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Limnological description of the Lakes Zürich, Lucerne, and Cadagno

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ABSTRACT

This introductory article of the special GAP issue gives an overview on general limnological characteristics of the prealpine Lakes Zürich and Lucerne and the alpine Lake Cadagno and reports on the specific situation of primary production parameters during the international GAP Workshop in mid September 1999. Furthermore, it describes methods used for water analysis and fieldwork in these lakes.

A comparison of data related to primary production in the three lakes in September 1999 during stratification shows that (i) phytoplankton community structure varied considerably between the lakes. The dominating algae were *Planktothrix rubescens* in Lake Zürich, various chrysophytes and diatoms in Lake Lucerne, and *Echinocoleum elegans* in Lake Cadagno, (ii) the euphotic zone in Lake Lucerne was considerably deeper (app. 15 m) than in the other two lakes (app. 10 m), (iii) chlorophyll *a* standing crop was highest in mesotrophic Lake Zürich (August: 121 mg m^{-2}), followed by oligotrophic Lake Lucerne (August: 75, September: 34 mg m^{-2}) and mesotrophic Lake Cadagno (August: 33, September: 25 and 14 mg m^{-2}), and (iv) areal primary production was highest in Lake Zürich (August: 105, September: 124 mg C m^{-2} h^{-1}), followed by Lake Cadagno (August: 102, September: 52 mg C m^{-2} h^{-1}) and Lake Lucerne (August: 90, September: 52 mg C m^{-2} h^{-1}). Physiological parameters, determined *in situ* from *P* versus *I* relationships, showed a lower initial slope α in Lake Lucerne (August: 0.03, September: 0.02 mg C mg^{-1} chl *a* h^{-1} µmol^{-1} m^2 s) than in the other two lakes (Lake Zürich in August: 0.05, in September: 0.11; Lake Cadagno in August: 0.05, in September: 0.11 and 0.28 mg C mg^{-1} chl *a* h^{-1} µmol^{-1} m^2 s). Lake Zürich showed the lowest AN_{max} (August: 2.6, September: 3.2 mg C mg^{-1} chl *a* h^{-1}, as compared to 5.9 – 7.4 mg C mg^{-1} chl *a* h^{-1} in the Lakes Lucerne and Cadagno), while in Lake Cadagno the highest inhibitory effects of C-assimilation were found (highest slopes of inhibition β, 0.007 –0.011, as compared to 0.0003 – 0.0026 in the other two lakes), due to a higher UV-exposure in this alpine lake.

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Introduction

The Lakes Lucerne, Zürich and Cadagno (Fig. 1) were chosen as sites of investigation for the 7th International GAP Workshop (9–17 September 1999) on the dynamics of primary production in spatially and temporally heterogeneous aquatic environments. All sampling sites are easily accessible and backed up by well equipped field stations nearby. Furthermore, a large variety of limnological data is available about these lakes, which differ in their altitudes and thus in the proportion of UV radiation of the total irradiance, but also in the underwater light climate, chemical composition, trophic state and the diversity of the plankton community.

Figure 1 shows the outlines of the three lakes with the sampling sites used during the GAP Workshop. The fjordlike lake system of Lake Lucerne in the Swiss prealpine calcareous region and the trough-shaped Lake Zürich in the moraineous sedimentary lowland are relatively large and deep lakes. Lake Cadagno is a small bowl-shaped basin in an alpine valley of the crystalline mountain range, whose bedrock contains dolomite and gypsum. All three lakes are mainly of glacial origin. Lake Cadagno is covered with ice up to two meters thick each winter, while the Lakes Lucerne and Zürich hardly ever freeze.

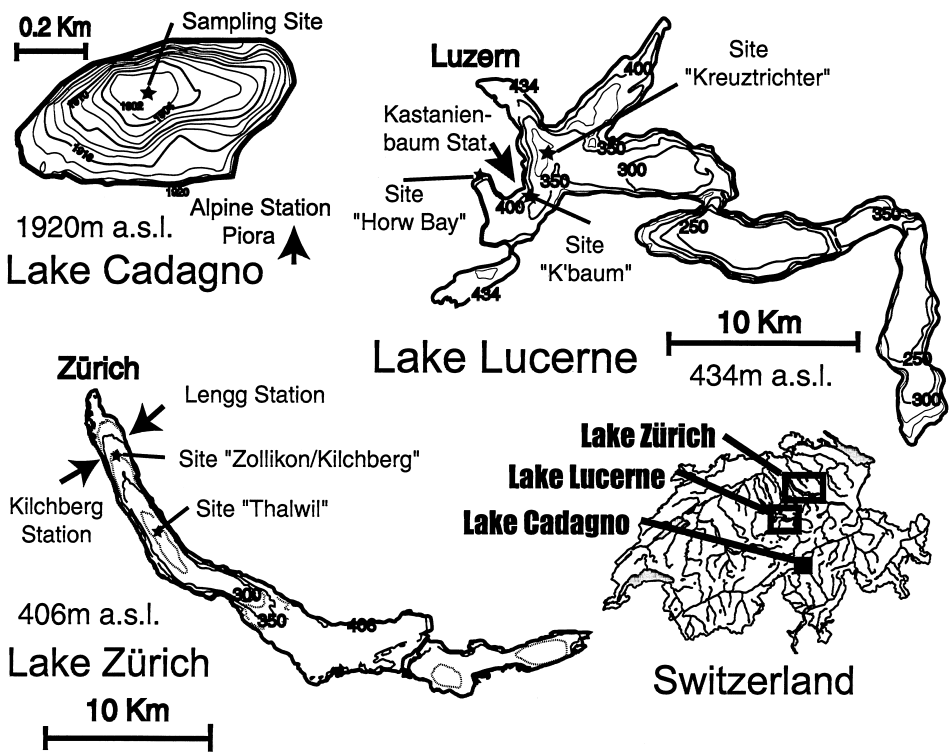

Figure 1. Lakes Lucerne, Zürich and Cadagno with field stations and sampling sites in the GAP-Workshop 1999

Table 1. Limnological description of the Lakes Lucerne, Zürich and Cadagno

a) Geographical and physical characterization:

Lake	region, catchment	altitude (m a.s.l.)	max. depth [m]	mean depth [m]	surface area [km^2]	residence time [years]	turnover
Zürich	lowland	406	136	51	68	1.4	monomictic
Lucerne	pre-alpine	434	214	104	113	3.4	monomictic
Cadagno	alpine	1921	20	9	0.27	n.d	meromictic

b) Limnological characterization of the epilimnion

Lake	trophic state	P_{tot} [µg l^{-1}]	NO_3-N [µg l^{-1}]	annual APP [g C m^{-2} y^{-1}]	APP in summer [mg C m^{-2} h^{-1}]	*Chl *a* in summer [mg m^{-2}]
Zürich	mesotrophic	**34 ± 10	**785 ± 52	*217 ± 45	*100 ± 59	*133 ± 60
Lucerne	oligotrophic	**6.5 ± 1.7	**592 ± 37	$^{+}$176 ± 35	$^{+}$73 ± 30	$^{+}$73 ± 32
Cadagno	mesotrophic	^{x} <10	^{xxx}<50	n.d.	^{xx}54 ± 19	^{xx} 36 ± 14

Lake	Secchi depth in summer [m]	Conductivity [µS cm^{-1}]	DIC [mg C l^{-1}]	DOC [mgl C l^{-1}]	Silicate [mg SiO_2 l^{-1}]
Zürich	*4.4 ± 1.7	**260 ± 5	**32.2 ± 1.7	*1.2 ± 0.2	**2.9 ± 0.3
Lucerne	*5.8 ± 1.4	**203 ± 5	**23.5 ± 1.2	**0.9 ± 0.1	**2.2 ± 0.3
Cadagno	$^{+}$6.8 ± 0.6	^{x}160–300	^{x}app. 10	^{x}app. 1.5 - 2	^{x}app. 1

c) Phytoplankton communities

Lake	dominating algae in winter	dominating algae/bacteria in summer
Zürich	*Planktothrix rubescens*, centric diatoms	pennate diatoms, *Dinobryon, Cryptomonas, P. rubescens* (metalimnion)
Lucerne	*Rhodomonas*, centric diatoms	pennate diatoms, chrysophytes, cryptophytes
Cadagno	n.d., under ice cover	diatoms, chlorophytes, cyanobacteria, phototrophic sulfur bacteria

Averages ± standard deviation. * Average 1990–1999 (**at full circulation); $^{+}$ Average 1990–1997. ^{x} estimation based on recent sampling campaigns in summer (Peduzzi at al., 1998). ^{xx} Average of a sampling campaign in summer 1986 (by Friedl, 1987). ^{xxx} Average of a sampling campaign in 1984/85 (by Del Don, 1986)

Table 1 gives a short overview on some limnological characteristics of the three lakes. Details about the long term development of the lakes are published elsewhere (for Lake Lucerne see Bührer and Ambühl, 1996 and 2001; Bürgi et al., 1999; Bloesch et al., 1995; for Lake Zürich: Gammeter et al., 1997; Gammeter and Zimmermann, 2001; Schanz, 1994; for Lake Cadagno: Peduzzi et al., 1998).

