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The main features of seasonal variability in the external forcing and dynamics of a deep mountain lake (Redó, Pyrenees)

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ABSTRACT

*Lake Redó, a dimictic oligotrophic mountain lake, was monitored for two complete years from July 1996 to July 1998. The main seasonal variations in the physical, chemical and biological parameters are described, with special emphasis on the comparison of external forcing (weather and atmospheric deposition) with internal lake dynamics. Annual mean air temperature was estimated to be 3.6 °C. The duration of ice cover on the lake was 4.5 months in 1996/97 and 5.8 months in 1997/98. The lake water was very ion-poor (mean annual conductivity 12 $\mu S\ cm^{-1}$); however, ion concentrations in the lake were higher than in the precipitation, the differences being due mainly to Ca^{2+} and bicarbonates originating in the catchment. NH_4^+ was the main ion in the precipitation, with an average concentration of 17 μM, while in the lake it was always below 3 μM. However, the concentration of dissolved inorganic nitrogen always exceeded that of soluble reactive phosphorus by two or three orders of magnitude, so the latter is likely to be the limiting nutrient for phytoplankton growth. Four main production episodes were identified, occurring during spring and autumn overturn, in the upper hypolimnion during summer stratification, and under the ice at the beginning of the ice-covered period. The highest chlorophyll-*a *concentrations (1.2-2.2 $\mu g\ l^{-1}$) were attained during spring overturn; concentrations of chlorophyll-*c *were high during both spring and autumn overturn, while chlorophyll-*b *was comparatively important in the upper hypolimnion during the stratification period.* Daphnia pulicaria *was the most abundant macrozooplankton species; its abundance was highest during the ice-covered period, when its biomass was comparable to the measured sestonic particulate carbon concentration. The* Daphnia *maximum was associated with higher concentrations of NH_4^+ and dissolved organic carbon, suggesting that it may play an important role in the pelagic biogeochemical compartment of the lake under ice. Winter respiration rates for the lake were estimated to be 339 mg $O_2\ m^{-2}\ d^{-1}$ for 1996/97 and 281 mg $O_2\ m^{-2}\ d^{-1}$ for 1997/98.*

Key words: seasonal variability, ice cover, oligotrophic lakes, seston, chlorophyll, macrozooplankton, precipitation, water chemistry

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1. INTRODUCTION

Alpine lakes, located above the tree-line, are distributed throughout many regions of the world. Their remoteness and their exposure to extreme climatic conditions are the two most distinctive characteristics of such lake systems. Because of their geographical location - either at high latitudes or high altitudes - local anthropogenic influence tends to be low. They are, therefore, ideal sensors for monitoring transboundary air pollution and global change (Schindler *et al.* 1990). In alpine lakes, at least three different habitats can be distinguished: pelagic, benthic, and the most peculiar, the slush habitat, located within the snow and ice covering the lake. Felip *et al.* (1995, 1999a) have described the succession of organisms found in this habitat, showing how in some cases these organisms can grow at higher rates within the slush than in the lake itself, despite temperatures close to zero.

Although the main seasonal patterns have been described for lakes in the Alps (Pechlaner *et al.* 1970; Tilzer & Schwarz 1976; Mosello *et al.* 1992), in the Pyrenees (Capblancq & Laville 1983; Catalan 1988) and in other mountain ranges (Pienitz *et al.* 1997a, b), the understanding of their seasonal variability is still partially limited by the shortness of the sampled time series, or, in the case of some events, by low sampling frequencies. In particular, there is a lack of studies relating variations in water column features to simultaneous variations in external forcing, i.e., in weather and atmospheric deposition. In this study, we describe the seasonal changes occurring in the main physical, chemical and biological parameters of Lake Redó (central Pyrenees) during two complete annual periods, with special emphasis on comparing internal lake dynamics with external forcing.

2. MATERIALS AND METHODS

Lake Redó (Fig. 1) is a glacial cirque lake located at 2240 m a.s.l. in the central Pyrenees (42° 38' N, 0° 46' E). It is relatively large compared with its catchment area (Tab. 1) and has an average water renewal time of 4 y (Catalan 1988). There are two main inlet streams which dry up at the end of the summer, and one surface outlet (Fig. 1). The catchment is of granodiorite bedrock; 76% of its area is covered by a poorly-developed soil layer with an average thickness of 0.35 m. The main vegetation communities are *Carici-Festucetum eskiae*

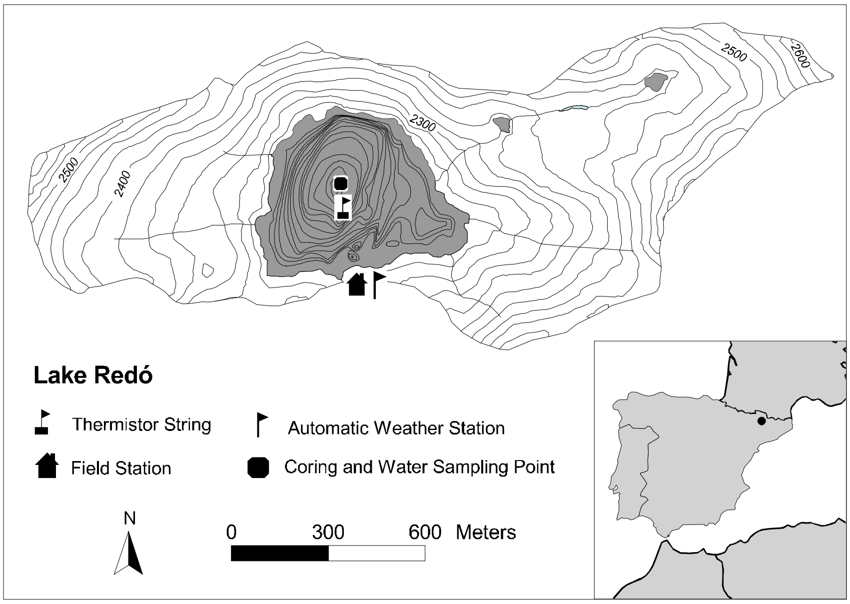

Fig. 1. Bathymetric map of Lake Redó (isobathic interval = 5 m) and its catchment. Maximum depth is 73 m at the raft.

(36%) and *Ranunculo-Festucetum eskiae* (23%), *Festuca eskia* being the dominant species.

Tab. 1. Main limnological characteristics of Lake Redó.

