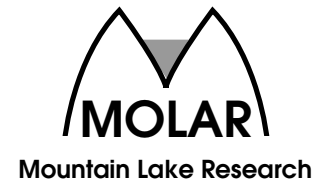


Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records



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Abstract

Weather variation and climate fluctuations are the main sources of ecosystem variability in remote mountain lakes. Here we describe the main patterns of seasonal variability in the ecosystems of nine lakes in Europe, and discuss the implications for recording climatic features in their sediments. Despite the diversity in latitude and size, the lakes showed a number of common features. They were ice-covered between 5–9 months, and all but one were dimictic. This particular lake was long and shallow, and wind action episodically mixed the water column throughout the ice-free period. All lakes showed characteristic oxygen depletion during the ice-covered-period, which was greater in the most productive lakes. Two types of lakes were distinguished according to the number of production peaks during the ice-free season. Lakes with longer summer stratification tended to have two productive periods:

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one at the onset of stratification, and the other during the autumn overturn. Lakes with shorter stratification had a single peak during the ice-free period. All lakes presented deep chlorophyll maxima during summer stratification, and subsurface chlorophyll maxima beneath the ice. Phosphorus limitation was common to all lakes, since nitrogen compounds were significantly more abundant than the requirements for the primary production observed. The major chemical components present in the lakes showed a short but extreme dilution during thawing. Certain lake features may favour the recording of particular climatic fluctuations, for instance: lakes with two distinct productive periods, climatic fluctuations in spring or autumn (e.g., through chrysophycean cysts); lakes with higher oxygen consumption, climatic factors affecting the duration of the ice-cover (e.g., through low-oxygen tolerant chironomids); lakes with higher water retention time; changes in atmospheric deposition (e.g., through carbon or pigment burial); lakes with longer stratification, air temperature changes during summer and autumn (e.g., through all epilimnetic species).

Introduction

Remote mountain lakes above the treeline in sparsely vegetated catchments are suitable for studying the impact of weather and seasonal and long-term changes in natural ecosystems (Battarbee et al., 2002, this issue). The study of the meteorological forcing in these lakes is more direct than in lowland lakes, since they are not as affected by complex soil and vegetation responses and by human activities in their catchment, all of which might modify the external loading of carbon, nutrients, major ions and suspended sediments.

The physical conditions of mountain lakes undergo major seasonal changes, which affect the chemical and biological dynamics of the lake. The extent to which the various components of the lake ecosystem are affected may vary significantly depending on when the changes occur. The morphological and hydrological characteristics of the lake determine whether the responses of the ecosystem are recorded in sediments.

The ecosystem response is based on the differential growth of distinct components in the food web, which eventually modify fluxes of matter or, at least, assemblage composition. Differences can arise from changes in the length of the growing season of organisms, in their intensity of growth within a given period, or both. Changes in intensity might be related to variations in resource availability (nutrient loading, food availability), temperature, and environmental conditions (e.g., pH and oxygen), and may therefore favour the growth of certain species. Furthermore, some organisms may be more sensitive because of their habitat within the lake (e.g., epilimnion vs. hypolimnion, plankton vs. benthos) or because of their way of living (e.g., autotrophic vs. heterotrophic). The signal preserved has greater information for organisms that produce identifiable microfossils (e.g., diatoms, chrysophytes, cladocerans, and chironomids). Other sedimentary proxies

only record signals for a whole group (e.g., pigments for chlorophytes, dinoflagellates, cryptophytes) with the risk that responses from different species with contrasting behaviour may mask the signal. Finally, other organisms will lack any direct signal, and their fluctuations will only be recorded in a subsidiary way if they affect the bulk fluxes of organic matter to sediments.

This paper discusses the implications of seasonal ecosystem variability in remote mountain lakes as regards their capacity to record weather and climatic signals in sediments, particularly by means of biotic proxies. We describe the main patterns of seasonal ecosystem variability in nine remote mountain lakes at various locations throughout Europe, and discuss the features they share and the range of variability that can be expected in their behaviour. Finally, we discuss how some seasonal features and lake morphology affect the recording of climatic signals in the sediments of remote mountain lakes.

Site description and methods

The lakes studied cover a large latitudinal gradient within Europe (40–69° N) and most major mountain ranges were included (Figure 1). All lakes were situated above the treeline in similar alpine environments of small, steep, and sparsely vegetated catchments. The more extreme climatic conditions at the latitudes of Fennoscandia compensated for lower altitudes (Table 1). The lakes covered typical depth (9.4–73 m) and surface area (1.7–70 ha) ranges for alpine and subarctic lakes. However, the Fennoscandian lakes had much larger area/maximum depth ratios than those at lower latitudes.

A regular survey of a number of key descriptors of lake dynamics was carried out from July 1996 to August 1998. Temperature, oxygen, pH and chlorophyll-a were selected for the synoptic description of the seasonal

Table 1. Lake location and morphology, catchment features and sampling features at each site. Lakes are ordered from the shallowest to the deepest

	Laguna Címera	Gossenköllesee	Jezero v Ledvici	Hagelseewi	Øvre Neádašvatn	Saanajärvi	Laghetto Inferiore	Nižné Terianske pleso	Estany Redó
Latitude	40° 16' N	47° 13' N	46° 20' N	46° 40' N	62° 46' N	69° 03' N	46° 28' N	49° 10' N	42° 38' N
Longitude	5° 18' W	11° 0' E	13° 47' E	8° 02' E	9° 00' E	20° 52' E	8° 35' E	20° 00' E	0° 46' E
Altitude (m a.s.l)	2140	2417	1830	2339	728	679	2074	1941	2240
Mountain range	Gredos	Tyrolian Alps	Julian Alps	Central Swiss Alps	Caledonian	Northern Finland	Central Southern Alps	Tatra	Pyrenees
Maximum depth (m)	9.4	9.9	15	18	18	24	32.5	44.4	73
Mean depth (m)	4.8	4.7	5.7	8.3	4.0	5.1	10.5	18.4	32.3
Lake area (ha)	4.49	1.7	2.37	2.37	50	69.9	4.85	4.83	24
Lake volume (106 m ³)	0.217	0.08	0.135	0.197	1.996	3.6 *	0.511	0.891	7.750
Watershed area (ha)	85	20	not defined	36	1600	461	178	114	155
Renewal time (years)	0.2	0.2*	0.1	0.3*	0.07	1*	0.2	0.8	4
Watershed to lake area ratio	18.9	11.8	-	15.2	32.0	6.6	36.7	22.8	6.5
Main lithology	Granite	Granite, gneiss, amphibolite	Limestone	Limestone	Gneiss	Schist, gneiss and limestone	Gneiss, amphibolite	Granite	Granodiorite
Soil cover (%)	-	20	<10	-	40	-	7	50	60
Main vegetation	Alpine meadows	Alpine meadows	Alpine meadows	Alpine meadows	Alpine heath, pasture	Subalpine vegetation	Meadows and sparse shrubs	Alpine meadows	<i>Festuca eskia</i> meadows
Sampling period	Jul 96–Jul 98	Oct 96–Sep 98	Jun 96–Oct 98	Jun 96–Sep 98	Jul 96–Apr 98	Jul 96–May 98	Jul 96–Jul 98	Aug 96–Jul 98	Jul 96–Aug 98
Ice-free period sampling frequency	Biweekly	Weekly	Monthly	Monthly	3 times	Biweekly	Monthly	Monthly	Monthly
Ice-covered period sampling frequency	Biweekly	Weekly	3 times	Monthly	3 times	3 times	3 times	Biweekly	Monthly
Sampling depths	0.5, 2.5, 5, 7.5, 8.5 m	Every 1 m	Every 2.5 m	0, 3, 6, 9, 12, 15, 16 m	1, 3, 5, 10, 15 m	Every 2 m	Every 2.5 m	Every 4 metres	Every 3 m



Figure 1. Map indicating the location of the lakes.

variability of physical, chemical and biological properties of the lake. Nutrients, major ions and organisms were also measured in most of the lakes but at lower spatial and temporal resolutions. These complementary data were extensively reported in Straškrabová et al. (1999a). The sampling effort was adapted to the sampling facilities available for each lake, but common minimum requirements were established as follows: during the ice-free season the lakes were sampled at least monthly while during the ice-covered period a minimum of three times. For lakes shallower than 20 m, a minimum of five regularly spaced sampling depths were required, which covered the entire lake depth, while ten depths were established for deeper lakes. Temperature and oxygen were instrumentally measured every metre at the deepest part of the lake. Chlorophyll-a was extracted using acetone (90%) and evaluated spectrophotometrically using wavelengths and equations following Jeffrey and Humphrey (1975). Alternatively, for Nizné Terianske Pleso, chlorophyll-a was determined fluorometrically after extraction in a mixture of acetone and methanol (Fott et al., 1999). At the

beginning of the survey both methods were applied simultaneously and no differences in chlorophyll-a estimation were observed (Stuchlík, personal communication). Details on sampling, chemical and biological analyses and quality control are described in Wathne and Hansen (1997), The MOLAR Water Chemistry Group (1999), Straškrabová et al. (1999b).