This article provides information for better understanding the results of the works achieved during the GAP VII Workshop published in this special issue. We also describe limnological key parameters and basic techniques of their assessment and analysis. The limnological situation of the three lakes, relevant for primary pro-

duction in summer 1999 (before and during the GAP-Workshop), is presented. A thorough orographical, biogeochemical and microbial description of Lake Cadagno is given in a separate article by Del Don et al. (2001).

Materials and methods

Vertical profiles of limnological key parameters, such as temperature, pH, alkalinity, DIC, O_2, PO_4-P, total P, NO_3-N, SiO_2, underwater light regime, and ^{14}C-assimilation, were assessed in the euphotic zones of the three lakes before (in August 1999) and during the workshop (in the period from 10 to 14 of September 1999).

Physical factors

Under water light regimes: Photosynthetically available radiation (PAR) was measured in $\mu mol\ m^{-2}\ s^{-1}$ with a scalar quantum sensor (LI 190 SB) connected to an integrating quantum meter (LI 188) made by LI-COR Inc, USA. A second sensor served as a reference, measuring PAR simultaneously above the water surface. The measurements were corrected for the immersion effect. Ultraviolet radiation (UV-A, UV-B) was assessed in $\mu W\ cm^{-2}$ with flat cosine corrected sensors (SD 104/UV-A and SD 104/UV-B) of the same type as used for measuring surface radiation. The inherent difference between the two sensor types, the PAR sensor measures photons while the UV sensors measure energy, impedes a precise direct comparison of the two types of measurement. The vertical light attenuation coefficient (K_d) was calculated using the formula presented by Schanz (1985). After linearisation the slope (= vertical light attenuation coefficent, m^{-1}) was calculated by the least square method.

Surface radiation: During the GAP Workshop PAR was measured at the three experimental sites; for Lake Cadagno at the Biological Alpine Station Piora, for Lake Lucerne at the Lake Research Institute, and for Lake Zürich on the roof of Sprüngli Factory (near the Limnological Station, Kilchberg) and on the roof of the City of Zürich Water Supply building at Lengg. UV-A and UV-B were continuously monitored at the field stations near the sampling site. Integrators (LI 1000, LI-COR) yielded a continuous output of PAR, and/or UVR integrals over intervals of 10 min. We used cosine corrected PAR sensors (LI 190), and cosine corrected UV sensors (SD 104/UV-A and SD 104/UV-B). For more technical details and comparison of instruments: see Neale et al. (2001 b, this issue).

Temperature, conductivity, turbidity and oxygen

In Lake Lucerne *temperature* and *conductivity* were measured *in situ* with a WTW probe (Conductometer LF 191, Weinheim, Germany). *Dissolved oxygen* was determined with the Winkler method modified by Carpenter (1965).

In Lake Cadagno profiles (0–21 m) were measured routinely for *temperature, conductivity, dissolved oxygen* and *turbidity* using the YSI 6920 multisonde (Yellow Springs Instruments, USA).

In Lake Zürich *temperature* was measured *in situ* with a digital thermometer (DMP, Switzerland) connected to a LI 1000 datalogger (LI-COR Inc., USA.), *dissolved oxygen* was determined as in Lake Lucerne, c*onductivity* was measured in bottled water samples in the laboratory (with a Conductometer E518, Metrohm, Switzerland).

Chemical parameters

Alkalinity was titrated according to Standard Methods (1971). *Dissolved inorganic carbon* (DIC) was determined from alkalinity and *pH* according to Rodhe (1958) and Goltermann et al. (1978).

In Lake Lucerne water samples, *ortho-phosphate* (SRP) and *total phosphorus* (P_{tot}) were analyzed with the molybdenum blue method according to Vogler (1965) and Schmid and Ambühl (1965).

Ammonia (NH_4-N), *nitrate* (NO_3-N) and *nitrite* (NO_2-N) were determined colorimetrically according to DEV (1985). *Silicate* (SiO_2) was analyzed with the heteropoly blue method (APHA 1989). *Sulfate* (SO_4) was determined according to DEW 1996.

In Lake Cadagno water samples, SRP and P_{tot}, NH_4-N and NO_2-N were determined colorimetrically according to DEV (1972), NO_3-N photometrically at 220 nm (Standard Methods, 1975), *sulfide* (H_2S) according to Gilboa-Garber (1971), SO_4 with anion chromatography (ion exchange column Wescan W-498) according to Hanselmann and Hutter (1998).

In Lake Zürich water samples, SRP and P_{tot} were determined according to DIN/EN1189 (DEW 1996), NO_3-N according to DIN/EN/ISO 10304-1 (DEW 1996), and SiO_2 according to DIN 38405 (DEW 1996).

Biological parameters

Phytoplankton: Samples from different depths (Lake Zürich, Lake Cadagno) or integrated samples from 0–20 m (Lake Lucerne) or 0–15 m (Lake Cadagno) were immediately fixed with Lugol solution. The biovolume of phytoplankton genera and species was obtained by counting and measuring cells by means of an inverted microscope (Utermöhl, 1958). Results of fresh weight (FW) given in this paper are determined from biovolumes, using a specific weight factor of 1.0.

Chlorophyll: In Lake Lucerne and Lake Cadagno, sample preparation and chlorophyll extraction was performed according to DEV, 1986: Samples were filtered through Whatman GF/F filters. The filters were put into Sovirel tubes filled with 8 ml of 90 % ethanol. Chlorophyll was extracted by heating the samples (for 10 min) in a water bath at 75 °C and subsequent sonification (for 5 min) at room temperature. Before HPLC analysis the chlorophyll extracts were filtered through Millipore Millex FG 0.2 µm membrane filters. Chlorophyll species were determined according to Meyns et al. (1994) and Murray et al. (1986): Chlorophyll *a* and *b* were separated isocratically by HPLC at a flux rate of 1.0 ml min^{-1} in a mixture of 49.5 % methanol, 45 % ethyl acetate and 5.5 % water, and quantified with photometric detectors at 430 nm (for chl *a*) and 460 nm (for chl *b*).

In Lake Zürich, samples were filtered through Whatman GF/F filters and the filters immediately stored at –20 °C. The filters then were homogenised in 10 ml 90 % acetone. The chlorophyll extracts were filtered through Whatman GF/F filters. Chlorophyll *a*, *b* and *c* and up to 15 carotenoids were separated by a quaternary HPLC column at a flux rate of 1.0 ml min^{-1} and determined by their spectra between 350 and 600 nm.

Primary Production (PP; ^{14}*C-Assimilation,* in mg C m^{-3} h^{-1}): Water samples were taken at 0.2, 0.5, 1, 1.5, 2.5, 3.75, 5, 7.5, 10, 12.5, 15, and 20 meters depth, and *in situ* measurements were performed in 120 ml Duran bottles (transmission properties, see Köhler et al., this issue) at each specific depth. Incubations took place for four hours from 10 to 14 h local time (CET), after addition of 5–10 µCi $NaH^{14}CO_3$ per bottle. From each of the samples taken in the Lakes Lucerne and Cadagno between 0.2 and 5 meters, sub-samples were incubated *in situ* in Duran bottles covered with a UV-screen (transparent hard PVC tube according to Bühlmann et al., 1987) to measure the difference in ^{14}C-assimilation, when UV radiation is removed. After incubation, the ^{14}C samples were immediately transported to the field station and processed by the acidic bubbling method, according to Gächter and Mares (1979). Radioactivity was determined in liquid scintillation counters (Model Tricarb, Packard, USA.), after addition of 10 ml of Instagel™ (Packard, USA.) to 7 ml water sample in glass vials of 20 ml volume. The glass quality of the bottles used in Lake Zürich for the in situ incubation on 4 August 1999 was less transparent to UV (93 % absorption at 325 nm, 40 % at 350 nm) than the Duran bottles (22 % absorption at 325 nm, 4 % at 350 nm).

The Specific Photosynthetic Rate (*SPP,* often defined as P^B or Assimilation Number *AN*) was calculated as C-assimilation per chlorophyll *a* [mg C (mg chl *a*)$^{-1}$ h^{-1}]. *P* versus *I* curves were calculated with a least square fit of the mathematical equation (Platt et al., 1980):

$$P^B = P_S^B \left(1 - e^{-\frac{\alpha \cdot I}{P_S^B}}\right) e^{-\frac{\beta \cdot I}{P_S^B}} \quad \text{(or shorter: } P^B = PBS\,(1 - e^{-\alpha I/\,PBS})\,e^{-\beta I/\,PBS}\text{)}$$

where P^B is gross primary productivity per unit biomass (in mg C · (mg chl *a*)$^{-1}$ · h^{-1}), and *I* is the ambient light intensity (µmol m^{-2} s^{-1}). In this paper P_S^B and AN_{max} are not identical. P_S^B (PBS) was calculated by curve fitting as the hypothetical maximum photosynthetic output the algae could sustain if there were no photoinhibition, while AN_{max} was determined *in situ* as the maximum *AN* measured in bottle samples at light saturation protected from exposure to UV radiation by filter screens.

The coefficient α (mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$), the slope of the linear part of the *P* versus *I* curve, is the increase of *AN* per unit increase in *I* that is in effect at $I = 0$ (initial slope) in the absence of photoinhibition. The coefficient β (dimensionless) is the fractional decrease in P^B caused by photoinhibition.