Lake area (A)	24 ha
Maximum length (NW-SE)	655 m
Maximum width	565 m
Maximum depth	73 m
Mean depth	32 m
Volume (V)	7.75 x 10^6 m^{-3}
Mean slope	46%
Catchment Area (Ac)	155 ha
Ac/A	6.5
Ac/V	0.2 m^{-1}
Water renewal time	3-4.2 y

The local meteorological conditions prevailing at Lake Redó from 1996-98 were characterized on the basis of measurements made by an automatic weather station (AWS) deployed about 30 m from the southern lake shore (Fig. 1). The base of the mast was 30 m above the lake surface and the sensors were located a further 6-10 m above ground level, i.e. between 2276 m a.s.l. and 2280 m a.s.l. The meteorological variables measured were air temperature, incident and reflected (short wave) solar radiation, net radiation, air pressure, relative humidity, precipitation, wind speed and wind direction. Precipitation measurements were conducted using a Geonor automatic gauge, in which a mixture of methanol and ethylene glycol was used to melt snow, allowing measurements to be made at both positive and negative air temperatures. The data storage interval was 30 min, and with the exception of air temperature, all values stored were 30 min mean values.

Temperature and dissolved oxygen in the water column were measured monthly at 1-m depth intervals using a WTW TA-197 oxygen meter. In addition, a thermistor chain delivered continuous information on lake water temperatures from January to April 1997 and from August 1997 to February 1998. During the ice-covered period, descriptions of the ice and snow cover were made at the same time as the water column sampling using the criteria proposed by UNESCO/IAHS/WMO (1970).

Using a Rüttner bottle, water column samples were taken once a month at 3 m intervals from July 1996 to July 1997 and at 9 m intervals from July 1997 to July 1998. The samples were divided into sub-samples immediately for analysis in a hut at the lake shore. Glass-fibre filters were used for pigment and particulate matter analyses; samples were frozen immediately after filtration. Bulk precipitation (rainfall and snowfall) samples were also taken daily from the end of August 1997 to June 1998 at a nearby field station, which is situated at less than 1 km in distance but at a lower altitude (1600 m). This data will be referred as Lake Redó precipitation, since no altitude differences have been found in a previous study (Camarero & Catalan 1996). The procedure followed for the chemical analysis of precipitation was the same as that employed in the case of the water column samples. Finally, samples from the two main inlet streams, located at the eastern basin (Fig. 1) were taken once a month during the snow-free period of 1997.

Water column samples were analysed for pH, alkalinity, conductivity, Na^+, K^+, Ca^{2+}, Mg^{2+}, NH_4^+, NO_2^-, NO_3^-, Cl^-, SO_4^{2-}, dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), soluble non-reactive phosphorus (SNRP), soluble reactive phosphorus (SRP), dissolved organic nitrogen (DON), dissolved silicon (DSi), particulate carbon (PC), particulate nitrogen (PN) and particulate phosphorus (PP). Precipitation samples were analysed for pH, alkalinity, conductivity, Na^+, K^+, Ca^{2+}, Mg^{2+}, NH_4^+, NO_3^-, Cl^-, SO_4^{2-}, total nitrogen (TN) and total phosphorus (TP). Conductivity was measured using a PTI-10 conductivity meter, and pH using an Orion Research model 720 pH meter with an electrode for low ionic-strength water. Alkalinity was determined by automated potentiometric Gran titration (Edmond 1970). Na^+, K^+, Ca^{2+}, Mg^{2+}, NO_3^-, Cl^- and SO_4^{2-} were analysed with a model CIA-4000 Waters Capillary Ion analyser. DIC and DOC were analysed using a Shimadzu TOC-5000 analyser. Sestonic PC and PN were measured by collecting the particles on pre-combusted Whatman GF/F filters (the samples were prefiltered through a nylon mesh to remove particles larger than 200 µm) and analysing them with a Carlo-Erba C-N-H-S analyser. NH_4^+ was determined by the phenolhypochlorite method (Solozano 1969). NO_2^- was determined by the sulphanylamide and n-naphthyl-etilenediamide method (Grasshof 1983). TN was determined by persulphate digestion (Grasshof 1983) followed by UV spectrophotometry. PP, PT and TDP were oxidized to phosphate by acid-persulphate digestion (Koroleff, cited by Grasshof 1983), and SRP was concentrated using chromatographic cartridges. Phosphate was analysed by the malachite green method (Camarero 1994b). For major ions, an analytical quality control was performed by ion balance and by comparing measured and estimated conductivities (Golterman *et al.* 1978).

Chlorophyll (Chl) was extracted using 5 ml of 90% acetone with sonication. Chl-*a*, *b* and *c* concentrations were calculated using the equations of Jeffrey & Humphrey (1975). The absorbance ratios A472:A664 and A433:A413 were used as a carotenoid index (Strickland & Parsons 1968) and a pheopigment index (Moss 1967), respectively.

Macrozooplankton samples were taken once a month following the protocol of Straškrabová *et al.* (1999). Biomass conversion for *Daphnia pulicaria* was carried out using the following regression of weight (W) on length (L), based on individuals from Lake Redó:

$$\ln W = 3.3 \ln L + 1.63 \quad (r^2 = 0.97, n = 29) \qquad (1$$

For *Cyclops abyssorum* and *Diaptomus cyaneus* the equations of Downing and Rigler (1984) were used (after validation based on some individuals from Lake Redó). Biomass was converted to carbon following the procedure of Straškrabová *et al.* (1999).

3. RESULTS

3.1. Meteorological data

Daily mean air temperatures (Fig. 2a) varied between –10.5 °C and +16.2 °C during the period of observation; they were negative for at least some of the time from October to May. In winter, long periods of generally negative air temperature were often punctuated by periods of a few days in which the air temperature rose above 0 °C. However, it is possible for daily mean air temperatures to remain consistently below 0 °C for at least 3 weeks in midwinter (e.g., 12 January – 6 February 1998). Based on the monthly mean data, and estimating the missing monthly means in October 1997 and November 1997 by linear interpolation, the annual mean air temperature at Lake Redó was estimated to be 3.6 °C.

Daily mean values of incident solar radiation (Fig. 2b) varied from less than 10 W m^{-2} on some winter days to over 380 W m^{-2} on cloudless summer days. Based on the approach described by Brock (1981), and using the atmospheric transmission coefficients of Hottel (1976), the daily mean clear-sky solar radiation at the latitude and altitude of Lake Redó could be calculated for each day of the year. A simple modification to this approach also allowed the influence of the local topography on the clear sky incident solar radiation to be calculated. Because of its southern exposure, the influence of local topographic effects on the clear-sky radiation at Lake Redó is slight, as is shown by the smallness of the discrepancy between curves B and C in figure 2b (<17 W m^{-2}). The percentage reduction in incident clear-sky solar radiation due to local topographic effects is strongly seasonally dependent, varying between a minimum of 4.1% in summer and a maximum of 13.4% in winter, with an annual mean of 7.6%. The radiation measurements from September to April agree well with the corresponding computed clear-sky radiation, implying generally low degrees of cloudiness. In fact, the maximum measured radiation during this period often exceeded the computed clear-sky values, sometimes by as much as 40%. During the same period, the ratio of reflected solar radiation (over land) to incident solar radiation was high (Fig. 2c), implying a snow-covered landscape with high albedo. The reason for the measured solar radiation exceeding the theoretical clear-sky radiation is therefore presumably the downward scattering and re-reflection of some of the radiation reflected upwards from the snowpack. In summer, reflection, absorption and scattering by cloud cover have a considerable influence on the solar radiation incident on the lake. During May - August 1997, for instance, the monthly mean measured solar radiation varied between 59% and 73% of the theoretical clear-sky radiation; this is substantially lower than the range of 91% - 105% found for February - April 1997.