Results

Thermal and mixing patterns

The lakes showed a distinctive seasonal thermal pattern, with a long ice-covered period, followed by rapid warming after melting, a short period of high heat content and a long cooling period until freezing (Figure 2). The peaks of the apparent heat fluxes depended on the sampling frequency; long sampling intervals tended to smooth out the values. However, the sampling frequency was sufficient to show that the deeper the lake, the larger the heat fluxes and the higher the seasonal

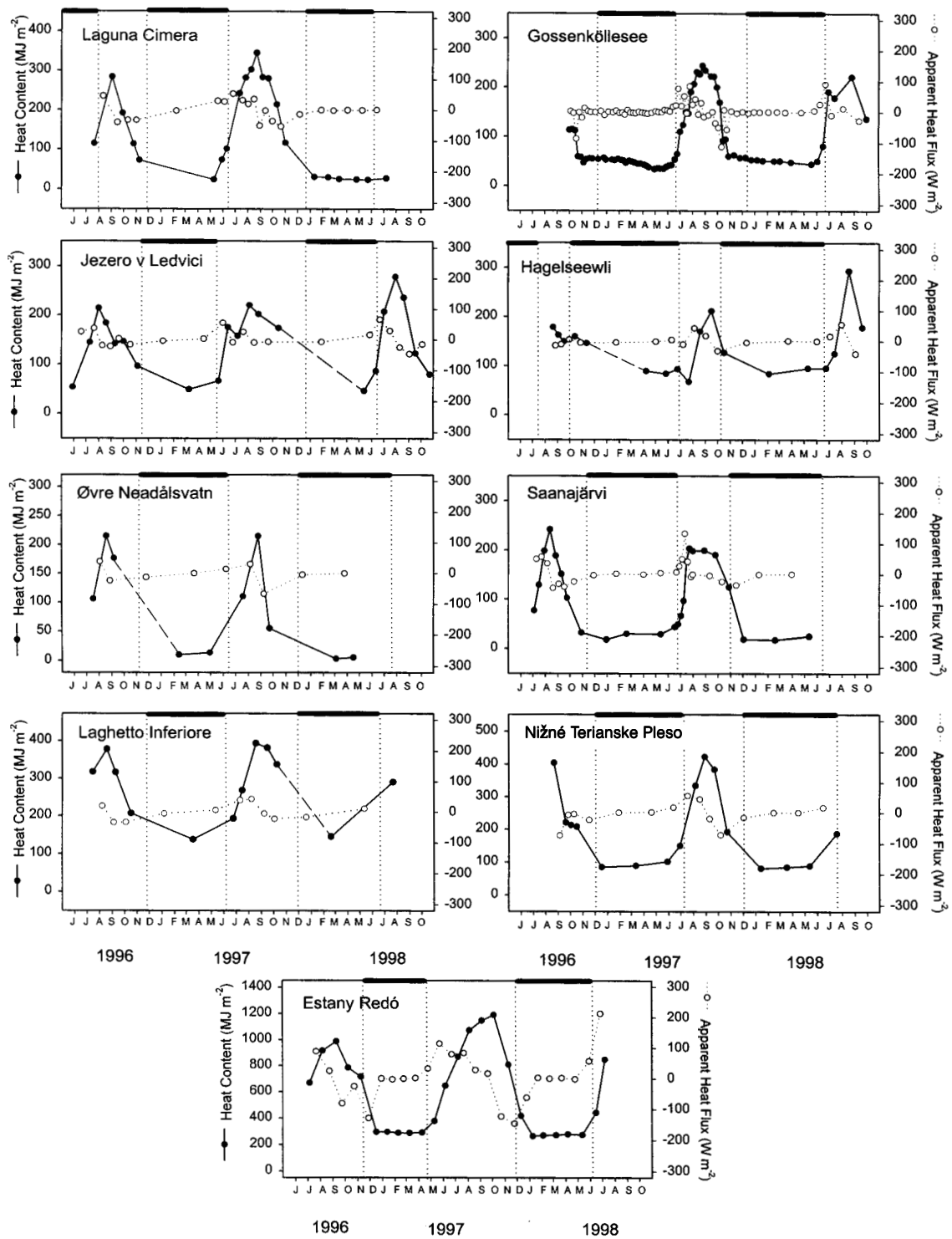


Figure 2. Seasonal changes in heat content and apparent heat flux in the lakes (inflow-outflow exchanges were not considered). The thick solid line indicates the ice-covered periods.

variability. Estany Redó, with the largest heat storage capacity, showed significantly larger cooling fluxes and for a longer period.

Heat exchanges determined a typical dimictic mixing pattern in most of these lakes, with an overturn during melting and a longer autumn mixing period associated with the deepening of the seasonal thermocline and eventual overturn. However, lakes with a large fetch compared to depth, such as Laguna Cimera and Øvre Neådalsvatn, experienced occasional episodes of whole lake mixing. The whole water column of these lakes behaved in a similar way to the epilimnion of other lakes – there was a permanently mixed surface layer and an inner layer that was normally stratified but which partially or completely mixed during episodes of high wind.

The wind speed necessary to start mixing the whole water column can be estimated using the Lake number (L_N), non-dimensional number that compares the stability of the water column with the disturbance caused by wind stress (Imberger & Patterson, 1990),

$$L_N = \frac{g S_t (1 - Z_T/Z_{max})}{\rho_a C_d U_*^2 A^{3/2} (1 - Z_{vol}/Z_{max})} \quad (1)$$

where g is gravity acceleration; Z_T , Z_{max} and Z_{vol} the thermocline, maximum and centre of volume depths, respectively, measured from bottom; ρ_a , air density, C_d , drag coefficient (0.0013); U_* , water friction velocity due to wind stress; A , lake area, and S_t , the Schmidt stability (Schmidt, 1928) defined as,

$$S_t = \int_{Z_o}^{Z_{max}} (Z_{vol} - z) A(z) \rho(z) dz \quad (2)$$

When $L_N = 1$, the whole water column is mixing and, if wind persists for long enough, the whole lake can be completely mixed. The seasonal thermocline was stable in most of the lakes, unlikely winds were required to obtain $L_N = 1$. However, in the long, shallow Laguna Cimera, wind speeds of 2–6 m sec⁻¹ sufficed to mix the lake during most of the ice-free period. Thermoclines were shallow (0.5–3 m) and ephemeral. Only during August were moderately strong winds (8–10 m sec⁻¹) required to mix the lake; deeper thermoclines (5–7.5 m) persisted for a few days during this month.

All the lakes were cold, being ice-covered for 5–9 months and having minimum bottom temperatures of between 1 and 4 °C. The lowest bottom temperatures were measured in Fennoscandian lakes. In these lakes, particularly in Øvre Neådalsvatn, the cooling of lake water continued for several months, while in alpine

lakes, snow decreased the heat exchange shortly after ice formation. Consequently, the thickness of black (clear) ice was greater in the former (up to 60 cm in Øvre Neådalsvatn in mid-winter) than in the latter (maximum of 30 cm). Maximum surface temperatures were reached during summer stratification, when differences between epilimnion and hypolimnion were as high as 10 °C in some lakes. Epilimnetic temperatures ranged between 10 and 15 °C, with the exception of the southernmost Laguna Cimera (18 °C).

Figure 3 shows the number of days in which a given temperature was recorded in the water column of a lake. In the shallow lakes (depth < 10 m), such as Laguna Cimera and Gossenköllesee, nearly the whole volume showed significant temperature changes throughout the year and two thermal states were observed: a long cold period (0–5 °C) and a short warmer one (10–14 °C). The transition through intermediate temperatures was rapid. Øvre Neådalsvatn, a slightly deeper (15 m) but much larger lake situated at higher latitude, also showed a similar pattern of temperature change, but the warm phase was short. In the lakes deeper than 10 m, there was a sharp transition in the thermal regime at specific depths (Jezero v Ledvici at 5 m; Hagelseewli at 8 m; Saanajärvi and Laghetto Inferiore at 10 m; Nižné Terianske Pleso and Estany Redó at 21 m), which divides the lakes into two distinct habitats in terms of temperature fluctuations. The upper layer showed a pattern similar to that in shallow lakes, with two extreme situations and a rapid transition between. An exception was Hagelseewli, which did not warm in summer. This lake is located close to a large cliff that keeps it in the shade for most of the year (Livingstone et al., 1999; Goudsmit et al., 2000). Within the shallower and warmer upper layer of most lakes, we also distinguished a sub-layer with an enhanced pattern. This layer (usually the first 3–5 m) corresponded to the permanently mixed surface layer during summer and the zone of direct ice-cover influence in winter. The bottom layer, comprising 40–50 % of the lake volume and corresponding to the summer hypolimnion, showed much less temperature oscillation, with nearly constant temperatures (2–4 °C, depending on the lakes) prevailing for half of the year.

