and 13 m. Furthermore, physical oscillations with frequencies of 0.2 h^{-1} and 0.1 h^{-1} have been observed depending on the depth of the measurement (Egli et al., 1998). During the summer season, the oxygen/hydrogen sulfide interface drops towards deeper zones due to the activity of the phototrophic bacteria (Figs. 5 and 8), from 11 m in early summer to 13.5 m depth in fall. The circulation in the mixolimnion in fall pushes the oxycline even deeper before the surface freezes in winter.

Besides sulfate and carbonate ions, the cations Ca^{2+} and Mg^{2+} are released from the gypsum containing dolomitic rock into the monimolimnion (Fig. 7). Since carbonate is the main buffer in the lake water, the pH is stabilized at a value of about 7.0 (Fig. 9). The pH in the mixolimnion, however, increases during the summer to values as high as 8.5 to 9.0 due to oxygenic photosynthesis. In contrast, during snow-melt (end of May) the pH of the surface water often drops to 5.3 due to the acidity of the lake ice and in the snow cover during the winter.

In summary, gradients in chemical parameters are more pronounced in summer and large concentration differences in many constituents of the water between mixo- and monimolimnion give rise to steep gradients in the redox transition zone. In contrast, in winter, concentrations of many compounds increase in the deeper layers while primary productivity in the upper zones is low. This leads to less pronounced gradients at the transition zone.

Biological dynamics of the lake during the annual cycle

In situ turbidity is a good measure for the distribution of bacterial biomass. Turbidity is low in the mixolimnion indicating lower bacterial biomass in the oxic production layer and no inorganic scattering material brought in by runoff water. Microscopy and pigment analyses of the turbidity below 11 m in summer