The daily mean net atmospheric (long-wave) radiation (Fig. 2d) was always positive, ranging from only slightly above zero to 137 W m^{-2}. There was no strong seasonal variation about the annual mean of 59 W m^{-2}. During the open-water period, the net long-wave atmospheric radiation accounted for an average of 25% of the total incident radiation and can therefore be considered to be important for the heat balance of the lake.

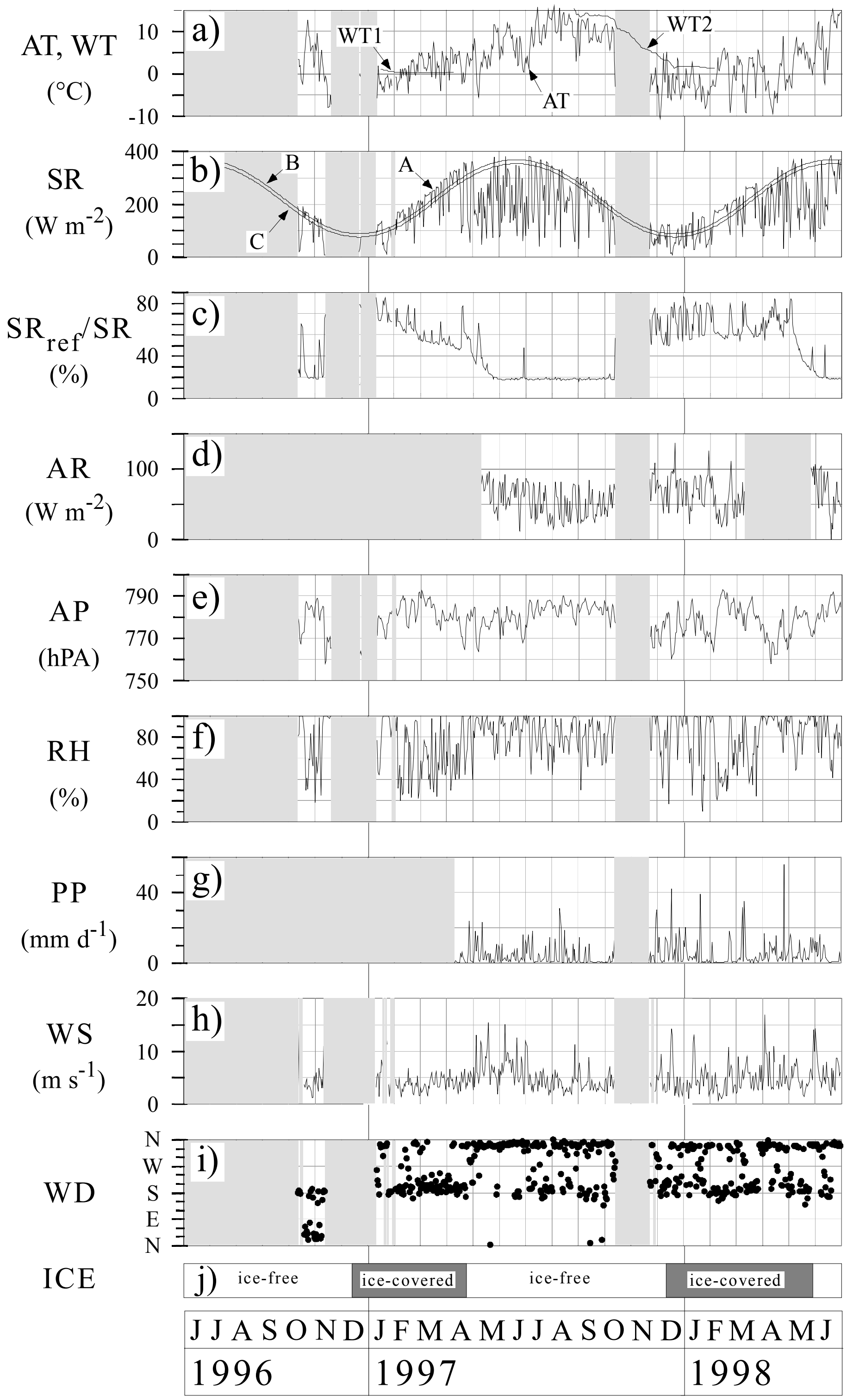

Fig. 2. Meteorological measurements and observations of ice cover made at the Redó AWS from October 1996 – June 1998: **a)** air temperature (AT) and water temperature at 1 m depth (WT1: January - April 1997) and 2 m depth (WT2: August 1997 - February 1998); **b)** incident short-wave solar radiation (SR); **c)** the ratio of reflected to incident short-wave solar radiation (SRref/SR); **d)** net long-wave atmospheric radiation (AR); **e)** air pressure (AP); **f)** relative humidity (RH), **g)** precipitation (PP); **h)** wind speed (WS); **i)** vector-averaged wind direction (WD); and **j)** ice cover (ICE). In **b)**, in addition to the measured data (A), the theoretical clear sky solar radiation calculated according to Brock (1981) using the atmospheric transmission coefficients of Hottel (1976) is shown, unmodified (B) and modified by the local skyline at the AWS (C). The grey panels indicate periods of missing data.

Although the air pressure at the lake (Fig. 2e) exhibited considerable day-to-day fluctuations, its seasonal variability was low. In summer 1997, for instance, the mean air pressure was 781.8 hPa, falling only slightly to 778.0 hPa in the following winter. The annual mean air pressure at the lake (± one standard deviation) was estimated to be 779.5 ±7.0 hPa. Applying the empirical formula of Bührer and Ambühl (1975), this implies an O_2 saturation concentration of 10.1 ±0.1 mg $O_2 \cdot l^{-1}$ at 4 °C (i.e., during overturn).

Relative humidity (Fig. 2f) exhibited a slight seasonal variability around the annual mean of 78%. Mean seasonal values were 70% and 84% in spring 1997 and 1998, respectively, 81% in summer 1997, and 72% in winter 1997-98 (autumn means could not be computed due to lack of data).