Production and respiration patterns

The oxygen concentration in a lake is indicative of the balance between respiration, production and the exchange between water and air. The lakes were well-oxygenated during most of the year, with values close

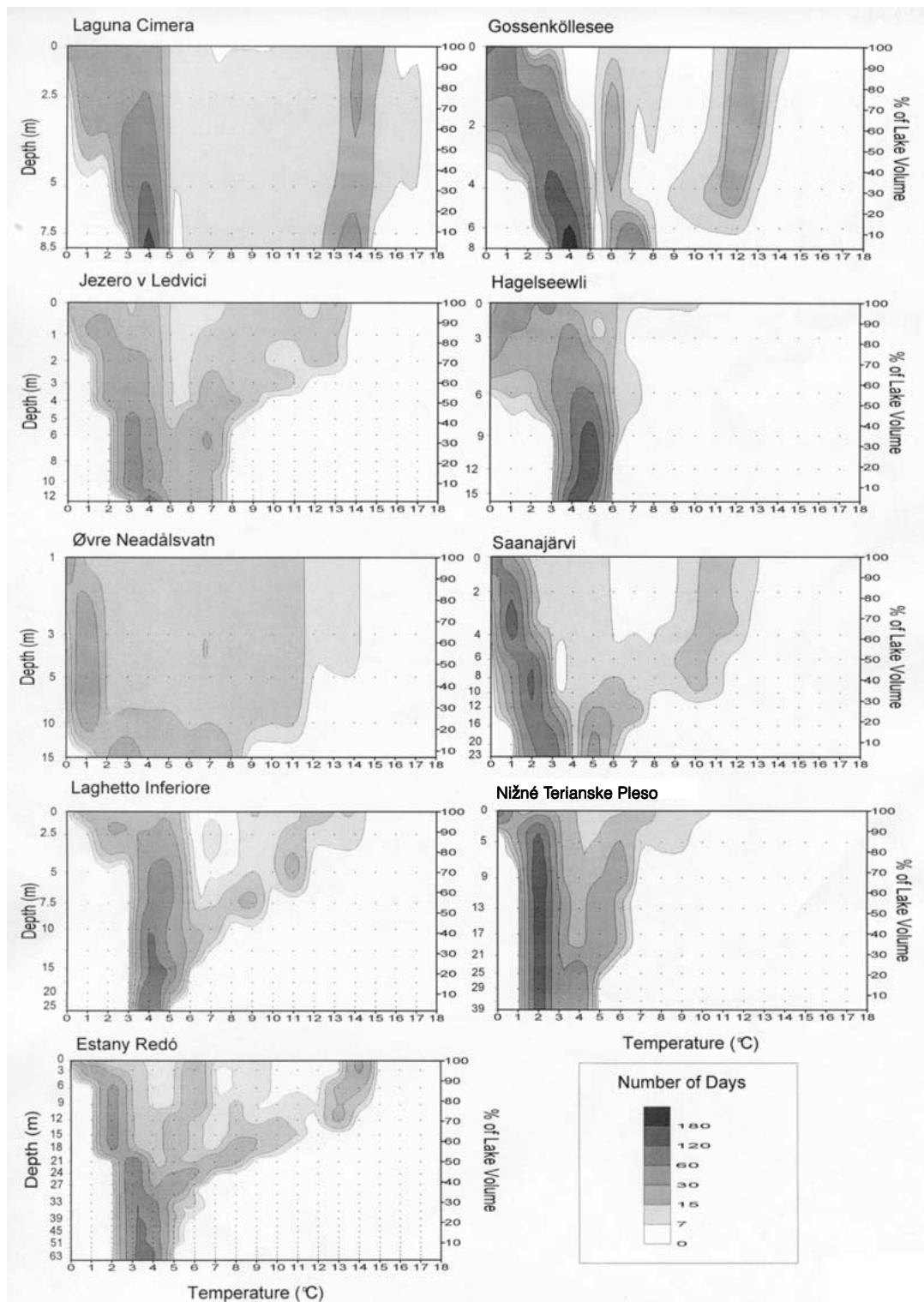


Figure 3. Isopleth diagrams showing the number of days that a lake layer remained at certain temperatures. Depth is scaled to lake volume percentages to illustrate the proportion of lake volume experiencing a given temperature. Number of days were estimated linearly by interpolating the temperature measurements to obtain daily values and then by counting the days a temperature was observed at each depth considering intervals of half a degree.

to saturation (Figure 4). However, all the lakes showed characteristic oxygen depletion during the ice-covered period. Bottom water values of about $1 \text{ mg O}_2 \text{ l}^{-1}$ were reached, indicating anoxic conditions at the water-sediment interface for a part of the ice-covered period. The rate of oxygen depletion was more pronounced in the small and shallow lakes, such as Laguna Cimera, Gossenköllesee and Hagelseewli, which also had the highest mean chlorophyll-a values (Thies et al., 2000). During the ice-free period, oxygen over-saturation occurred within the metalimnion and upper hypolimnion, and only the deepest lakes presented under-saturation in the deepest layers. Therefore, the annual cycle of the lakes was clearly divided into a predominantly productive period and an ice-covered period dominated by respiration and lack of aeration.

Further details of production patterns were provided by data on the changes in chlorophyll-a. In general, the deeper the lake the larger the accumulation of chlorophyll-a in the water column (Figure 5) but the lower the mean concentration. The average chlorophyll-a (Chl) was very low ($\leq 1 \mu\text{g l}^{-1}$) in most lakes, and slightly higher in the shallowest lakes ($2\text{--}3 \mu\text{g l}^{-1}$). Lakes with low averages showed peaks below $5 \mu\text{g l}^{-1}$, while those with higher averages showed peaks around $10 \mu\text{g l}^{-1}$.

Each lake had its own seasonal pattern, but this was similar for the two years studied. In lakes with a short ice-free season, a single peak of chlorophyll occurred from late August to October. Lakes with longer ice-free periods tended to have two chlorophyll peaks, one at the beginning of the ice-free season (July, August) and the other at the end. The absolute and relative magnitudes between the two peaks differed from lake to lake and from year to year within a lake.

In all lakes, a distinctive deep chlorophyll-a maximum occurred during summer stratification (Figure 6). In shallow lakes, the maximum was found close to the bottom (e.g., Laguna Cimera, Gossenköllesee, Hagelseewli), and in deep lakes in the lower part of the metalimnion (e.g., Saanajärvi, Nižné Terianske Pleso, Estany Redó). These maxima formed quickly after the onset of summer stratification. During the spring overturn, chlorophyll-a was low in all lakes. The deep chlorophyll-a maximum pattern lasted until the deepening of the seasonal thermocline reached fine sediments, which are usually located below the mean depth in this type of lake (e.g., October in Laguna Cimera and Hagelseewli; late August in Saanajärvi; end of September in Nižné Terianske Pleso; and November in Estany Redó, Figure 6). Then, chlorophyll values were higher within the mixed layer. After freezing, in some lakes a

sub-surface peak of chlorophyll-a formed, which progressively decreased throughout the winter. In Gossenköllesee, the chlorophyll peak under ice coincided with the annual peak (Thies et al., 1999) and was caused by *Cyclotella* growth (Koinig et al., 2000). In the lakes where chlorophyll-b and chlorophyll-c were estimated, it appeared that the proportion of the latter increased during phases of increasing chlorophyll-a, whereas that of chlorophyll-b rose in more stable or decaying periods (Figure 7). The phaeopigment ratio (A430:A410) indicated that senescent algal material mainly accumulated in deep water during ice cover (Figure 8), although patterns varied from lake to lake. In the shallow Laguna Cimera, fluctuations throughout the year were significantly larger than in deeper lakes, since in this lake chlorophyll-a maxima appeared close to the sediments in summer, and, due to the physical instability of the water column, resuspension of benthic algae was likely. However, even in the deepest lake, the differences in the degradation state of the algal material deposited between the ice-free and ice-covered period were quite significant.

The increase in chlorophyll-a when mixing reached the fine sediments indicates that internal loading drives seasonal productivity. Since the ratio of nitrogen to phosphorus was well above that of the Redfield ratio (Redfield et al., 1963) (Figure 9), the latter seems to be the limiting nutrient. Ammonium was low throughout most of the year ($< 2 \mu\text{mol l}^{-1}$), although significantly high values were observed during the melting of the snowpack ($5\text{--}40 \mu\text{mol l}^{-1}$), depending on the atmospheric long-range pollution at each site. In contrast, nitrate concentrations were higher in all lakes than those of ammonium, and differences among lakes reflected the distinct atmospheric loading of nitrogen among regions, as lakes in northern Norway, Finland and southwestern Spain showed significantly lower values than those in the Alps and Tatra mountains ($> 10 \mu\text{mol l}^{-1}$). The lakes with low nitrate levels revealed a higher variability in concentration than those with high nitrate values, suggesting that in the former nitrogen and phosphorus may alternate as limiting nutrients during the year. In the areas with high nitrogen deposition, nitrate in lake water was high throughout the year, and episodic low values occurred during the melting of the snowpack and the concomitant short dilution of lake water.