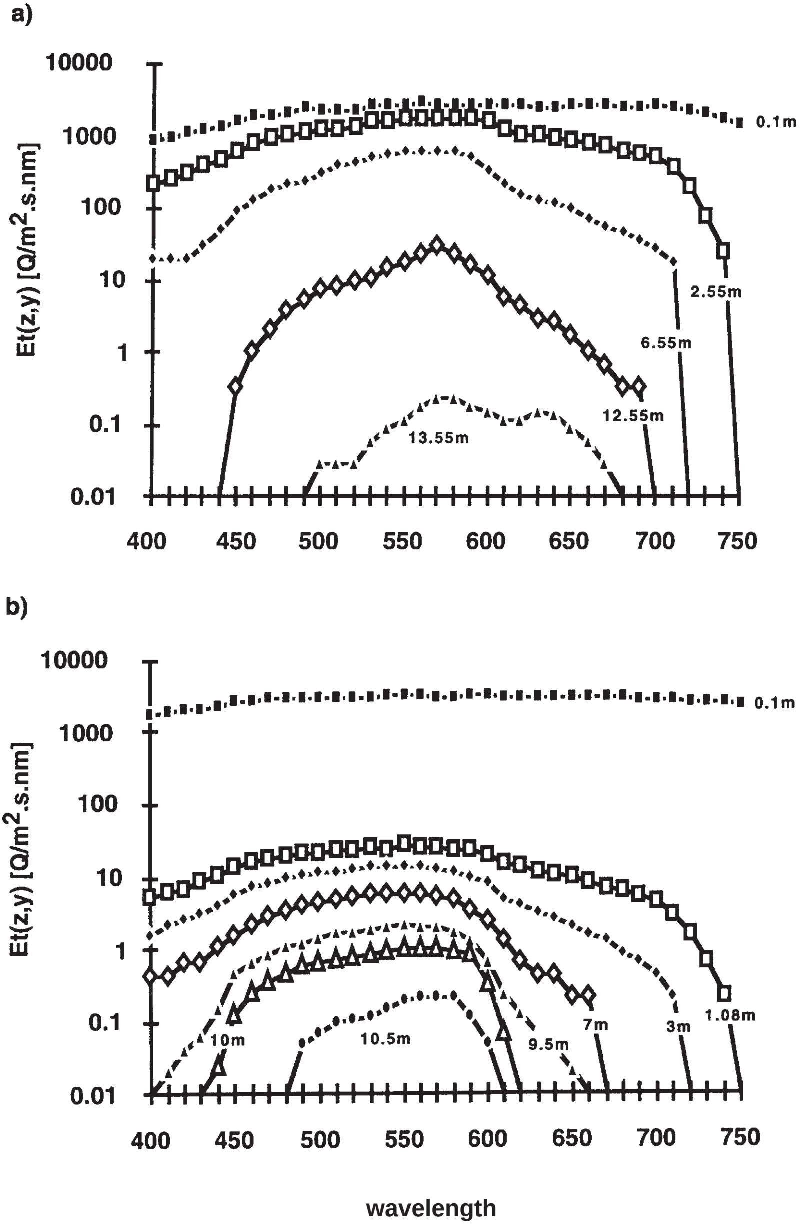


Figure 6. Spectral distribution of the sunlight at the surface and at various depths in summer (a, 24. 8. 1985) and in winter (b, 30. 3. 1985) and penetration of radiation as deep as the redox transition zone (c)

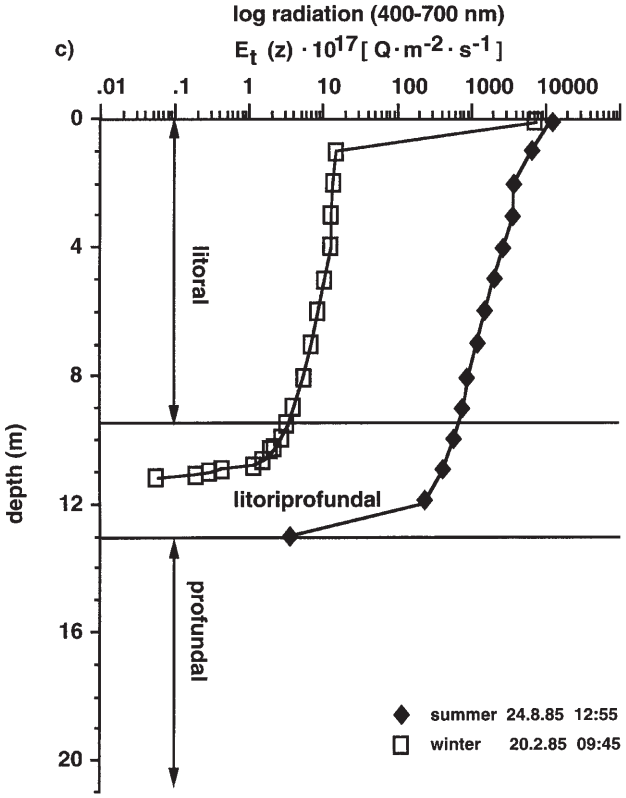


Figure 6 (continued)

indicate the presence of blooms of phototrophic sulfur bacteria, dominated by the large *Chromatium okenii* and colonies of *Amoebobacter purpureus* (Tonolla et al., 1999; Bosshard et al., 2000a and b). They reach densities of up to 10^6 per mL giving the water a purple color due to the presence of carotenoids, mainly okenone.

Bacteriochlorophyll a is the major chlorophyll found in the turbidity layer, but also chlorophyll a is present at the upper edge of the layer. Some of the Chl a may be associated with sedimenting algal biomass from the mixolimnion, but also populations of photosynthetically active phytoflagellates have been observed at these microoxic depths (Camacho et al., this volume). Many changes in the chemistry of the lake water are controlled by the metabolism of the bacterial populations. The bacteria maintain the strong gradients and act as a chemical nutrient filter between mixo- and monimolimnion. The pH of the water at different depths (Fig. 9) is a good indicator for the kind of metabolic processes which dominate (Hanselmann, 1986).