P_s^B, α, and β were determined by curve fitting by two approaches: Because a simultaneous calibration of the coefficients α, β and P_s^B yielded sometimes unrealistic values, they were also calibrated stepwise: α was first determined with equation $P^B = PBS\,(1 - e^{-\alpha I/PBS})$ from datasets containing only low light intensity data; β was

then determined with equation $P^B = PBS\, e^{-\beta I/PBS}$ from datasets containing only high light intensity data. *PBS* was thereafter calibrated with the full dataset with Platt's equation ($P^B = PBS\,(1 - e^{-\alpha I/\,PBS})\, e^{-\beta I/PBS}$) where α and β were kept as fixed constants.

Characteristics of the lakes investigated

Lake Lucerne

Lake Lucerne (Vierwaldstättersee) is an oligotrophic deep prealpine monomictic lake of a complicated morphological structure consisting of a chain of different basins. Chemical, physical and biological parameters have been monitored in monthly intervals from 1961 to 1992 (Bührer and Ambühl, 1996 and 2001) and since then twice per year (plankton monthly). Primary production (PP) has been assessed monthly from 1979 until 1997. Size related primary production was investigated by Uehlinger and Bloesch (1989).

The lake was originally oligotrophic. Between 1960 and 1980 it underwent a period of eutrophication which reached a peak in the late seventies (total P at maximum spring turnover: 30 mg m^{-3}, annual Areal Primary Production (APP): 300 g C m^{-2} yr^{-1}). Subsequently the lake turned from mesotrophic to oligotrophic again (total P at maximum spring turnover < 5 mg m^{-3}, annual APP < 200 g C m^{-2} yr^{-1}) within 15 years, due to a reduction of the phosphorus load from 103 to 14 t yr^{-1} (Bloesch et al., 1995). Nitrate as the major component of total dissolved nitrogen, however, continued to increase (measured at maximum spring turnover) from 340 µg N l^{-1} in 1960 to 600 in 1999.

The long-term development of phytoplankton is described in detail by Bürgi et al. (1999 and 1985). In the 1960s the phytoplankton community was dominated by cyanophytes (mainly *Planktothrix rubescens*) and pennate diatoms. The chlorophytes were rare. With increasing P-load the green algae added some distinct peaks, but diatoms (shifting from pennate to centric forms) and blue-greens remained dominant. At the peak of eutrophication (in the late seventies) chlorophytes were also abundant, while the *Planktothrix* biomass declined. During the phase of pronounced oligotrophication (1982–85) the biomass of cyanophytes decreased to minor densities, as well as diatoms, dinophytes and cryptomonads, while chrysomonads and green algae remained stable. Later on (1986–95) the phytoplankton composition tended to shift from netplankton to motile nannoplankton, e.g. towards small flagellates (Chrysophyceae). *Planktothrix rubesc*ens also recovered while the green algae decreased.

Today the community structure is dominated in winter by *Rhodomonas* and centric diatoms, in summer by pennate diatoms (*Fragilaria*) and in autumn by blue-greens, e.g. *Planktothrix rubescens* (Bürgi et al., 1999).

The euphotic zone (>1 % of surface PAR) expanded during re-oligotrophication from 15 m (in 1980) to 20 m (in 1999), thus considerably enlarging the layer of primary production. This may be one reason for an only moderate decrease of pelagic primary productivity in spite of the drastic decrease of SRP during that period.

Key parameters measured in summer 1999

Figure 2 presents a summary of the two sampling days on 25 August and 13 September 1999.

The summer 1999 was very rainy at the beginning, but ended with a warm, dry period in September. Compared to other years this resulted in a relatively low energy input into the lake until end of August. However, while in former years the upper lake epilimnion had already cooled down by mid-September, water temperatures were still rising in the first part of September 1999. During the GAP-Workshop (13 September) the epilimnion was stratified as reflected by an almost linear temperature decrease from 19.4 °C at 2.5 m to 8.5 °C in 20 m depth (Fig. 2a). Within the uppermost 2.5 meters the temperature difference was small (0.4 °C).

While there was still plenty of nitrate (230–330 µg NO_3-N l^{-1}) and silicate (430–1650 µg SiO_2 l^{-1}) available (Figs. 2e, f), the growth-limiting nutrient SRP (Fig. 2d) was hardly detectable (0–1 µg P l^{-1}) within the whole epilimnion.

The euphotic zone (> 1% of surface PAR) extended to a depth of 15.1 m during the GAP Workshop (Fig. $2g_1$). 10% of the surface radiation were measured on 13 September for PAR at a depth of 7.1 m ($K_{d,PAR}$ = 0.313 m^{-1}), for UV-A at 3.7 m ($K_{d,UV\text{-}A}$ = 0.618 m^{-1}), and for UV-B at 2.1 m ($K_{d,UV\text{-}B}$ = 1.047 m^{-1}) (see Figs. 2g, h, j, and Table 2). Good weather conditions with frequent cloudless periods during the GAP Workshop resulted in relatively high surface radiation intensities, which produced ideal conditions to assess the full scale of inhibition, saturation and light limitation within *in situ* PP depth profiles (Fig. 2*l*).

The phytoplankton community was dominated in August and September 1999 by chrysophytes (*Dinobryon, Erkenia, Ochromas* sp.) and diatoms *(Asterionella, Fragilaria, Synedra, Cyclotella, Stephanodiscus*). A sharp decline of pennate diatoms from 30 August to 7 September was compensated by an increase in centric diatoms (Fig. 3).

Both parameters for phytoplankton biomass, fresh weight and chlorophyll *a,* decreased in the period immediately before the GAP Workshop (Table 2, Fig. 3).

The depth profiles of primary production (PP) of 25 August and 13 September (Fig. 2), determined at full sunshine, showed typical near surface depressions. The production maxima were between 3.75 and 5.0 (on 13 September) and between 5 and 7.5 m depth (on 25 August), respectively, which corresponds approximately to the chlorophyll maxima in those depths.

Table 2. Lake Lucerne, key parameters for primary production in summer 1999

Date	Surface PAR I_0 [µmol m^{-2} s^{-1}]	10% of surface PAR, depth [m]	Phyto-plankton 0–20 m [g FW m^{-2}]	Chl *a* 0–20 m [mg m^{-2}]	Chl *b* 0–20 m [mg m^{-2}]	APP 0–20 m [mg C m^{-2} h^{-1}]	AN ave. 0–5 m [mg C (mg chl *a*)$^{-1}$ h^{-1}]
16-08-99			15.5				
25-08-99	1273	8.7		78.7	1.96	90.2	2.15 ± 0.76
30-08-99			16.3				
07-09-99			7.4				
13-09-99	1010	7.1		34.5	1.88	52.1	3.89 ± 2.12