Winds (Fig. 2h) were strong at Lake Redó and calm periods were rare. Daily mean wind speeds ranged from 0.8 - 17.0 m s^{-1}, exceeding 5 m s^{-1} during 40% of the time, and 10 m s^{-1} during 5% of the time. Based on all data, the annual mean wind speed was estimated to be 5.0 m s^{-1}. Prevailing wind directions (Fig. 2i), assessed in terms of vector-averaged daily means, were north (45%) and south (43%). Winds from the west (11%) were less common, and winds from the east (<1%) extremely rare.

3.3. Physical structure

Lake Redó is dimictic; the period of study therefore included five mixing periods (Fig. 3). Spring overturn occurred in late June 1996, at the beginning of May 1997 and at the beginning of July 1998. Both autumn overturn periods occurred during November; however, in 1996 the lake mixed at the beginning of the month, while in 1997 it mixed two weeks later. There would therefore seem to be more variability in the timing of spring overturn than in the timing of autumn overturn, probably because of the variability in winter ice-cover characteristics that influence spring mixing.

During the first open-water period (June to November 1996), the epilimnion had a mean temperature of 6.6 °C, while during the second open-water period (May to November 1997) it was substantially higher (8.1 °C), reflecting the high air temperatures prevailing in 1997 (Fig. 2a). Epilimnetic temperatures were generally about 5.2 °C higher than the corresponding air temperatures, which is not unusual in summer and autumn in both lowland lakes (Livingstone & Lotter 1998) and alpine lakes (Livingstone *et al.* 1999). In contrast to the epilimnion, the temperature of the hypolimnion was essentially the same during both open-water periods (4.6 °C in 1996 and 4.5 °C in 1997), as was the mean lake

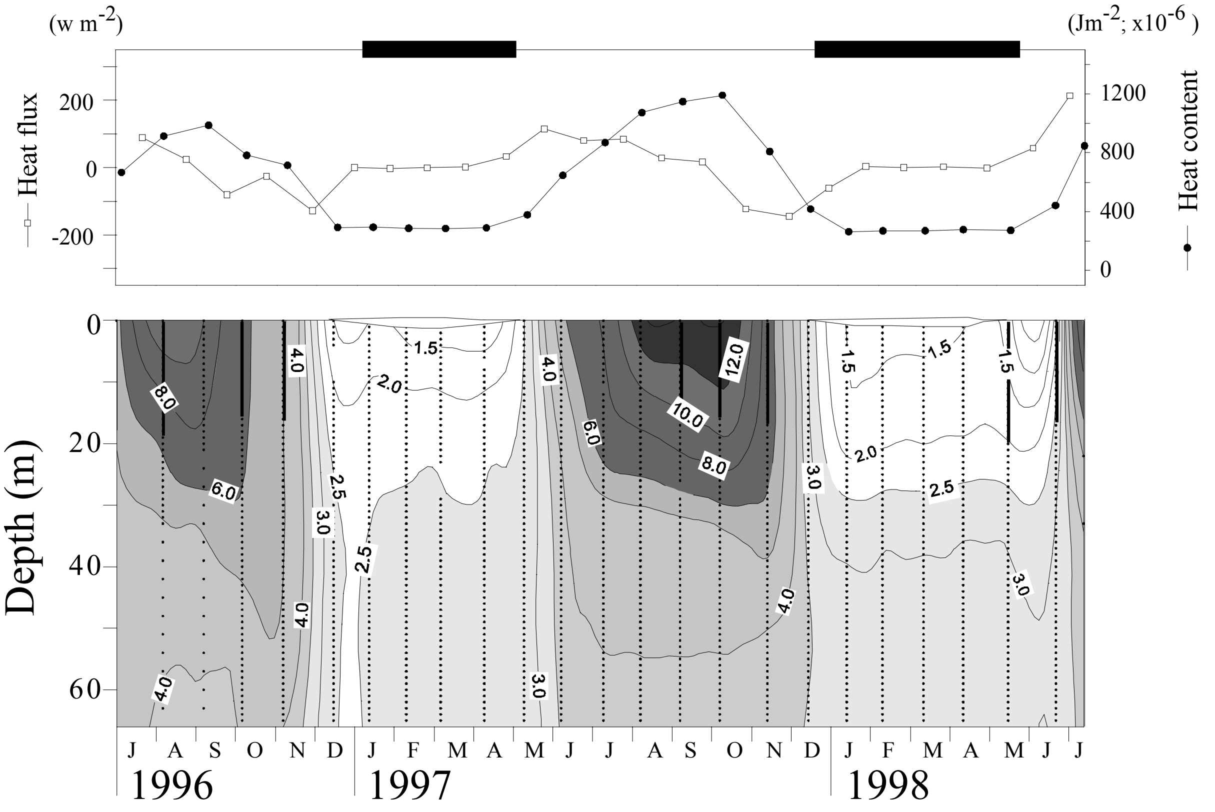

Fig. 3. **Upper panel**: Heat content and heat flux at Lake Redó during the study period (July 1996 to July 1998). The horizontal lines at the top of the panel represent periods of ice cover. **Lower panel**: Isotherm plot illustrating seasonal temperature changes (°C). Secchi depths are shown as vertical bars. The dotted lines indicate the measured profiles on which the isotherm interpolation is based.