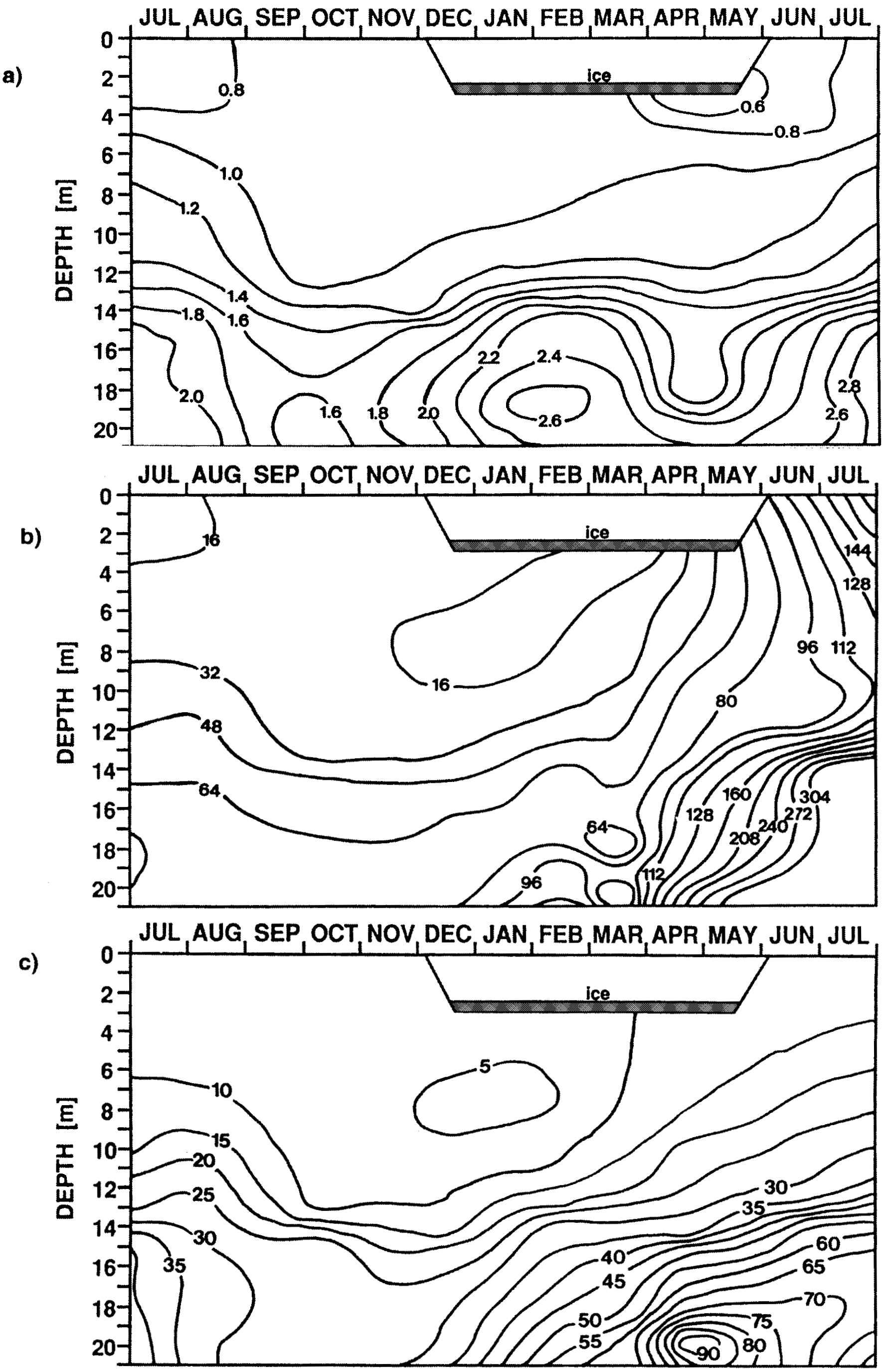


Figure 7. Concentration isopleths of (a) the sum of the carbonates (mval/L), (b) Calcium (mg/L) and (c) Magnesium (mg/L) during the annual cycle

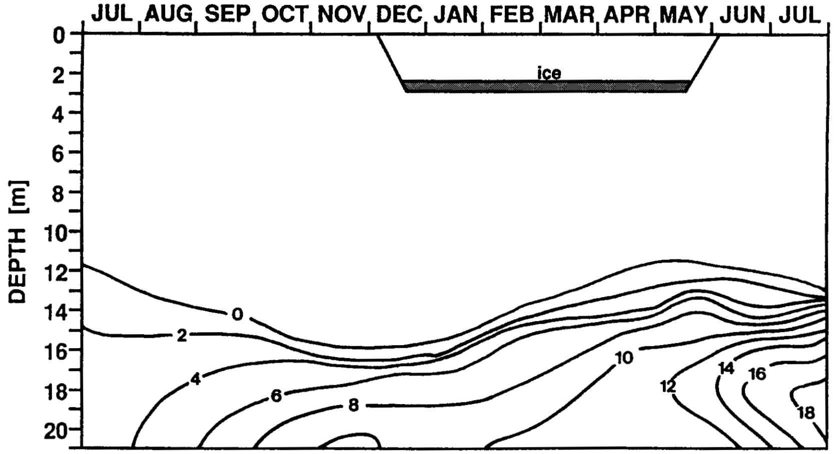


Figure 8. Sulfide concentration isopleths during an annual cycle. Compare with Fig. 5. Numbers are ΣH_2S in mg/L ($\Sigma H_2S = [H_2S] + [HS^-] + [S^{2-}]$)