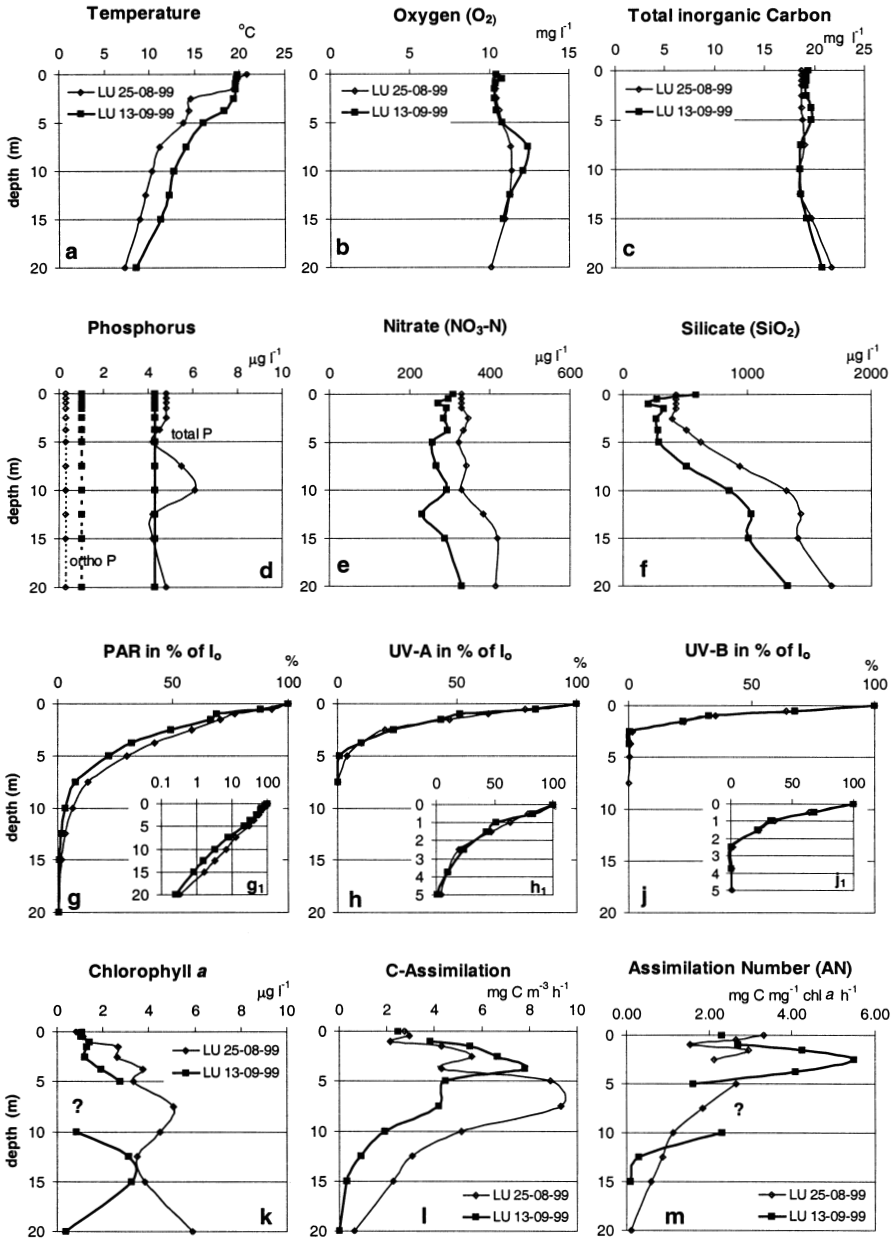

Figure 2. Lake Lucerne, Kreuztrichter, depth profiles of 25 August (diamonds) and 13 September (squares) 1999, for (a) temperature, (b) oxygen, (c) total dissolved inorganic carbon (DIC), (d) ortho-phosphate (SRP) and total-phosphorus (P_{tot}), (e) nitrate, (f) silicate, (g) PAR transparency in percent of incident radiation at the water surface, with inset (g_1) log representation, (h) UV-A transparency with inset h_1) zoom of the uppermost five meters, (j) UV-B transparency with inset (j_1) zoom, (k) chlorophyll *a*, (l) photosynthetic C-assimilation, and (m) chlorophyll-specific C-assimilation (assimilation number, AN)

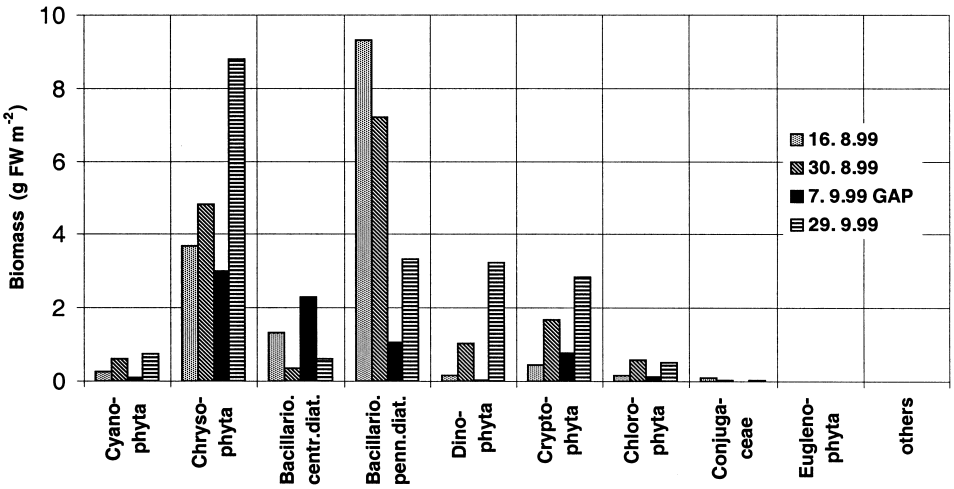

Figure 3. Phytoplankton community structure in the trophogenic layer (0–20 m) of Lake Lucerne, Kreuztrichter, of 16 August, 30 August, 7 September, and 29 September 1999; biomass in g FW m^{-2}

The profiles of *AN* showed equal shapes of curves. However, the maximum *AN* were closer to the surface than those of PP, namely between 2.5 and 3.75 m depth at both days. In the period of 1995–1997, when C-assimilation was measured monthly, *AN* never rose above 4 mg C mg^{-1} chl *a* h^{-1} at any depth at any season. The Assimilation Numbers in the depths of 1.5 m (*AN* of 7.2) and 2.5 m (*AN* of 5.5) seem to be quite high (Fig. 2m) due to low chl *a* values. They fit, however, into the general picture obtained from long term data of past years that *AN* values tend to increase in late summer and early fall.

Lake Zürich

Lake Zürich is a deep, and based on the sediments (Züllig, 1982), an originally oligotrophic lake in a densely populated region. It suffered from sewage discharges since the beginning of the 20th century (Thomas, 1965). The lake has been monitored intensively for many decades as it serves as a major source for drinking water production. In the period from 1937 to 1975 chemical and physical measurements have been done routinely at several sites along the length axis of the lake by the Cantonal Laboratory Zürich (Oern, 1980). During the past 25 years monthly profiles of chemical, physical and biological parameters, in particular phytoplankton and primary productivity, have been measured by Zürich Water Supply (Gammeter et al., 1997).

Since 1955 over 90% of the population around the lake have been connected to wastewater treatment plants with enhanced P-removal (today eliminating up to 99% of total P). As a result, Lake Zürich returned from an eutrophic (Total P, TP, at maximum spring overturn >100 µg l^{-1} around 1970) to a mesotrophic state with

Table 3. Lake Zürich, key parameters for primary production in summer 1999

Date	Surface PAR I_0 [µmol m^{-2} s^{-1}]	10% of surface PAR, depth [m]	Phyto-plankton 0–15 m [g FW m^{-2}]	Chl *a* 0–15 m [mg m^{-2}]	Chl *b* 0–15 m [mg m^{-2}]	APP 0–15 m [mg C m^{-2} h^{-1}]	AN ave. 0–5 m [mg C (mg chl *a*)$^{-1}$ h^{-1}]
04-08-99	1251	3.7	43.9	104.5	3.5	104.6	2.12 ± 0.35
18-08-99	180	5.0	28.0	n.d.	n.d.	n.d.	n.d.
08-09-99	1245	4.9	42.4	65.6	2.35	124.5	2.71 ± 0.53

TP concentrations of 30 µg l^{-1}. A first report on the oligotrophication of Lake Zürich was given by Schanz and Thomas (1981). P load is relatively stable since 1990. During the past 10 years the annual APP was 217 g C m^{-2} yr^{-1} and the mean phytoplankton biomass (0–15 m) remained relatively stable at 2.5 g FW m^{-3} (Gammeter and Zimmermann, 2001).

The lake is usually monomictic, but holomixis is rather exceptional (Kutschke, 1966; Oern, 1980). In warm winters, or in such with poor wind activities, mixing depth reaches only 60 to 100 m. Inverse stratification is observed only in cold winters mostly during a short period at the beginning of March. Complete ice cover occurs (statistically) once in every 25 years, the last one dating back to 1963. From May until October a stable thermocline develops between 8 and 15 m depth, with maximum gradients of 3.5 °C m^{-1}. Temperature in the epilimnion exceeds 20 °C for usually 2 months and reaches maximum values of 25 °C at the surface. The euphotic zone extends down to 10.0 ± 2.5 m depth during summer stratification (April–September).

In the 10 to 12 m layer *Planktothrix rubescens* grows to very high densities (up to 10 mg FW l^{-1}) in late summer (Micheletti et al., 1998; influence on spectral light attenuation, see Schanz, 1986). Usually at the end of September the *Planktothrix* filaments are distributed within the whole epilimnion. *P. rubescens* accounts for more than 50% of the total phytoplankton biomass from September to March. The biomass reaches low values between end of May and mid of July (Walsby et al., 1998). Several other cyanobacterial genera appear regularly in early autumn: *Aphanothece*, *Aphanocapsa*, *Microcystis* and *Aphanizomenon*. Numerous Chlorophyta species occur, but they account for less than 10% of phytoplankton biomass. Typical autumn Chrysophyta species are *Dinobryon* and *Fragilaria crotonensis*. Cryptophyta (*Cryptomonas*, *Rhodomonas*) and Dinophyta (mainly *Ceratium hirundinella*) make up for the remaining 20% of total biomass. In winter diatoms and flagellates are frequent besides the dominating *Planktothrix* and in spring centric diatoms and cryptophytes (*Rhodomonas*) are regularly blooming (Bleiker and Schanz, 1989).

Key parameters measured in summer 1999

Figure 4 presents a summary of the two sampling days of 4 August and 8 September 1999. Temperature in the epilimnion reached maximum values of 24 °C in August. By the time of the GAP Workshop, a stable thermocline had established