Data on silicate were available for only some of the lakes (Figure 9). Large differences between lakes and significant oscillations within lakes were observed. Planktonic diatoms were scarce in lakes with low sili-

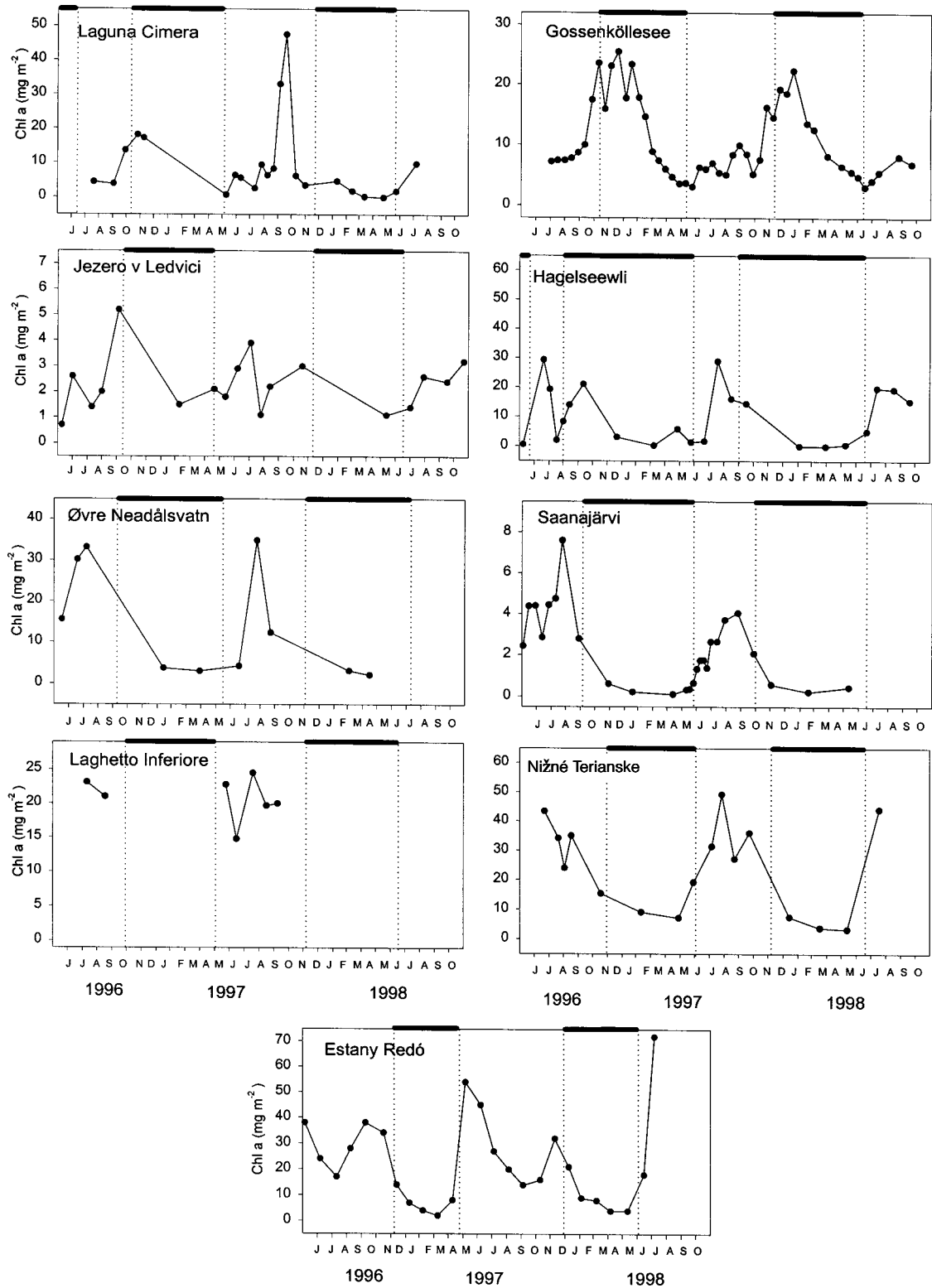


Figure 5. Seasonal changes in chlorophyll in the lakes. The thick solid line on top of the plots indicates the ice-covered period.

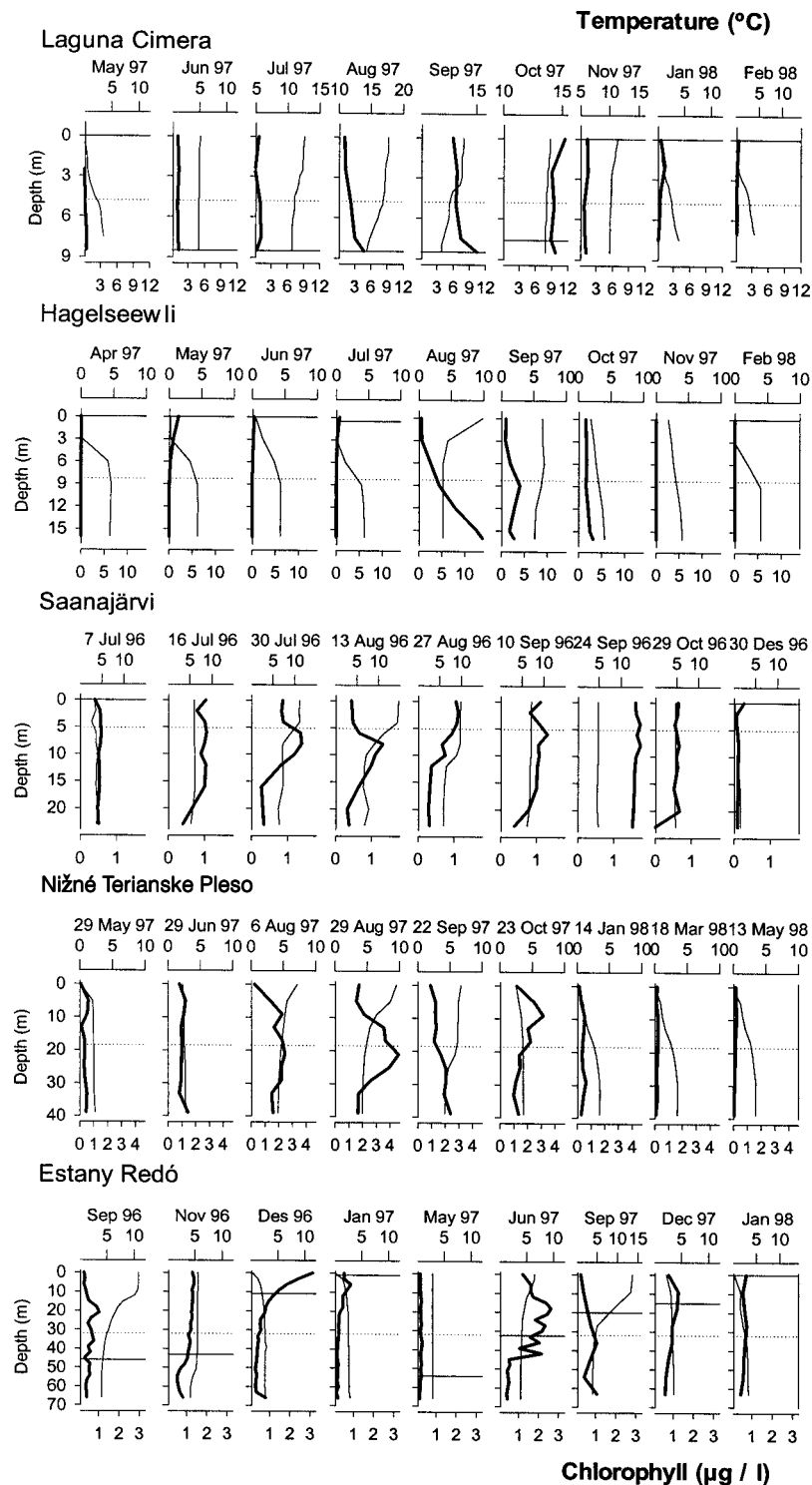


Figure 6. Profiles of chlorophyll (thicker line) and temperature (thinner line) selected to illustrate the vertical patterns throughout the year of certain representative lakes. The mean depth (dotted line) and photic zone (solid line) are indicated to illustrate the critical depths in each lake. The photic zone limit was estimated as 2.7-fold the Secchi disc depth during the ice-free period, and according to Catalan (1988) during the ice-covered period, considering the snow and ice cover structure.