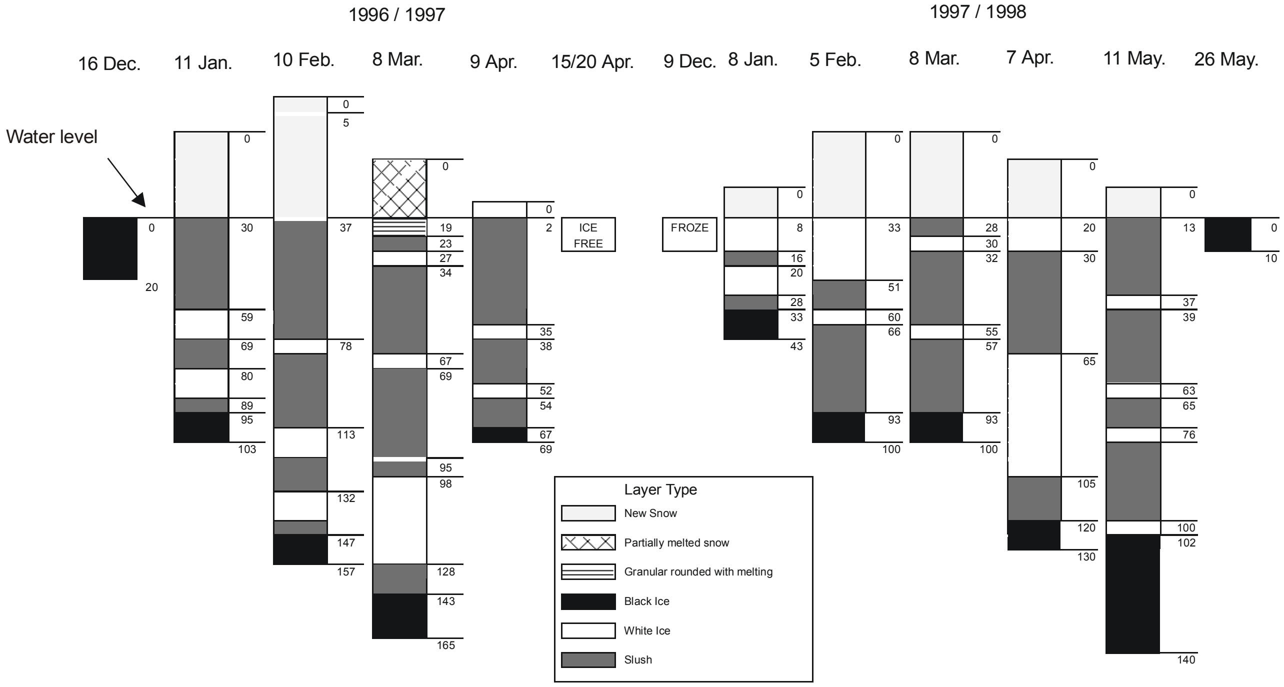

Fig. 4. Ice cover profiles for the winters of 1996/97 and 1997/98 in Lake Redó. The depths of the different layers are given in cm, starting from the snow surface.

temperature during the ice-covered periods (2.2 °C in 1996/97 and 2.0 °C in 1997/98). Thus interannual variability in climate forcing would appear to be reflected only in open-water epilimnion temperatures. The annual heat budget of the lake was calculated to be 71,600 J m^{-2} y^{-1} in 1996-97 and 90,288 J m^{-2} y^{-1} in 1997-98. Both these values substantially exceed the annual heat budget of 63,582 J m^{-2} y^{-1} calculated by Catalan (1988) for 1984-85.

Lake Redó was ice-covered from early December 1996 to late April 1997, and from late December 1997 to early June 1998. Because local topographic effects on incident solar radiation at the lake are slight, the onset and end of the period of ice cover are likely to be determined to a large extent by synoptic-scale climate integrated over several weeks (cf. Palecki & Barry 1986), and especially by air temperature (e.g. Ruosteenoja 1986). At Redó, the timing of freeze-up and break-up is thus likely to reflect the air temperatures prevailing at the lake around November and April, respectively. The fact that the lake remained frozen substantially longer in 1998 than in 1997 can thus be associated with the considerable difference in the air temperatures prevailing during spring in these two years (Fig. 2a). The mean spring air temperature (March - May) was 2.6 °C lower in 1998 than in 1997, and the mean April air temperature was 4.7 °C lower. The end of the snow cover in April 1997 is earlier than that observed in previous years (Catalan 1989, 1992; Camarero 1994a).

The structure of the ice cover (up to four layers of white ice alternating with slush) was similar during both winters (Fig. 4), as was the maximum ice thickness (165 cm in 1996/97 and 140 cm in 1997/98). In the first winter, ice thickness reached its maximum during February/March 1997, subsequently melting fairly rapidly (Fig. 4) as a result of the high air temperatures and the lack of snowfall prevailing from January to May. In the second winter, maximum ice thickness occurred later, i.e. during April/May 1998.

Light was able to penetrate quite deeply into the lake: Secchi depths ranged from about 15 - 16 m during the stratification periods to about 18.5 - 20.5 m after the snowmelt (Fig. 3).

3.4. Deposition chemistry and lake water chemistry

Precipitation samples were collected only from June 1997 to June 1998. Concentrations and precipitation rates are summarised in table 2. A total of 1600 mm fell during this period, corresponding to a monthly mean of 122 mm. Mean conductivity was 9 µS cm^{-1}. The most abundant cations were NH_4^+, Ca^{2+} and Na^+, while NO_3^-, SO_4^{2-} and Cl^- were the most abundant anions. The alkalinity of the precipitation was very low (6 µeq l^{-1} on average) since most of the rain events were acidic (median pH = 5.2).

Lake water chemistry was dilute (Tab. 3), with a mean conductivity of 12 µS cm^{-1}, and an average pH of 6.3. Ca^{2+} was the most abundant cation, and HCO_3^- and SO_4^{2-} the dominant anions. Ionic concentrations were higher in the lake water than in the precipitation, mainly because of higher concentrations of Ca^{2+} and HCO_3^-. Concentrations of NO_3^- and SO_4^{2-} in the lake water and in the precipitation were similar, while concentrations of Cl^- and Na^+ were slightly lower in the lake than in the precipitation, suggesting a dilution effect because of differential elution during the thawing of the snowpack (Camarero 1994a). There were no significant seasonal variations in the concentrations of major ions in the water column during the sampling period.

Tab. 2. Volume weighted mean chemical composition of the precipitation at Lake Redó during the second year of the study period (July 1997 to July 1998), calculated on the basis of daily samples.

	Mean	Max.	Min.
Precipitation (l m^{-2} $month^{-1}$)	122	300	24
H^+ (µM)	9	23	1
Alkalinity (µeq l^{-1})	6	38	-17
Conductivity (µS cm^{-1})	9.0	13.1	3.9
Na^+ (µM)	16	48	4
K^+ (µM)	3	11	0
Ca^{2+} (µM)	13	47	4
Mg^{2+} (µM)	2	5	0
Cl^- (µM)	12	37	5
SO_4^{2-} (µM)	12	20	4
NO_3^- (µM)	13	30	3
NH_4^+ (µM)	17	39	4
TN (µM)	35	50	19
TP (µM)	0.176	0.308	0.024

Tab. 3. Mean chemical composition of the Lake Redó water column during the study period (sampled at monthly intervals from July 1996 to July 1998).