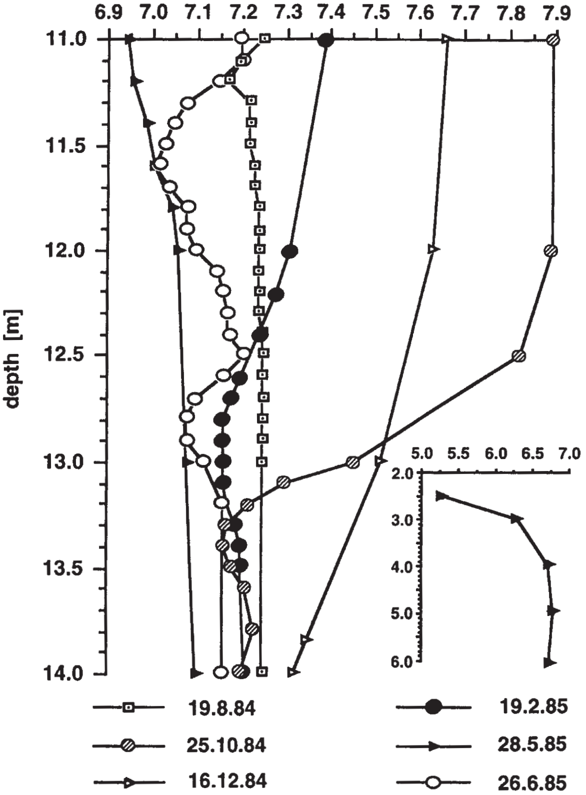


Figure 9. Variation of pH in the bacterial layer during the annual cycle. Insert: pH drop in the surface water during melting of the ice

Discussion

The data presented demonstrate that the meromictic Lake Cadagno is an excellent model to study biological processes occurring at chemical redox transition zones and of their consequences on water chemistry.

The anoxic monimolimnion is characterized by high concentrations of hydrogen sulfide since the sulfate contained in the subaquatic spring water presents a readily available electron acceptor for anaerobic respiration. Through sulfate-reducing and fermenting activities sedimenting biomass is degraded and partially oxidized in the hypolimnion and in the upper layers of the sediment thereby producing carbon dioxide and hydrogen sulfide which are released into the overlaying water.

The year-round stratification is stabilized through the higher density of the water fed to the monimolimnion by underwater springs, this prevents fall circulation from reaching depths below 14 m. It would hardly be sufficient, however, to prevent full circulation in winter in the absence of a protective ice cover. In general, the density decreases continuously from the lake bottom to the surface showing two depths with more pronounced changes. They correspond to the two pycnocline indicated in Fig. 3. This is best seen in the changes in local stability expressed as N^2.

The dense microbial populations may themselves create density changes in the water column. A significant drop in stability is observed especially in summer in the bacterial layer between 11 and 12 m depth. Under typical summer conditions (Figs. 2a, 3a, and 4a) the total bacterial counts reach concentrations of up to 10^6 to 10^7 cells mL^{-1}. Such large numbers would give a density increase of $7.7 \cdot 10^{-5}$ to $7.7 \cdot 10^{-4}$ g/cm^{-3}. Thus, the large number of suspended particles contribute to the density increase as much as the sum of the dissolved salts. The bacterial particles are responsible for a layer of nearly constant density and high instability within the overall density gradient (Fig. 3, inserts). In this layer of high bacterial density, sedimenting dead biomass becomes accessible for degradation by fermenting or anaerobically respiring organisms. On the other hand, the same bacterial layer acts also as a chemical filter for compounds produced within it and those diffusing from the monimolimnion towards the surface. This role of the bacterial layer is especially important for the removal of the toxic sulfide but also for many other nutrients which are liberated in the sediments and in the monimolimnion.

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