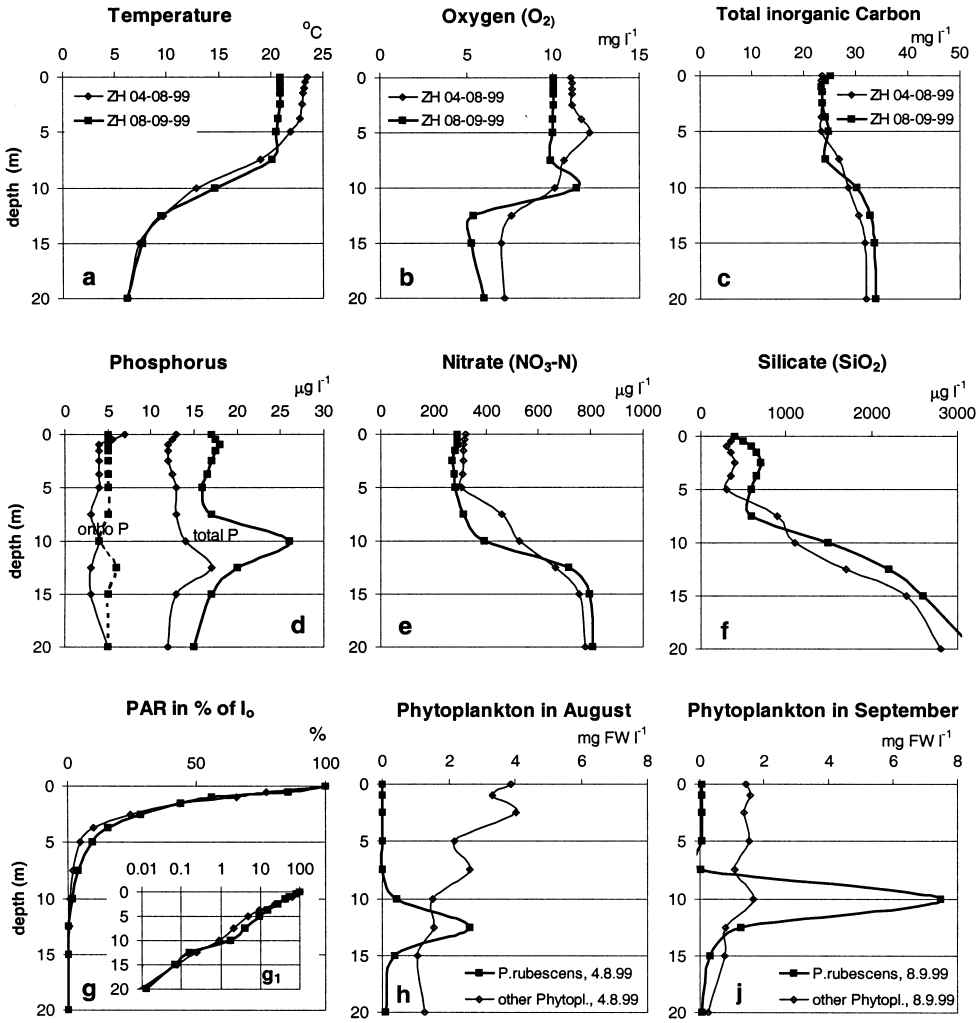

Figure 4. Lake Zürich, Thalwil, depth profiles of 4 August (diamonds) and 8 September (squares) 1999, for (a) temperature, (b) oxygen, (c) total dissolved inorganic carbon (DIC), (d) ortho-phosphate (SRP) and total-phosphorus (P_{tot}), (e) nitrate, (f) silicate, (g) PAR transparency in percent of incident radiation at the water surface, with inset (g_l) log representation, (h) phytoplankton biomass *and Planktothrix rubescens* on 4 August in mg FW l^{-1} (j)

between 8 and 12 m (temperature difference 9 °C, or 2.25 °C m^{-1}). This resulted in a clear separation of epilimnion (0–8 m), metalimnion (8–12 m) and hypolimnion (Fig. 4a).

The phytoplankton community was dominated in early August by chrysophytes, followed by cyanophytes, diatoms and dinophytes. Thereafter, the cyanophytes increased their biomass drastically in the deep trophogenic layer (Figs. 4h and j) and dominated total phytoplankton biomass in late summer and fall, while the bio-

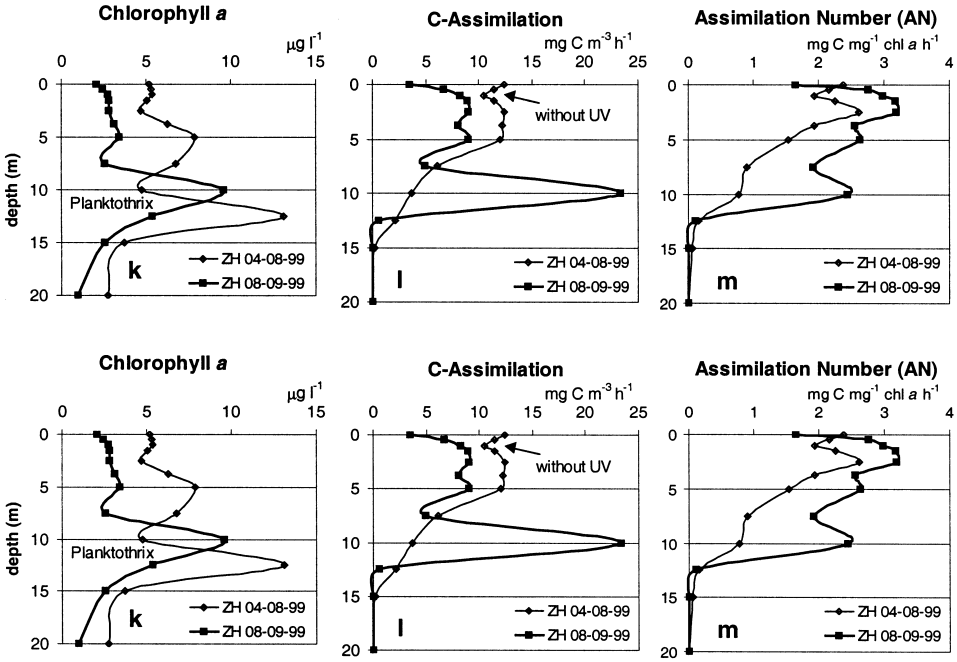

Figure 4 (continued) (j) phytoplankton biomass and *Planktothrix rubescens* on 8 September in mg FW l^{-1} (k) chlorophyll *a*, (l) photosynthetic C-assimilation, and (m) chlorophyll-specific C-assimilation (assimilation number, AN)

mass of chrysophytes and diatoms decreased considerably (Fig. 5), also in the upper epilimnion (Figs. 4h and j).

The epilimnetic nutrient concentrations do not appear to be limiting (Fig. 4d–f): SRP on 4 August was 4 µg l^{-1}, on 8 September 5 µg l^{-1}; nitrate on 4 August 350 µg N l^{-1}, on 8 September 290 µg N l^{-1}; silicate on 4 August 500 µg SiO_2 l^{-1}, on 8 September 575 µg SiO_2 l^{-1}. However, chlorophyll *a* concentrations were only moderate (6 µg l^{-1} in August, 2.5 µg l^{-1} in September) as were the phytoplankton fresh weights (3.2 mg l^{-1} in August and 1.4 mg l^{-1} in September, see Fig. 4 h, j). Most of the biomass was concentrated in the metalimnion, at 10 m depth. This metalimnetic phytoplankton consists to about 80% of the filamentous cyanobacterium *Planktothrix rubescens* (Fig. 4 h, j). A peak at 10 m depth in oxygen (Fig. 4 b) and total phosphorus (Fig. 4 d) underpin the significance of this metalimnetic production. *Planktothrix rubescens* is avoided by most zooplankton species, probably because of its high microcystin content (Kurmayer and Jüttner, 1999).

Euphotic depth (1% of surface PAR) was 9.7 m on 4 August and 10.7 m on 8 September 1999. The attenuation coefficient (K_d) in the epilimnion was 0.466 m^{-1} on 4 August and 0.462 m^{-1} on 8 September. In the *Planktothrix* layer in September K_d was much higher (0.967 m^{-1} between 10 and 12.5 m).

The PP was only moderate in the 0 to 7.5 m layer showing values between 5 and 13 mg C m^{-3} h^{-1}. The PP of *Planktothrix* filaments at 10 m depth was quite high during the GAP-workshop (PP = 23 mg C m^{-3} h^{-1}; *AN* = 2.4 mg C mg^{-1} chl *a* h^{-1}),

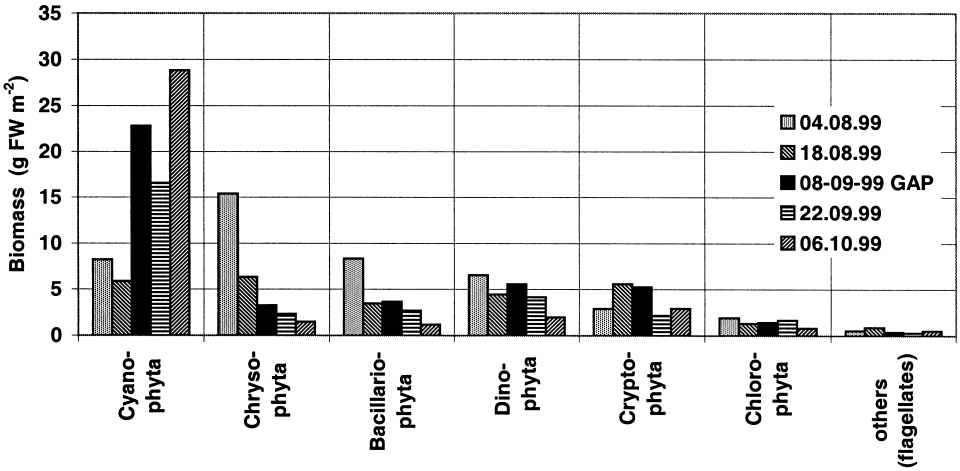

Figure 5. Phytoplankton community structure in the trophogenic layer (0–20 m) of Lake Zürich, Thalwil of 4 August, 8 September, and 6 October, and Zollikon of 18 August and 22 September 1999; biomass in g FW m^{-2}

although the mean light intensity during the exposition period was only 5 µmol m^{-2} s^{-1}. On 4 August, the majority of the filaments were too deep in the metalimnion (12.5 m) to support a considerable PP, in spite of the high chlorophyll *a* content of 13 mg m^{-3} (PP = 2; *AN* = 0.2). In the upper 5 m the main contribution to the PP at that day was caused by *Dinobryon*, *Peridinium* and centric diatoms (see also Fig. 5). On 8 September the scarce phytoplankton in the epilimnion was more active in terms of assimilation per chlorophyll *a* (*AN* = 2.85, mean of 0 to 5 m depth layer) than on 4 August (*AN* = 2.2), probably due to the presence of *Rhodomonas* and *Cryptomonas* species.