	Mean	Max.	Min.
pH	6.3	6.6	6.0
Conductivity (µS cm^{-1})	11.5	13.7	9.4
Alkalinity (µeq l^{-1})	46	54	40
Na^+ (µM)	10	14	7
Mg^{2+} (µM)	4	4	3
K^+ (µM)	1	3	0
Ca^{2+} (µM)	36	42	32
SO_4^{2+} (µM)	13	15	12
Cl^- (µM)	7	14	4
NO_3^- (µM)	12	13	10
NO_2^- (µM)	0.13	0.22	0.06
NH_4^+ (µM)	1.3	2.9	0.1
DON (µM)	5	7	2
PN (µM)	1	1.6	0.6
SRP (µM)	0.009	0.021	0.003
SNRP (µM)	0.046	0.134	0.003
PP (µM)	0.061	0.193	0.000
DIC (µM)	83	100	67
DOC (µM)	125	208	50
PC (µM)	9	17	3
DSi (µM)	10	13	7
Chl-*a* (µg l^{-1})	0.70	2.24	0.07
Chl-*b* (µg l^{-1})	0.03	0.10	0.00
Chl-*c* (µg l^{-1})	0.09	0.25	0.01
O_2 (mg l^{-1})	9.1	9.9	8.2

The carbon budget in Lake Redó during 1996/97 has been studied by Camarero *et al.* (1999), and is illustrated in figure 5. DOC was the most abundant carbon fraction, followed by DIC and PC (Tab. 3). During summer 1996, variations in all three carbon fractions were similar, although DIC was highest in July, while PC and DOC were highest in August. Mean DOC and PC concentrations were highly correlated during the first year ($r^2 = 0.70$, $p < 0.001$), but much less correlated during the second year ($r^2 = 0.34$, $p < 0.05$), when the linear regression had a similar linear trend, although the datapoints were much more scattered. In October of both years there was a peak in carbon concentrations; the highest concentrations of both DIC and DOC during the whole sampling period occurred in October 1997.

The main nitrogen component was dissolved inorganic nitrogen (DIN, the sum of NH_4^+, NO_3^- and NO_2^-). DON concentrations were approximately half those of DIN concentrations, and concentrations of PN much lower than DON concentrations (Tab. 3). NO_3^- was the most abundant ion of the DIN pool, as observed in most Pyrenean lakes (Catalan *et al.* 1994). However, concentrations of NH_4^+, the most abundant ion in the precipitation, were very low in the lake. PN had a similar pattern to that of PC; viz. high concentrations during the open-water period that decreased during the subsequent ice-covered period. The main difference in the behaviour of the PC and PN concentrations occurred in August and October 1996, when very high concentrations of PC, but not of PN, were measured at the surface. Both sampling dates were preceded by heavy rainfall, which could have resulted in high allochtonous inputs of PC and DOC. Variations in PN and DOC were similar ($r^2 = 0.61$, $p < 0.001$), particularly during the second half of 1997 and 1998, when they were very highly correlated ($r^2 = 0.80$, $p < 0.001$). The main mismatch between DOC and PN variations occurred during the 1997 spring overturn, when PN showed an increase very similar to that of Chl-*a*, while DOC concentrations remained low. Phosphorus was present mainly as PP and SNRP, the concentrations of which were similar. SRP concentrations were comparatively low (Tab. 3) and showed no significant changes throughout the sampling period.

During both winters, DSi concentrations in the deeper layers of the lake lay between 15 and 17 µM, compared to 10 µM in the upper layers, indicating a release of DSi from the sediments.

3.5. Biological activity

Four different peaks can be distinguished in the chlorophyll measurements (Fig. 6). Two of these are associated with the mixing periods (spring and autumn overturn), while the other two are associated with the stratification periods. A chlorophyll maximum was observed in the upper layers of the hypolimnion in summer, and another chlorophyll maximum was observed under the ice, where some algal communities are able to

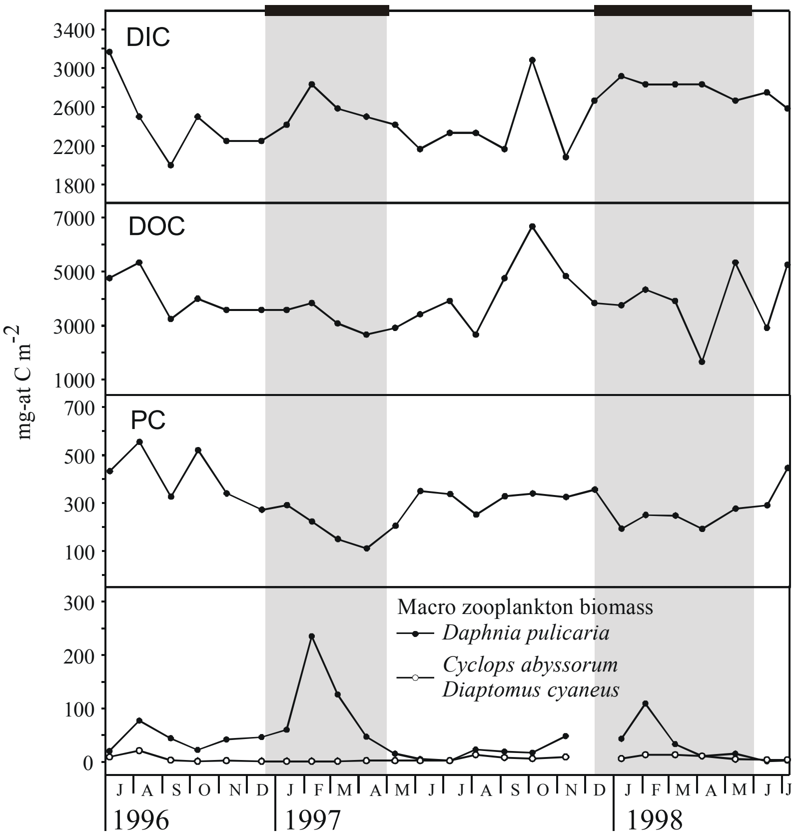

Fig. 5. Areal mean concentrations of DIC, DOC, PC and macrozooplankton biomass in Lake Redó during the study period (July 1996 to July 1998). The thick black lines indicate periods of ice cover.

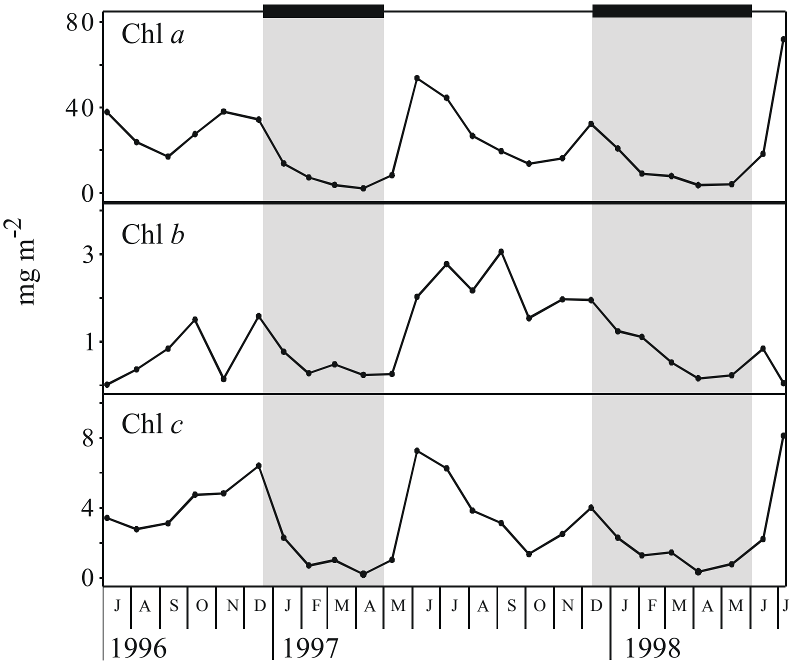

Fig. 6. Areal mean concentrations of Chl-*a*, Chl-*b* and Chl-*c* in lake Redó during the study period (July 1996 to July 1998). The thick black lines indicate periods of ice cover.