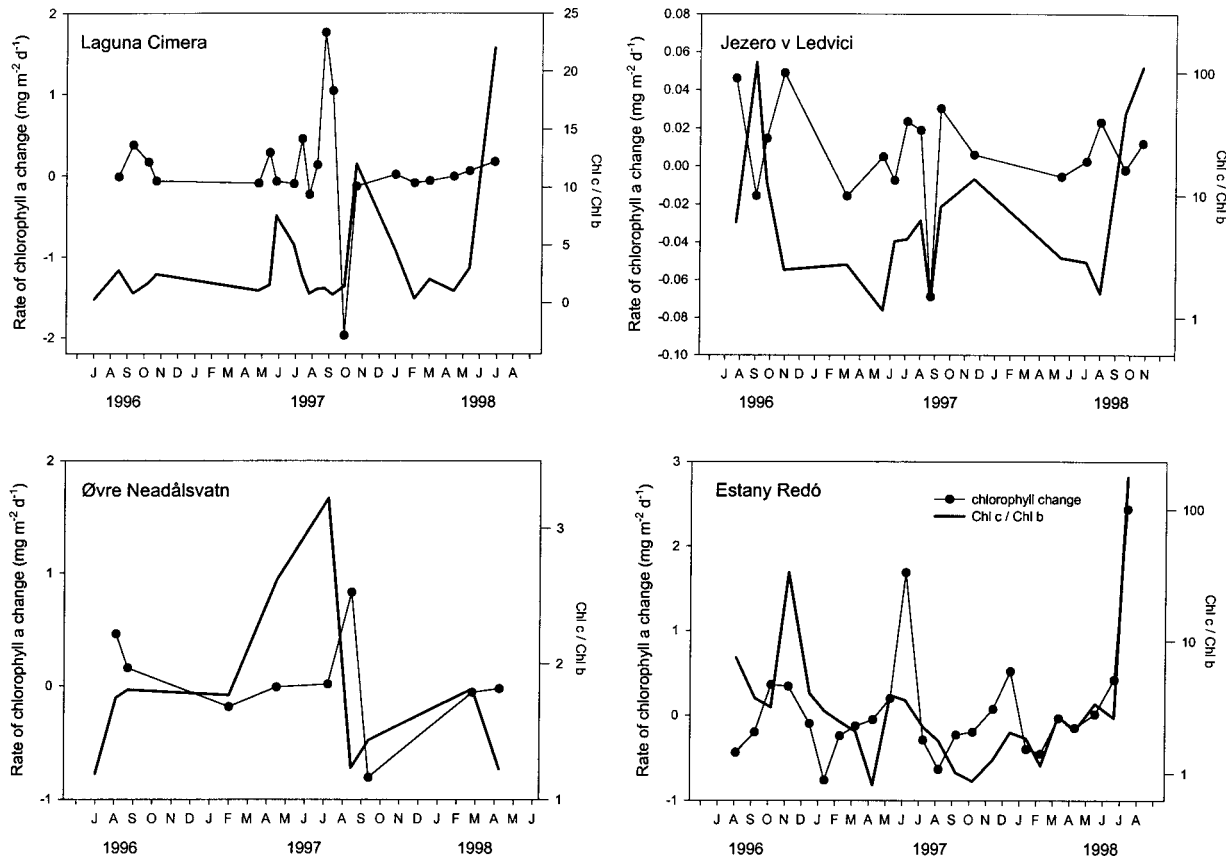


Figure 7. Plots of the rate of chlorophyll-a change and the ratio between chlorophyll-c and chlorophyll-b for lakes where the three types of chlorophyll were estimated as proxies for total phytoplankton, chlorophytes and chrysophytes+diatoms, respectively.

cate levels (Felip et al., 1999; Fott et al., 1999; Simona et al., 1999), while those with a higher concentration showed rich and diverse *Cyclotella* populations (e.g., Gossenköllesee) (Konig et al., in press). Nevertheless, more data are needed to give a conclusive interpretation of this relationship.

Variability in major chemical features

Some major chemical features (e.g., alkalinity, sulphate, dissolved organic carbon) are key factors in determining differences in organism composition between lakes (Margalef, 1983). The seasonal variability of these features within lakes was very low (Figure 10) and concentrations remained largely constant except during thaw, when differential migration of ions within the snowpack periodically caused short events of very low concentrations, preceded by a similar short-term increase in major ions. The within-lake alkalinity production during winter was low in all lakes, being

drastically compensated by the dilution phase during ice-melt, which was also an acidic pulse. Overall, the pH fluctuations during the rest of the year were negligible and mainly related to production-respiration patterns. Fluctuations in pH were more noticeable in the layers corresponding to the hypolimnion, because of the CO_2 up-take for photosynthesis in the deep chlorophyll maximum during summer, and release of CO_2 by respiration during ice-cover. Dissolved organic carbon (DOC) was generally below 1 mg l^{-1} and showed no apparent seasonal pattern in the lakes where it was measured (Gossenköllesee (Thies et al., 1999), Nižné Terianske Pleso and Estany Redó (Ventura et al., 2000)).

Discussion

Two main types of signals in the sediment record can reveal the effects of weather and climate on lake ecosystems (e.g., Schindler, 1997). On the one hand, the

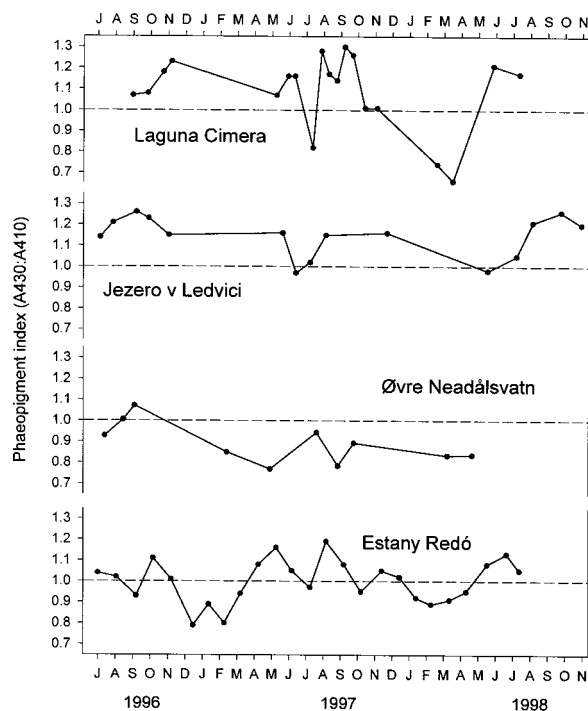


Figure 8. Phaeopigment index for the deepest part of the lakes during the study period (Laguna Cimera 8.5 m, Jezero v Ledvici 12.5 m, Ovre Neådalsvatn 15 m, Estany Redó 63 m).

signals related to the biogeochemical functioning of the lake, which comprise sediment parameters such as carbon content, metal composition, sub-fossil pigments, etc. The fluctuations of these parameters are mainly related to how climate affects the transport involved in the production, and decomposition processes of the lake. On the other hand, the remains of organisms may provide better information on climatic fluctuations, especially where changes in the seasonal characteristics of climate change the dynamics of the populations of some species.

Sensitivity of ecosystem productivity to climate change

The development of chlorophyll maxima deep in the water column in the lakes studied is indicative of a high response potential to any enrichment in nutrients, either external or internal. Any enrichment by external loading will cause an increase in production. However, we have no data on the variability of external nutrient loading and the extent of its dependence on climate and weather fluctuations in remote mountain lakes (Thies et al., 1998). A large proportion of the catchment of

most of the lakes studied consists of bare rock or lithosols and, when present, soils are thin and poor. Therefore, the direct fertilising effects of atmospheric deposition cannot be excluded. Snow cover accumulated during about half a year may be a potentially significant source of nutrients to the lake (Nickus et al., 1998). Phosphorus rather than nitrogen is the primary limiting factor for production – however, further studies on the variation of external loading of phosphorus over the season and how this loading can be affected by climate change are required (Catalan, 2000). In some cases, the factors which affect external nutrients are bizarre, such as the case of Jezero v Ledvici, where it has been found that land-slides linked to earthquakes play a significant role in nutrient enrichment (Brancelj et al., 2002, this issue).

Due to the effects of climate on mixing, the internal loading of nutrients changes. Figure 11 illustrates a simplified view of lake productivity (Catalan, 1991). The lakes studied here are largely deficient in phosphorus, so we can assume that the annual production of the water column is mainly driven by the amount of phosphorus made available to the column by internal and external loading. Production in the water column will eventually be either exported from the system through outflow or will sink and contribute to an increase in the stored pool in the active sediment. We can characterise this partition by non-dimensional sedimentation coefficient (s) that will depend on the opposing influences of sedimentation and flushing rates,

$$s = 1 - \frac{z_{\text{mean}}/v_s}{t_r} \quad (3)$$

where z_{mean} is the mean depth; v_s , a mean sedimentation velocity; and t_r is the renewal time. The mean velocity of sedimentation depends on the phytoplankton composition over the year. Diatoms may sediment at a rate of 0.6–0.8 m day⁻¹ (Reynolds, 1997), but they are rare in the plankton of the lakes studied (Straškrabová et al., 1999b); and, at the other extreme, the sedimentation in winter, when small cells predominate, is about 0.14 m day⁻¹ (Catalan, 1992). Given the size of most phytoplankton species during the ice-free period, a reasonable estimate of the mean sedimentation velocity for the lakes studied is ca. 0.25 m day⁻¹. Based on this assumption, the sedimentation coefficient for these lakes will vary between 0.37 (Øvre Neådalsvatn) and 0.94 (Saanajärvi and Laghetto Inferiore).

Within the sediment, part of the phosphorus of the stored pool will become available and will be returned