Lake Cadagno

Lake Cadagno is an alpine meromictic lake in the Piora Valley at 1921 m a.s.l. in the southern part of Switzerland. The 21 m deep lake basin was formed by glacial erosion and dammed by a glacial moraine. Today it serves as one of the reservoirs for a hydroelectric power plant in Piotta and thus undergoes each winter water level fluctuations of 3 m. In summer the lake frequently receives loads of organic matter (cattle manure, waste products of cheese manufacture) which increases the nutrient level leading to a trophy shift during the summer months (Schanz and Stalder, 1998). This is reflected by the exceptionally high concentrations of dissolved organic carbon (DOC, 1.5–2 mg C l^{-1}) for an alpine lake at this altitude.

The mixolimnion of Lake Cadagno is fed by electrolyte-poor surface water. It spans down to 11–12 m water depth. The monimolimnion consists of salt-rich water (mainly sulfate, carbonate, calcium and magnesium) which is constantly supplied by subaquatic springs. The water masses of the lake are stabilized by the large density

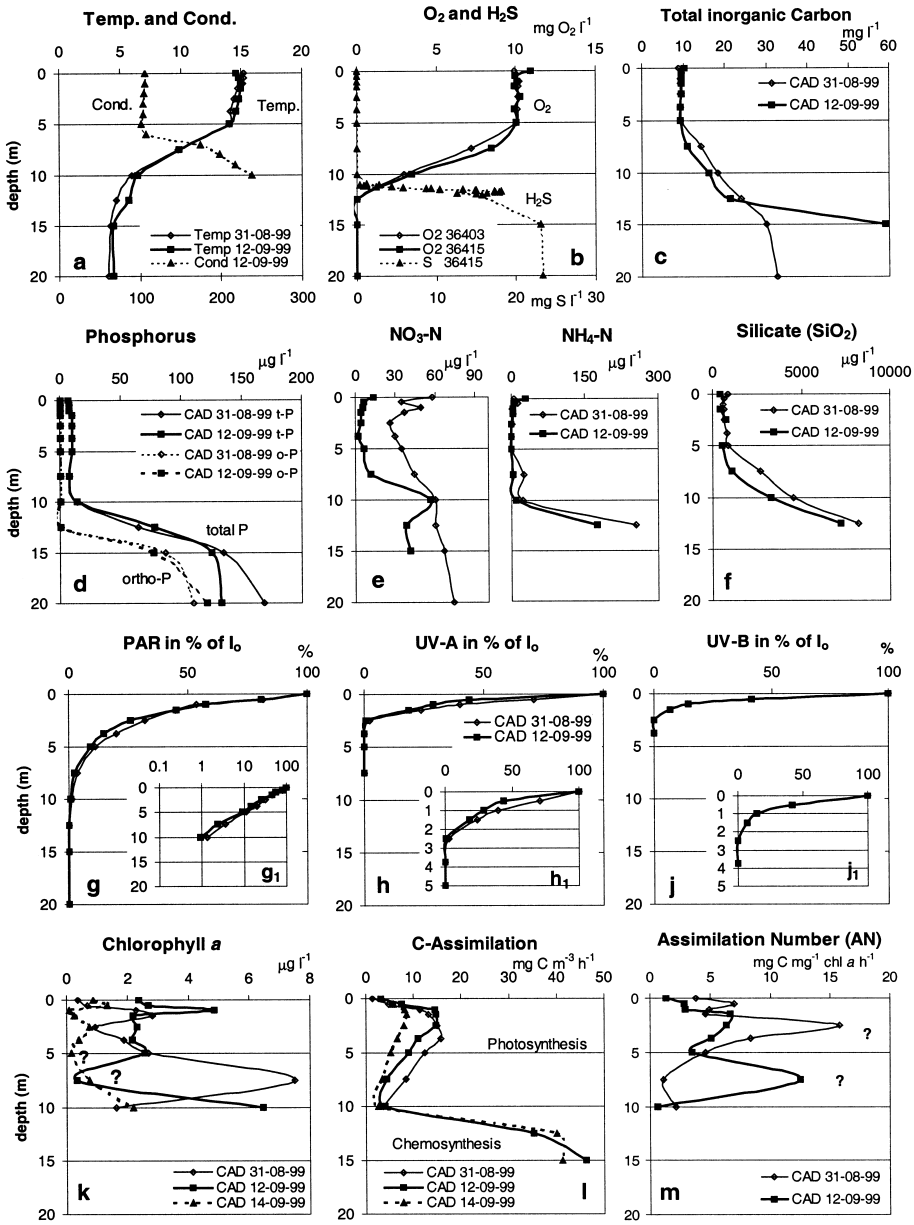

Figure 6. Lake Cadagno, center of the lake, depth profiles of 31 August (diamonds) and 12 September (squares) 1999, for (a) temperature and conductivity, (b) oxygen and sulfide, (c) total dissolved inorganic carbon (DIC), (d) ortho-phosphate (SRP) and total-phosphorus (P_{tot}), (e) nitrate and ammonia, (f) silicate, (g) PAR transparency in percent of incident radiation at the water surface, with inset (g_1) log representation, (h) UV-A transparency with inset (h_1) zoom of the uppermost five meters, (j) UV-B transparency with inset (j_1) zoom, (k) chlorophyll *a* (uncorrected), (l) photosynthetic C-assimilation, and (m) chlorophyll-specific C-assimilation (assimilation number, AN)

Table 4. Lake Cadagno, key parameters for primary production in summer 1999

Date	Surface PAR I_0 [µmol m^{-2} s^{-1}]	10 % of surface PAR, depth [m]	Phyto-plankton 0–10 m [g FW m^{-2}]	Chl *a* 0–10 m [mg m^{-2}]	Chl *b* 0–10 m [mg m^{-2}]	APP 0–10 m [mg C m^{-2} h^{-1}]	AN ave. 0–5 m [mg C (mg chl *a*)$^{-1}$ h^{-1}]
31-08-99	1140	5.4	n.d.	33.0		102.2	7.03 ± 4.16
12-09-99	833	4.9	43	24.9	4.3	86.1	4.11 ± 1.98
14-09-99	664			7.4	2.9	52.4	26.4 ± 28.6

differences between the mixolimnic and the monimolimnic water. The monimolimnion of the lake is constantly anoxic and sulfide is accumulated up to 23 mg l^{-1} (see e.g. Lehmann and Bachofen, 1999, and Fig. 6b), thus the pycnocline parallels a redoxcline and a chemocline, a depth where dense populations of phototrophic bacteria are naturally enriched. Fischer et al. (1996) studied the light environment and the synthesis of bacteriochlorophyll by populations of *Chromatium okenii*. Growth and production of the bacterial layer was described by Schanz et al. (1998). The peculiar phenomenon of crenogenic meromixis has attracted scientists already early in the 20th century and is described in detail by Del Don et al. (2001).

Most of the following generalizations are based on short term investigations mainly during the summer seasons of the past two decades (see also Peduzzi et al., 1998). Secchi depths, measured in July, averaged in the past decade 6.8 ± 0.6 m (Tonolla, unpublished results). Epilimnetic nutrient concentrations (in the uppermost 10 m) are low during summer. While PO_4-P approaches detection limits (< 1 µg P l^{-1}), NO_3-N is below 50 µg N l^{-1} and DIC ranges around 10 mg l^{-1}. The concentrations of these nutrients increase with depth in the anoxic monimolimnion to near bottom values of approximately 100 µg PO_4-P l^{-1}, 400 µg NH_4-N l^{-1} and 20 mg DIC l^{-1} (Del Don, 1986; Friedl, 1987; Tonolla et al., 1998 and 1999).

The epilimnetic phytoplankton community (0–10 m) starts out in early summer with a relatively even distribution of centric and pennate diatoms, green algae (mainly *Scenedesmus* and *Dictyosphaerium*), cryptophytes and dinophytes. During summer pennate and centric diatoms (*Fragilaria, Stephanodiscus, Cyclotella sp.*) take over. In late summer green algae (mainly *Sphaerocystis* and later *Oocystis*) dominate (Schanz and Stalder, 1998). Chlorophyll *a* concentrations vary considerably, e.g. in summer 1988 between 26 mg m^{-2} in late July and 4 mg m^{-2} in early September, or in summer 1986 between 18 and 65 mg m^{-2} (Schanz and Friedl, 1993).