benefit from the stable conditions generated by the black ice (Fig. 7; Catalan & Camarero 1991). Among the four production episodes observed, the highest Chl concentrations occurred during spring overturn. In both years, Chl concentrations during autumn overturn were lower than during spring overturn. In 1996 there was a Chl maximum under the ice following the autumn overturn maximum. However, in 1997 no Chl maximum was detected, probably because of the rapid accumulation of 30 cm of snow on the top of the black ice after the lake froze, which prevented the penetration of light necessary for algal growth.

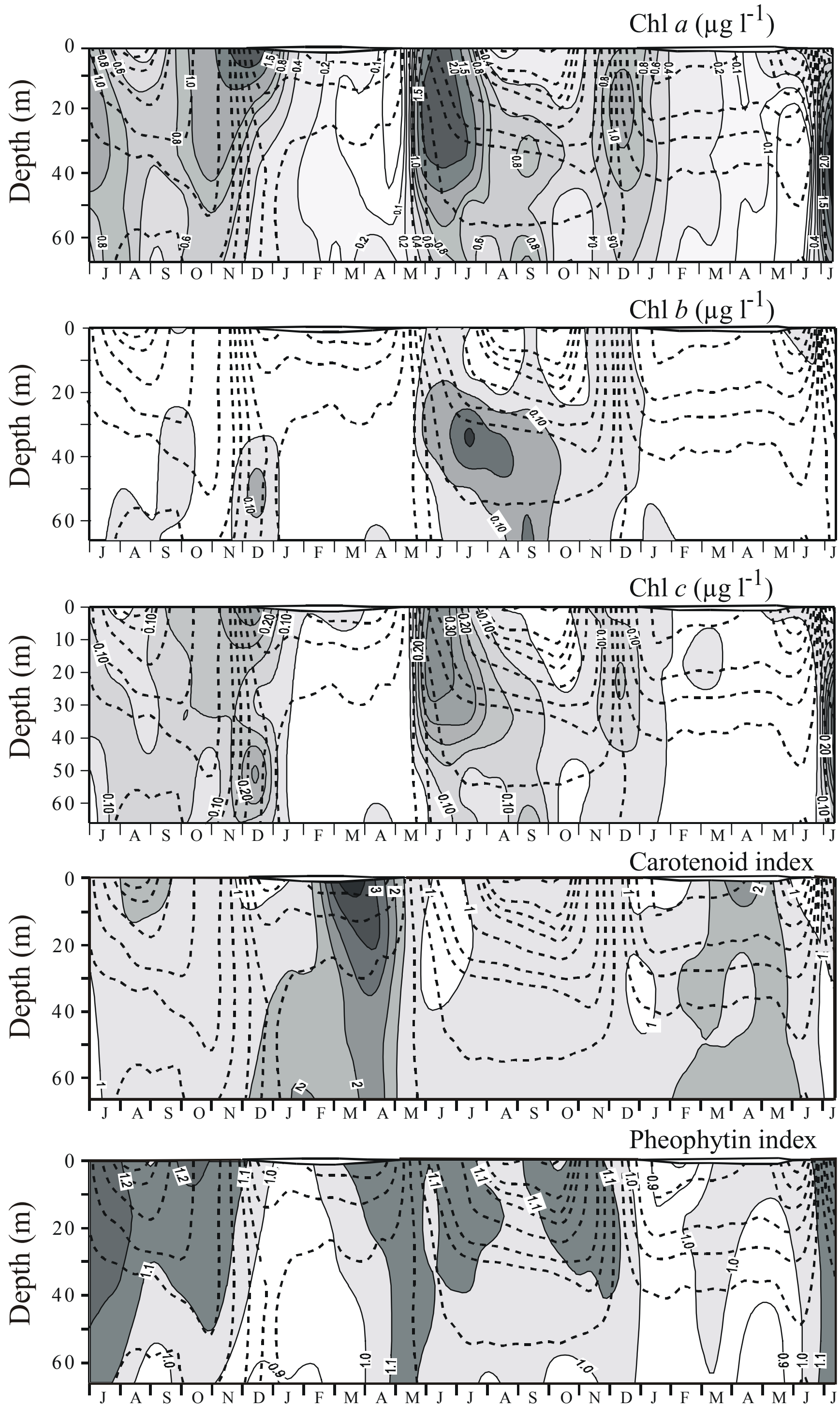

Fig. 7. Isoline plots of Chl-*a*, Chl-*b*, Chl-*c*, the carotenoid index and the pheopigment index for Lake Redó during the study period (July 1996 to July 1998). Isotherms (dashed lines) are also shown in order to facilitate comparison with seasonal patterns of stratification and mixing. Duration and thickness of ice-cover are shown at the top of each panel.

Mean lake Chl-*a* concentrations during spring overturn were low in 1996 (1.18 μg l^{-1}) and 1997 (1.39 μg l^{-1}), but in 1998 they were much higher (2.24 μg l^{-1}), closer to values found in other years (Catalan 1991).

As shown in figure 7, Chl-*b* and *c* peaks did not overlap in space and time, with the exception of the two autumn overturn periods. Chl-*c* was typical of the two mixing periods, while Chl-*b* appeared mainly in the upper layers of the hypolimnion.