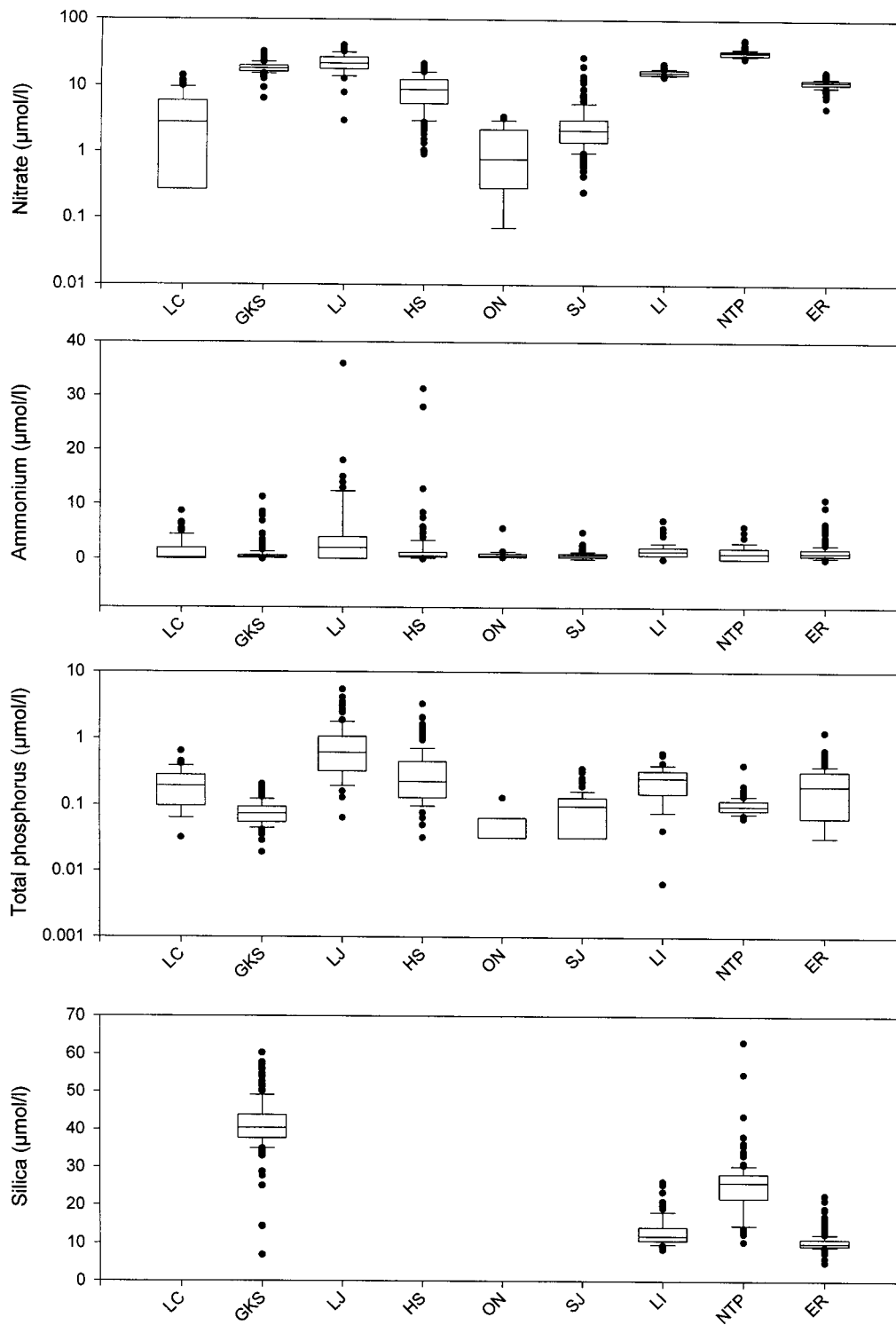


Figure 9. Box plots of nitrate, ammonium, total phosphorus and silica for the lakes (LC, Laguna Címera; GKS, Gossenköllesee; LJ, Jezero v Ledvici; HS, Hagelseewli; ON, Øvre Neådalsvatn; SJ, Saanajärvi; LI, Laghetto Inferiore, NTP, Nižné Terianske Pleso; ER, Estany Redó). 10%, 25%, 50%, 75% and 90% percentiles are indicated.

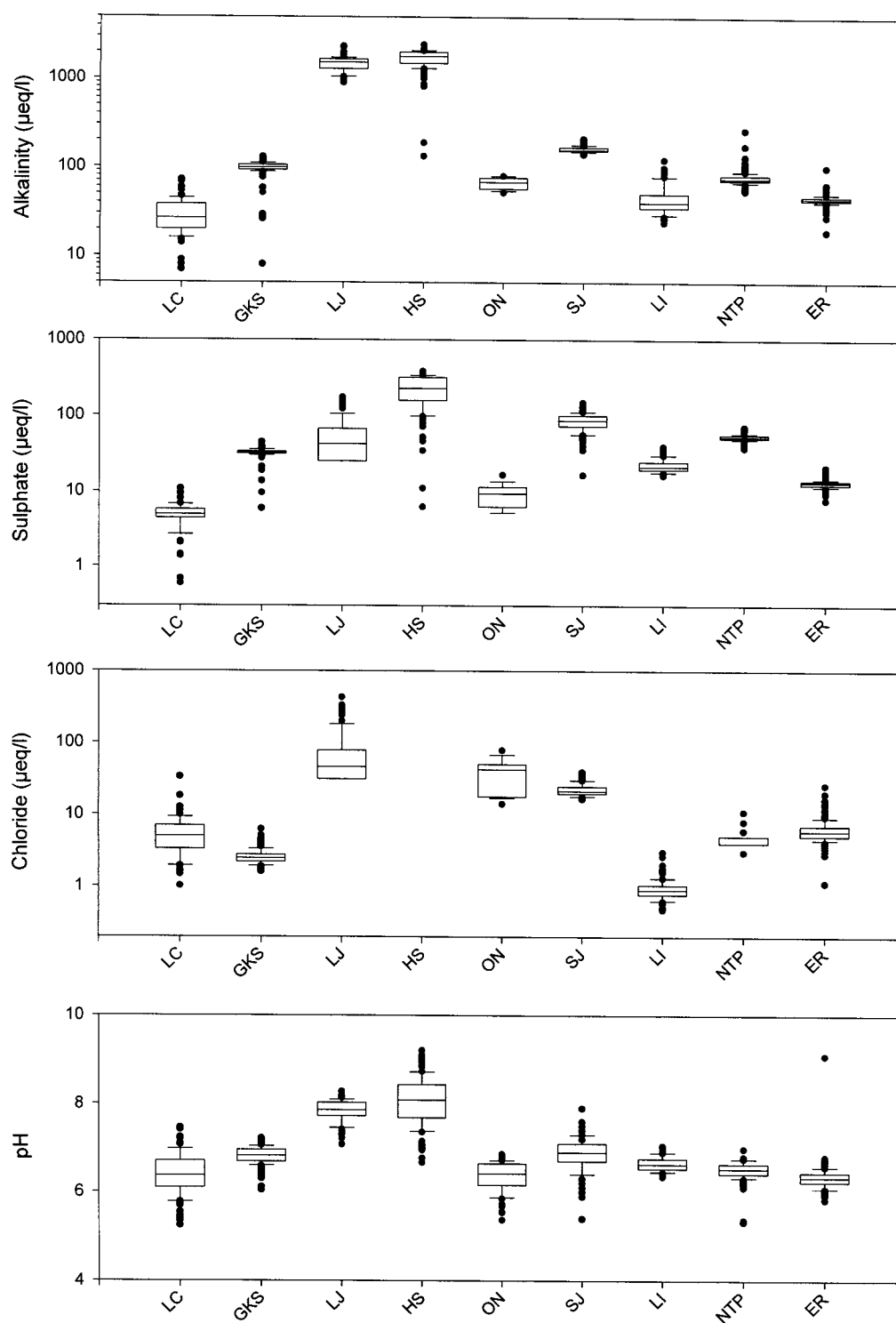


Figure 10. Box plots of alkalinity, sulphate, chloride and pH for the lakes (LC, Laguna Cimerá; GKS, Gossenköllesee; LJ, Jezero v Ledvici; HS, Hagelseewli; ON, Ovre Neädalsvatn; SJ, Saanajärvi; LI, Laghetto Inferiore, NTP, Nižné Terianske Pleso; ER, Estany Redó). 10%, 25%, 50%, 75% and 90% percentiles are indicated.

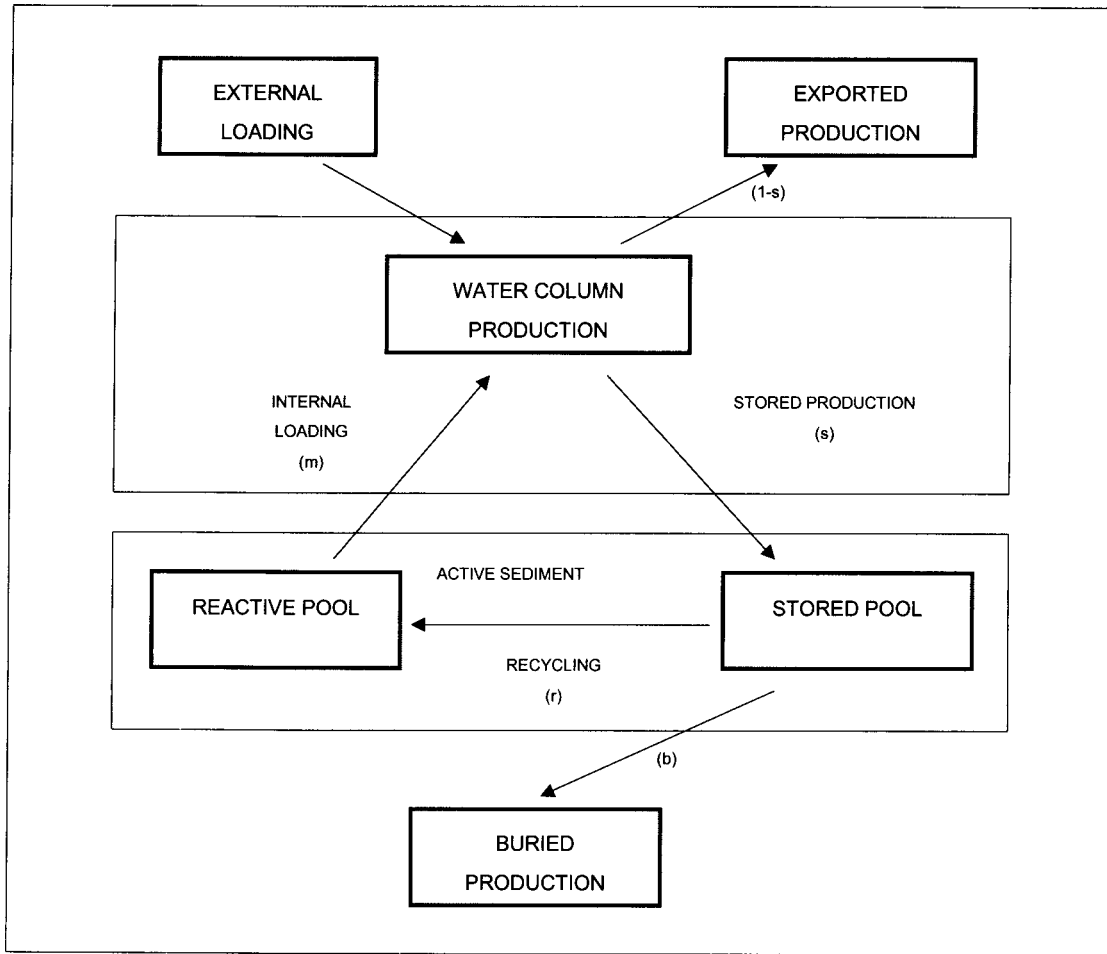


Figure 11. Simplified scheme of the relation between water column production, external and internal loadings of phosphorus and the buried production as a recorded signal of lake productivity.