The PP from July to September 1986 (Friedl, 1987) varied between 23 and 79 mg C m^{-2} h^{-1} in the layer from the surface down to 9.5 m depth which is the zone dominated by aerobic phytoplankton organisms. The euphotic zone (> depth of 1 % surface PAR) remained very stable during this period (11.6 ± 0.3 m). The low intensity of light below 9.5 m depth is efficiently used by phototrophic bacteria in anoxygenic photosynthesis with sulfide as electron donor (Schanz et al., 1998). According to the data of Friedl (1987) bacterial production below 10 m depth was in the average 50 % of the 0 to 9.5 m phytoplankton production (range 12–97 %). AN_{max} (in the 0–5 m depth layer) was between 1.8 and 6.7 mg C (mg chl *a*)$^{-1}$ h^{-1}, exceeding 5 mg C (mg chl *a*)$^{-1}$ h^{-1} only twice. The near surface *AN* (0 to 2 m layer), calculated

in August 1997 (Pasini, 1999; Pasini and Schanz, 1998), were in the range of 1.3 to 6.5 mg C (mg chl *a*)$^{-1}$ h^{-1} with a mean of 4.3 mg C (mg chl *a*)$^{-1}$ h^{-1}. Therefore, no statistical significant difference between the datasets of 1986 and 1997 is expected.

Key parameters for primary production in summer 1999

Figure 6 presents a summary of the two sampling days on 31 August and 12 September 1999.

The vertical temperature profile remained stable during the first two weeks in September. The lake had developed a pronounced thermocline between 5 and 12 m depth with a temperature difference of 10 °C (gradient 1.4 °C m^{-1}). The thermic stability was additionally strengthened by the density gradient which was most prominent between 5 and 10 m depth, as deduced from the conductivity data (increase from 100 µS cm^{-1} at 5 m water depth to 250 µS cm^{-1} at 10 m water depth). Vertical mixing above the thermocline caused homogeneous concentrations of all dissolved compounds in the mixolimnion, while in the meta- and hypolimnion steep gradients had established. This is deduced from the oxygen curve showing a sharp decline from 10 to 0 O_2 mg l^{-1} between 5 and 12 m depth. SRP was 0.5 µg P l^{-1} throughout the euphotic zone (0–5 m depth). Dissolved nitrate (< 50 µg N l^{-1}) was very low compared to Lake Zürich and Lake Lucerne, and decreased in the euphotic zone within two weeks by 66 % or 269 mg N m^{-2}. This resulted in an average nitrate concentration on 12 September of 13.4 µg NO_3-N l^{-1}. Such a loss is easily explained by N-consumption during growth at an average areal daily PP of 200 mg C m^{-2} d^{-1}. DIC concentration remained stable in the euphotic zone during the two weeks period, showing a relatively low value of about 10 mg C l^{-1} as a consequence of the incoming soft water from the crystalline rock region of the catchment area. The DIC concentrations increased considerably towards the lake bottom up to 30 mg C l^{-1} on 31 August and up to 58 mg l^{-1} on 12 September.

The euphotic depth (1 % of surface PAR) was 10 m and thus covered the epi- and metalimnion down to the layer of photosynthetic sulfur bacteria (Schanz et al., 1998). 10 % of the surface radiation were measured on 12 September for PAR at a depth of 4.9 m ($K_{d,PAR}$ = 0.47 m^{-1}), for UV-A at 2.0 m ($K_{d,UV\text{-}A}$ = 1.08 m^{-1}), and for UV-B at 1.3 m ($K_{d,UV\text{-}B}$ = 1.70 m^{-1}).

The vertical distribution of PP (Fig. 6l), measured on 31 August, 12 and 14 September, was of similar shape in all three depth profiles: a low production close to the surface, a distinct production maximum located at a depth of 1.5–3.75 m, and a production minimum at 10 m (depth of 1 % surface light intensity = compensation depth for oxygenic photosynthesis). Below 10 m very high values of phototrophic (caused by the sulfur bacteria *Amoebobacter* cf. *purpureus* and *Chromatium okenii*) and chemotrophic C-assimilation were observed (for details see Camacho et al., 2001).

While chlorophyll concentrations (Fig. 6k) showed large variations with depth on all sampling days, the PP profiles were smooth. As a consequence, the assimilation numbers (*AN*), calculated from C-assimilation and chlorophyll, varied accordingly and yielded in some depths incorrect values (Fig. 6m).

The phytoplankton community in early September is described in detail by Camacho et al. (2001). The upper water body of the euphotic zone was dominated

by the green algae *Echinocoleum elegans* and *Elakatothrix* sp. and the diatom *Cyclotella radiosa*. Furthermore various picoplankton were present in smaller concentrations. Total phytoplankton fresh weight in the euphotic zone from 0–10 m depth was 43 g FW m^{-2} (calculated from data obtained by Camacho et al., 2001). Immediately below the euphotic zone (at 10.8–11.2 m) a dense population of diatoms, mainly *Fragilaria capucina* and *Cyclotella comensis*, peaked in the oxic water at the upper edge of the chemocline and added considerably to the total phytoplankton fresh weight (from 0–12 m depth: 56 g FW m^{-2}).

Zooplankton species, mainly *Daphnia longispina, Acanthodiaptomus denticornis* and *Bosmina longirostris* among the crustaceans, as well as *Conochilus sp*. and, less abundant, *Asplanchna priodonta* among the rotifers, were observed.

Comparison of primary production properties in the Lakes Lucerne, Zürich and Cadagno

In August (Table 5a), all three lakes showed at nearly equal surface insolation (I_0, 1140–1273 µmol $m^{-2}s^{-1}$) similar areal primary production (APP, 90–105 mg C m^{-2} h^{-1}) despite different chlorophyll standing crops. Due to a higher water transparency the euphotic depth and thus primary production (PP) extended in Lake Lucerne into deeper zones than in Lake Zürich (Table 5). The lower areal chlorophyll standing crop in Lake Lucerne yielded a higher chlorophyll-specific areal production rate (AAN) and thus an APP similar to Lake Zürich.

AAN in the alpine Lake Cadagno were considerably higher than in the two lowland lakes. In September, AAN in all three lakes were higher than in August, as had been observed in former years.

It is notable that in Lake Zürich the APP was higher in September (124.5 mg C m^{-2} h^{-1}) than in August (105 mg C m^{-2} h^{-1}) in spite of a smaller chlorophyll standing crop (74.5 versus 120 mg m^{-2}), and nearly equal I_0 and K_d. *Planktothrix rubescens* must be responsible for the apparent discrepancy, as it is able to achieve high assimilation rates at very low light intensities (see Fig. 4l).

Table 5. Comparison of areal primary production in Lakes Lucerne, Zürich and Cadagno

Lake /Date	Chl *a* [mg m^{-2}]	APP [mg C m^{-2} h^{-1}]	AAN [mg C (mg chl *a*)$^{-1}$ h^{-1}]	Euphotic zone [m]	Surface PAR [µmol m^{-2} s^{-1}
a) in August					
Lucerne/25.8.99	78.7	90.2	1.15	17.7	1273
Zürich/4.8.99	120.8	105.2	0.87	9.8	1251
Cadagno/31.8.99	33.0	102.2	3.10	10.4	1140
b) in September					
Lucerne/13.9.99	34.5	52.1	1.51	15.1	1010
Zürich/8.9.99	74.5	124.5	1.67	10.9	1245
Cadagno/12.9.99	24.8	86.1	3.47	9.9	833
Cadagno/14.9.99	14.2	52.4	3.62		664

Plots of *AN* versus ambient light intensity (I_z) in the *in situ* depth profiles of the three lakes (Fig. 7) showed in September an (inhibitory) decrease in *AN* at $I_z >$ 500 µmol m^{-2} s^{-1}. *AN* in Lake Cadagno samples (outliers in Fig. 6 m were corrected with the help of simultaneous *in situ* incubations with UV-screens) were considerably depressed at even lower intensities (< 300 µmol m^{-2} s^{-1}) on both dates of 31 August and 12 September. In August no inhibition of *AN* occurred in the Lakes Lucerne and Zürich. Additional simultaneous incubations in bottles covered with UV absorbing material revealed, however, a distinct inhibitory effect on the PP by ambient UV, not only in September but also in August (Fig. 8). The PP profile in Lake Zürich of 4 August can be seen as a 'no UV experiment', since the bottles used for incubation absorbed most of the UV radiation (93 % absorption at 325 nm, 40 % at 350 nm). This may explain the missing inhibition of photosynthesis in the uppermost meter in August, compared to the September profile, when Duran glass bottles (38 % absorption at 325 nm, 5 % at 350 nm) were used.

Physiological parameters of primary production, such as calculated P^B_S, α, and β could not be calculated with high accuracy because of a considerable scatter in the data, but sufficient information was obtained to categorize the three lakes. Figure 9 shows some rough estimates calculated by different approaches: a) estimates from selected measured data (open bars) and b) curve-fitting (shaded bars) according to Platt et al. (1980) as described in "Materials and Methods".