to the water column. The recycling rate, which controls the path from the stored to the reactive pool, depends on the pH and redox conditions in the sediments (Stumm & Morgan, 1981). The higher the oxygen depletion in deep waters (which for a given lake is related to the duration of ice-cover), the higher the available free phosphorus in the sediments. Since transport by molecular diffusion from the top of the sediment is very slow, periods of mixing will enhance transport. On the other hand, part of the stored pool will be permanently buried and therefore the production signal is recorded in the sediments. If the burying depends mainly on the sediment accumulation rate, we can assume that the buried production will be a fraction of the stored pool proportional to the sediment accumulation rate. The dynamics of such a system can be described by the following equations,

$$\frac{\partial R}{\partial t} = rS - mR \quad (4)$$

$$\frac{\partial W}{\partial t} = aE + mR - lW \quad (5)$$

$$\frac{\partial S}{\partial t} = s l W - S(r + b) \quad (6)$$

where aE is the annual external loading (MT^{-1}); W , S , R are, respectively, the water column, stored and reactive pools (M); m , l , r and b are the mixing, loss, recycling and burying rates (T^{-1}), respectively; and s , is the non-dimensional sedimentation coefficient.

We can assume that, annually, the water column pool will either export or sediment, thus $l = 1 \text{ year}^{-1}$. In a

steady state, the values in the different compartments (water column production, reactive pool, stored pool) can be expressed as a function of external loading and the coefficients of sedimentation (s), recycling (r) and burying (b). For instance, the increase in the water column pool (production) caused by internal loading with respect to production based on external loading is given by,

$$W/E = 1 - \frac{rs}{rs - r - b} \quad (7)$$

and, the buried production with respect to external loading by,

$$B/E = 1 - \frac{-sb}{rs - r - b} \quad (8)$$

The latter expression allows us to analyse the suitability of lakes for recording climate change. Figure 12 plots the results of a simulation using a range of values for r (0.3–0.8 year⁻¹) and s (0.3–0.95) which probably cover most remote mountain lakes. To simplify the analysis, we assumed a constant value of 0.05 year⁻¹ for b , after considering a characteristic thickness of about 1 cm for the active sediment, and a sediment accumulation rate of 0.05 cm year⁻¹.

The model output suggests that, for a given external loading forcing lake production, the recorded signal (buried production) may vary up to an order of magnitude under different hydrological and climatic conditions (Figure 12). Plotting the position of the lakes studied on the graph, according to the estimated r and s values, allows us to identify their sensitivity to record a change in (r) as a proxy for the duration of the ice cover (thus inversely related to air temperature), and (s) inversely related renewal time (thus inversely related to changes in total deposition for a given lake). In the graph, sensitivity to (s) is shown by the distance between consecutive isolines – the closer the lines the less sensitive the buried production is to fluctuations in (s), thus to deposition. Sensitivity to (r) is indicated by the slope of the (s) isolines – the steeper the lines the more sensitive the buried production is to changes in (r), thus to ice-cover duration. In general, the potential changes due to fluctuations in (s) within a fixed (r) are larger than the changes due to fluctuations in (r) at a fixed (s). Therefore, according to this model, lake productivity is more sensitive to a change in deposition than to ice-cover fluctuations. However, there may be significant differences between lakes. The less sensi-

tive ones lie in the lower right corner of Figure 12, and the most sensitive in the upper left part. Therefore, among the lakes studied, particularly Øvre Neådalsvatn and Hagelseewli appear to be unsuitable for recording weather and climatic fluctuations in terms of productivity. However, whereas the latter might increase its sensitivity with increased warming, Øvre Neådalsvatn can hardly increase its sensitivity under any climatic scenario.

The model also shows that changing the buried production without significantly changing the external load is difficult in all lakes. This result emphasises the need to study the catchment processes which affect runoff characteristics and how they are affected by climate in remote mountain areas. Moreover, lakes are only close to a steady state or in a transient state, and therefore we can conclude that recording climate changes in terms of variations in productivity is only feasible under severe fluctuations or persistent long trends. Species growing exclusively or predominantly in one of the productive periods of the year may be more appropriate for recording weather fluctuations and climate changes in sediments, even if annual productivity is not significantly affected. Amongst algae, planktonic species show more seasonality than benthic species. Thus, it is likely that early responses to trends or finer tuning with fluctuations could be found in the former;

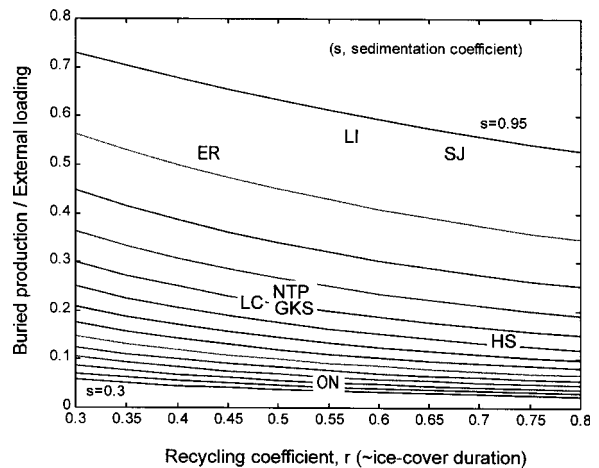


Figure 12. Mapping of the relationship of the buried production normalised to external loading with the recycling coefficient (assumed to be a function of the ice-cover length) and the sedimentation coefficient (assumed to be a function of the renewal time). Lines indicate isolines of equal sedimentation coefficient (s), from 0.3–0.95 at 0.05 intervals. The slope of the lines indicates the sensitivity of the buried production to changes in the recycling coefficient and the density of lines to changes in the sedimentation coefficient.

particularly when climate change is short-term. Species with chlorophyll-c (diatoms and chrysophytes) are particularly dominant during the growing phases of total phytoplankton biomass. Since both groups leave microfossil records, it is likely that changes in productivity patterns could be recorded in the sediments by fluctuations in assemblage percentages.

Sensitivity of the species to seasonal changes

Differential growth of species may result from changes in either the availability of resources they require (e.g., light, nutrients, prey) or in environmental conditions (e.g., temperature, pH, oxygen saturation). The biota of lakes includes species with contrasting generation times, which cover from a few hours to several years. Therefore, the sensitivity and time responses of community components may be quite different. Many present a preference for growing in a particular season, therefore the probability that their population dynamics will be affected by climatic changes that occur in that season is higher.

Throughout the year, the environment in the lakes studied showed periods of certain stability followed by short episodes of sudden and significant changes. This sequence of change permits a partition of seasonality to be defined, which may be a useful conceptual reference for the purpose of our discussion. The beginning of the periods considered can be defined as follows: overturn, when the mixed layer reaches mean depth; clear-cover, when the lake freezes; opaque-cover, when snow accumulation reduces penetration of photosynthetically active radiation to < 1% of radiation outside the lake; thaw, when the ice-cover breaks along the shoreline because of an increase in water level due to the thawing of snow in the catchment; and, finally stratification, when the surface water reaches 4 °C. In Table 2, we give an estimation of the length of each period in the lakes studied.

Overturn period: solar radiation decreases rapidly in autumn, and air temperatures are low, the deepening of the seasonal thermocline accelerates. When the mixed layer reaches the mean depth of the lake, or slightly deeper, it enters in contact with fine sediment (Catalan, 1988) and transport from the active surface sediment to the water column is enhanced. The response of phytoplankton production was quite different among the lakes (Figure 5). A significant increase in chlorophyll was mainly found in lakes with a relatively long stratification period (Gossenköllesee, Jezero v Ledvici, Estany Redó), suggesting that after spring mixing, some time is required to refill the free phosphorus in sediment porewater. Since the growing conditions for phytoplankton are quite different from the previous period because of mixing, a significant number of the species might be characteristic of this period, at least in those lakes that show an increase in production. This is the case for Gossenköllesee and Estany Redó where characteristic diatom and chrysophytes have been found (Pla, 1999; Koinig et al., 2000). The sediment record of these species may be indicative of fluctuations in the duration of summer stratification.

Clear ice-cover period: when lake temperature drops below 4 °C, rapid cooling brings the water surface to the freezing point, because of the change in buoyancy behaviour that restricts heat lost to the upper layers. A transparent ice sheet develops, but light can still penetrate to a significant depth, thus allowing episodic high productivity under the ice (Catalan & Camarero, 1991). The chlorophyll distribution below the ice suggests that this is a common feature for most of the lakes (Figure 6). However, a slight chlorophyll increase does not necessarily mean a productive peak. Suppression of wind permits a redistribution of chlorophyll depending on the light field and, in addition, the chlorophyll content per cell can increase because of acclimation to low irradiance (Felip & Catalan, 2000). In Gossenköllesee, peaks under the ice are much higher than in the other

Table 2. Estimated duration (months) of the different seasonal periods in the study lakes

Lake/Period	Overturn	Clear-cover	Opaque-cover	Thaw	Stratification
Laguna Cimera	3	0.5	5	0.5	3
Gossenköllesee	1.5	0.5	5.5	1	3.5
Jezero v Ledvici	3	0.5	5.5	0.5	2.5
Hagelseewli	0.5	0.5	8	2	1
Øvre Neådalsvatn	2	2	4.5	1	2.5
Saanajärvi	1	2	6	1	2
Laghetto Inferiore	1	1.5	5.3	1	3.2
Nižné Terianske pleso	2.5	0.5	5.5	1	2.5
Estany Redó	1.5	0.5	4.5	1	4.5

lakes (Figure 5). In this case, gentle convective mixing, induced by radiation heating, favours the growth and suspension of small planktonic diatoms (*Cyclotella*) in a way not found in any of the other lakes studied. During clear-ice cover the lake is still cooling, thus the longer this period the thicker the ice sheet and the lower the temperature within the lake for the rest of the ice cover period. Consequently, the Fennoscandian lakes (Øvre Neådalsvatn, Saanajärvi) show lower winter temperatures (1–2 °C) in the whole water column than the rest of the lakes (3–4 °C) (Figure 3). It is unknown if this slightly lower temperature significantly affects organisms. Except for lakes with peculiar communities, such as Gossenköllesee, sediment signals corresponding to changes in this period are probably difficult to detect.

Opaque ice-cover period: the below-ice growing phase finishes as soon as enough snow accumulates to prevent light penetration. Most of these lakes easily accumulate more than one meter of snow. Then, a period of usually several months starts in which phytoplankton and non-living suspended matter slowly sink. The oxygen consumption progressively produces an under-saturation that is higher in the deepest layers because of the large sediment surface (Figure 9). In other studies, it has been shown that CO₂ production from the decomposition of organic matter causes the pH to fall (Psenner & Catalan, 1994), and there is a point at which these trends allow the diffusion of reduced ions from the sediment (e.g., Mn²⁺, Fe²⁺) (Catalan, 1992), nutrients (SRP) and cations (Ca²⁺, Na⁺) (Catalan & Camarero, 1993). The long duration opaque-cover appears to render ecosystems relatively insensitive to air temperature fluctuations during winter and early spring, unless the duration of the ice-cover is affected.

Climate change and weather fluctuations can leave their mark on the sediment record by modifying the habitats within the lake. The period of opaque-cover is the longest in the seasonal divide and the only one that is exclusively respiratory. Apart from providing signals through their influence on biogeochemical pathways, we would expect oxygen levels, to provide a signal as an environmental factor which conditions the survival of species. The extent of the hypoxic sediment surface during winter could be a key factor in recording climate signals, e.g., affecting the relative abundance of low-oxygen resistant chironomids (Granados & Toro, 2000). Lakes with high oxygen consumption rates may react more strongly to fluctuations in the length of cover, hence we may expect signals that better match extreme events within the range of inter-annual variability. Lakes with low rates are perhaps

better recorders of long-term trends. Calibration of an oxygen factor (e.g., relating microfossils with, for instance, percentage of sediment surface below 50% oxygen saturation after 3 months) may well be a useful proxy for reconstructions of ice-cover length over long time scales. The shallower the lake (Laguna Cimera, Gossenköllesee) the larger the percentage of water volume and sediment surface affected by low oxygen content. The higher deposition of phaeopigments during ice-cover is another potential sign of the length of this period (Figure 8); however, this signal may be altered by degradation of the chlorophylls in the sediments, which depend on oxygen levels and pH (Guilizzoni et al., 1992).

As mentioned above, the ice-covered period is also the time in which the internal generation of alkalinity occurs. Although, at first, we might expect a shift in species related to variations in alkalinity, because some groups are particularly sensitive (diatoms, chrysophytes), response to annual variability is unlikely: the increment in alkalinity produced by the longer duration of the ice-cover can be largely offset by the acidic event during thaw, which is produced by the differential elution of ions. It seems more likely that the external supply of alkalinity during ice-free periods plays a more relevant role as suggested by Sommaruga-Wögrath et al. (1997). An improved understanding of catchment processes is necessary to clarify this point.

Thaw period: the transition between the ice-covered and ice-free period is characterised by a relatively quick and spatially heterogeneous melting of the snow and ice cover, followed by deep mixing while warming, and by a high flushing rate of the lake because of the thaw of the catchment snowpack (Catalan, 1988, 1989). The light environment in the water column quickly changes from darkness to the highest radiation levels during the year. The biological response during this period is probably highly conditioned by the renewal time of the lake, but remains to be elucidated. In small, shallow lakes the plankton community can be washed out. In deep lakes, water flushing occurs mainly within the upper layers (0–15 m), deep layers being insignificantly affected during peak water flow (Barbieri & Mosello, 2000). When flow decreases and convection drives deep mixing, phytoplankton communities are stressed by high dilution, a fall in pH and fluctuations between exposure to harmful radiation and light limited conditions (Catalan, 1992). When flow through the lake decreases but temperature is still below 4 °C, complete mixing of the water column takes place. The heat flux towards the lake is very high (Figure 2), since radia-

tion is about its annual maximum, and thus convection is strong. This is the most differentiated period of the year in terms of water chemistry. Extremely low values and acidic peaks over the year mainly correspond to this period (Figures 9 & 10). However, very little is known about the consequence of these stress conditions for the lake community, and their potential to generate sediment signals.

In extremely cold conditions, the cover in some lakes such as Hagelseewli may not completely melt; a moat of open water is found around the shore but most of the lake is covered by ice even in summer. In such cases, periphytic organisms are favoured and plankton is restricted (Douglas & Smol, 1999). For instance, the ratio between chrysophycean cyst and benthic diatoms could be an indicator of cold summers in this type of lakes.

Stratification period: as soon as the lake water reaches 4 °C, the water column stratifies and phytoplankton blooms. A chlorophyll maximum occurs just below the thermocline (Figure 6). Winter temperatures modify the length of the winter cover (Livingstone, 1997) and thus change the length of the mixing period during thaw, and, consequently, the period in which convection distributes nutrients from deep layers or from sediments into the whole water column. This mechanism may eventually determine the intensity of the chlorophyll peak at the onset of stratification. It is likely that the duration of ice cover, particularly changes in ice-out timing, is reflected in the chrysophyte cyst record, since the productivity peak at the stratification on-set corresponds to chrysophytes, as indicated by the rise in the ratio of chlorophyll c to chlorophyll b (Figure 7). There is some evidence of species preferentially growing in this period (Pla, 1999). Over a few weeks, winds usually deepen the initially shallow thermocline down to a depth where it is stable to common winds. The chlorophyll maximum deepens too, and is then located at the base of the metalimnion in deep lakes (Estany Redó, Nižné Terianske Pleso, Saanajärvi) or close to the lake bottom in shallow lakes (Gossenköllesee). In most lakes, stratification is quite stable, but in the case of lakes like Laguna Cimera, which is long and shallow, the water column could resist wind action only for a short period in the middle of August, when maximum heat content was recorded.

This is the period, when the uppermost metres of the lake have the highest temperature. The transition from low to the highest temperatures is rapid and the number of days of intermediate values is low (Figure 3). Planktonic species growing in the epilimnion and invertebrates inhabiting the littoral and epilimnetic bottom are

more likely to respond to fluctuations in air temperature in the summer and early autumn. Although temperature generally enhances growth if resources are available, we cannot rule out a negative relationship with temperature, because most of the invertebrate species found in these lakes are cold stenotherms (Lotter et al., 1999, Catalan et al., 2002, this issue). Differences in the highest temperatures recorded were significant between lakes; even allowing for the differences in size, depth and shading, a latitudinal gradient could be distinguished. The epilimnion in the southernmost lakes had more than a month of temperatures of about 13 °C. In the case of insect larvae, the number of degree days for development may play a relevant role in the relationship between climate and fluctuations in their populations (Williams & Felmate, 1992; Armitage et al., 1995). In this sense, we found (Figure 3) that most of the lakes presented bimodal distributions in the number of days that the epilimnion maintained a certain temperature. The implications for species distribution of this temperature bimodality requires further study.

The potential consequences of a summer–autumn warming in the internal supply of nutrients during the autumn overturn appear unclear. The thermal cycle of the lake during the ice-free period is mainly driven by seasonal variation in radiation (Catalan, 1988). While changes in air temperature will only slightly affect the timing of the mixing patterns, they can significantly affect the temperature of the epilimnion during the late phase of stratification. Therefore, changes in community composition are more likely than significant changes in total productivity.

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