These calculations show that the initial slope α tends to rise from August to September in all three lakes, being the lowest in Lake Lucerne with the deepest euphotic zone. The considerable increase of the coefficient α in Lake Zürich from August to September can be explained with the rôle of *Planktothrix* which shows an efficient utilization of light at low light intensities. The coefficient β (characterizing the slope of inhibition) is highest in Lake Cadagno, followed by Lake Lucerne and Lake Zürich. The hypothetical parameter P^B_S (the calculated maximum photosynthetic output the algae could sustain if there were no photoinhibition), is highly dependent on the shape of the calculated *P* versus *I* curve (especially on β) and therefore affected by the data scatter in the upper epilimnion. If inhibition is mainly caused by UV radiation and less by high light intensities, as Figure 8 suggests for most cases (see also Neale et al., 2001 a, this issue), calculated P^B_S should be only slightly higher than or equal to the measured AN_{max} as observed in samples covered with UV fil-

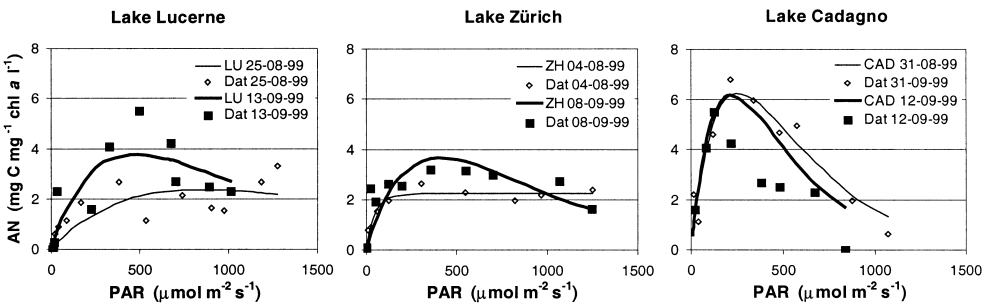

Figure 7. *P* versus *I* curves of the Lakes Lucerne, Zürich and Cadagno, in August and September 1999, calculated with equation $P^B = PBS\ (1\text{-}e^{-\alpha I/PBS})\ e^{-\beta I/PBS}$

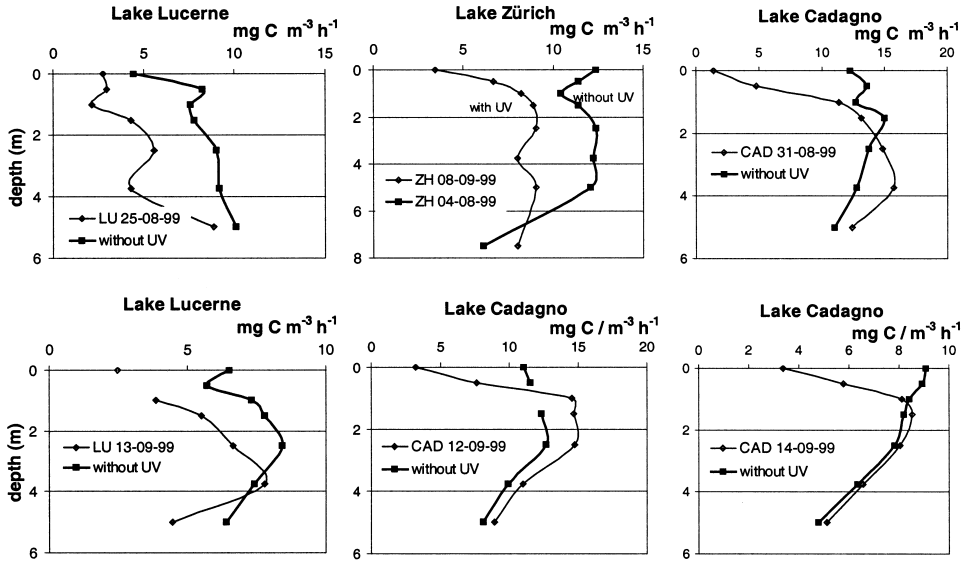

Figure 8. Depth profiles of photosynthetic *in situ* C-assimilation. In the Lakes Lucerne and Cadagno bottles incubated with and without exposure to UV radiation using Duran glass and UV-filters. Lake Zürich samples incubated in bottles of two different glass qualities (incubation on 4 August with plain glass bottles being more opaque to UV than the Duran bottles used on 8 September)

ters or in samples exposed to low UV radiation. Calculated P_S^B exceed in most cases measured AN_{max} in the Lakes Cadagno and Lucerne, especially when determined by simultaneous calibration of all three coefficients. For calculated P_S^B higher than 10 [mg C (mg chl *a*)$^{-1}$ h^{-1}] we hesitate to quantify the influence of the solar radiation on the observed inhibition of C-assimilation. In Lake Zürich, however, where little inhibition was observed, calculated P_S^B and measured AN_{max} correspond rather well.

In conclusion, the biological and physiological properties of phytoplankton in the three lakes during the GAP workshop in mid-September 1999 can be categorized as follows:

Lake Lucerne: A relatively low phytoplankton biomass (app. 7 g FW m^{-2}), with a high chlorophyll content (35 mg chl *a* m^{-2}), originating from mainly chrysophytes and diatoms, spread through a stratified euphotic zone of 15 m extension and increased with depth. The phytoplankton population in this oligotrophic lake is phosphate limited and yields a moderate APP of the same size as the mesotrophic Lake Cadagno. *AN* at low light intensities is rather low (flat initial slope α), while AN_{max} and β are moderate, when compared to the other two lakes.

Lake Zürich: A relatively high phytoplankton biomass (app. 42 g FW m^{-2}) combined with a low chlorophyll content (66 mg chl *a* m^{-2}) originating from cyanophytes, chrysophytes, diatoms and dinophytes peaks in the lowest part of the

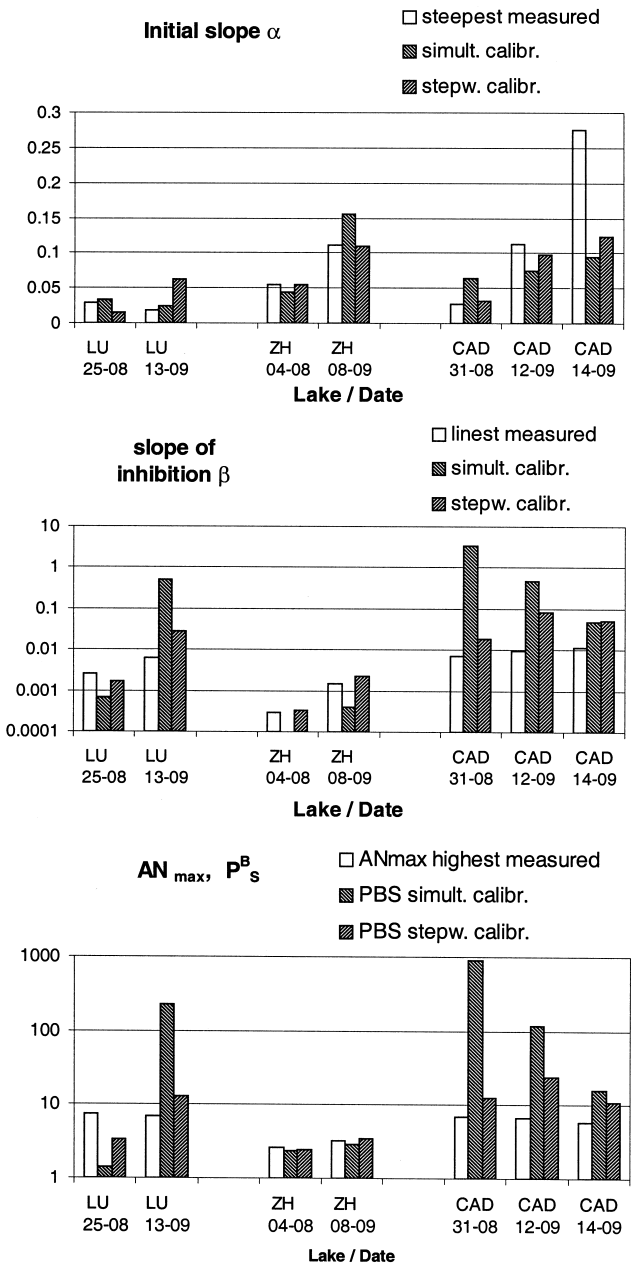

Figure 9. Characteristic factors of P versus I curves: AN_{max}, P^{B}_{S}, α, and β, determined in the Lakes Lucerne, Zürich and Cadagno in August and September 1999. The factors (coefficients) were determined (i) from measured data (α: steepest slope measured, β: straight line calculated by using the least squares method, AN_{max}: highest value of AN in the depth profile), (ii) by curve fitting with equation $P^{B} = PBS\ (1 - e^{-\alpha I/PBS})\ e^{-\beta I/PBS}$ (simultaneous and stepwise calibration of the coefficients). For further explanations see text

euphotic zone (dominated by Cyanobacteria) of 11 m extension. APP is rather high compared to the other two lakes. *AN* at low light intensities is high, due to the *Planktothrix* layer. AN_{max} and β are low.

Lake Cadagno: A relatively high phytoplankton biomass (app. 43 g FW m^{-2}) combined with a rather low chlorophyll content, (app 7–20 mg chl *a* m^{-2}) is dominated by the chlorophyte *Echinocoleum elegans*. It spreads through a stratified euphotic zone of about 10 m extension. APP is moderate. The vertical distribution of photosynthetic C-assimilation peaks at 1–3 m depth and again, caused by the phototrophic sulfur bacteria *Amoebobacter* cf. *purpureus* and *Chromatium okenii,* at 11–12 m. High rates of dark C-assimilation by chemolithotrophic bacteria are observed in the chemocline (Camacho et al., 2001). *AN* at low light intensities is rather high, due to the *Amoebobacter-Chromatium* layer. AN_{max} and β are high. The high inhibition coefficient below the water surface of this alpine lake is mainly caused by the high UV-intensity at this altitude compared to the two lowland lakes.

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