The carotenoid index, which indicates the ratio of the concentration of carotenoid pigments to the concentration of Chl, increased during both winters from

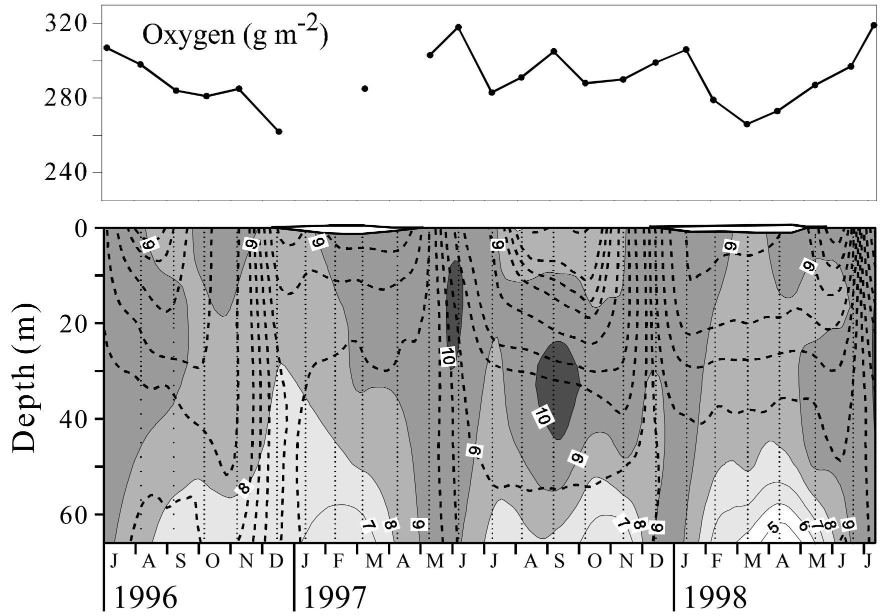

Fig. 8. **Upper panel**: Seasonal variations in in the oxygen content Lake Redó (g m^{-2}) during the study period (July 1996 to July 1998). **Lower panel**: Isoline plot of oxygen concentration (mg l^{-1}) in Lake Redó, 1996-98 (solid lines). Isotherms (dashed lines) are also shown in order to facilitate comparison with seasonal patterns and mixing. The dotted lines indicate the measured profiles on which the isoline interpolation is based. Duration and thickness of ice-cover are shown at the top of each panel.

March to April, with minimum values occurring during the episodes of maximum Chl. The carotenoid index therefore reacted more sensitively to variations in Chl concentrations than to variations in carotenoid concentrations, indicating that carotenoid concentrations were quite constant in comparison to Chl concentrations during the sampling period. The pheopigment index, which indicates the ratio of the concentration of Chl-*a* to that of pheophytin-*a* and pheophorbides, was high during the open-water periods, decreasing both below the ice-cover and below 60 m throughout the year.

The macrozooplankton biomass (Fig. 5) was dominated by *Daphnia pulicaria* during most of the study period, with the exception of the open-water period of 1997 and the beginning of the open-water period of 1998, when the *Diaptomus cyaneus* population was as large or larger than the *D. pulicaria* population. *D. cyaneus* grew only during the open-water periods, while *Cyclops abyssorum* was present throughout the year, although in terms of carbon it represented a low proportion of the total macrozooplankton population. *D. pulicaria* biomass during both ice-covered periods was very high, reaching higher mean lake values than PC in February 1997 (235 and 223 mg at C m^2 for *D. pulicaria* and PC, respectively) and half of the PC in February 1998 (109 and 250 mg at C m^2, respectively).

Oxygen concentrations (Fig. 8) decreased during winter, especially in the deeper layers of the lake. Anoxia was reached below 66 m in April 1998. In 1997, two oxygen peaks (with saturation values of 100% - 120%) occurred during spring overturn and during summer, indicating high primary production.

During winter, when the lake can be considered to be isolated from the atmosphere by the ice cover and photosynthesis is practically nil because of the lack of light, total lake respiration rates can be calculated by areal integration of the measured oxygen profiles (Welch *et al.* 1976). Areal respiration rates were higher during the first ice-covered period (339 mg O_2 m^{-2} d^{-1}) than the second (281 mg O_2 m^{-2} d^{-1}). However, they were of a similar magnitude to those calculated for Lake Redó in other years (232 mg O_2 m^{-2} d^{-1}, Catalan 1992) and similar lakes from the Canadian Shield (131-306 mg O_2 m^{-2} d^{-1}, Welch & Bergmann 1985).

4. DISCUSSION

The comparison of the lake chemistry with the chemistry of the precipitation falling on the lake can be very informative for understanding the origin of the chemical composition of the lake water (Margalef 1983). The chemistry of the precipitation during the second half of the present study period showed significant differences compared to previously measured values (Camarero & Catalan 1993, 1996): NO_3^-, SO_2^{2-}, alkalinity and Ca^{2+} were lower during this study. Despite these decreases, Ca^{2+} and alkalinity were much higher in the lake than in the precipitation, indicating that, although the basin is mainly composed of granite bedrock, there was a very significant source of Ca^{2+} in the catchment. A mean Ca^{2+} concentration of 72 µM and a mean alkalinity of 130 µeq l^{-1} in the two main inlets during the snow-free period confirmed that Ca^{2+} and alkalinity must have been generated in some parts of the lake catchment.

NH_4^+, which was the dominant cation in the precipitation, was present at much lower concentrations in the lake water. Since NH_4^+ concentrations in the inlet streams were below the limit of detection during the 1997 open-water period, this discrepancy could be explained by its retention in the soil (Schimel & Parton 1986). Thus, the only source of NH_4^+ to the lake during the snow-free period was its direct input to the lake surface in the precipitation. During the snow-covered period, when the precipitation accumulated in the snowpack, most ions were eluted during snowmelt (Camarero 1994a). In early May during the two ice-covered periods studied, NH_4^+ concentrations were very high at the surface (0-5 m: 3.1 and 5.3 μM) compared with the rest of the water column (5-66 m: 1.3 and 1.9 μM).

Although NH_4^+ concentrations in the lake water were much lower than in the rain, they were probably sufficient for the requirements of the algae, since the NH_4^+: SRP ratio was usually significantly greater than 16, the Redfield ratio. NH_4^+ concentrations increased with increasing Chl concentration ($r^2 = 0.37$, $p < 0.001$), as did DON ($r^2 = 0.50$, $p < 0.001$), suggesting that the NH_4^+ was mainly a product of cellular exudation.

Lake Redó had very low TP concentrations during the whole study period (mean concentration: 3.6 $\mu g\ l^{-1}$). Since TP $< 5\ \mu g\ l^{-1}$, according to the classification scheme of Vollenweider and Kerekes (1982) Lake Redó is ultra-oligotrophic. In addition, the magnitude of the mean DIN:SRP ratio (1333:1 by atoms) indicates that Lake Redó is severely limited by P in comparison to N.

Although the chlorophyll maximum does not exactly match the biomass maximum (Felip & Catalan 2000), chlorophyll measurements are still acceptable indicators of the main patterns of primary production in the lake. Also, chlorophyll-*b* and *c* concentrations may be used as a first approach to characterize the algal composition. In Lake Redó, chlorococcal chlorophytes were the most important group of algae containing Chl-*b*, while cryptophytes, chrysophytes and dinoflagellates contributed to Chl-*c*. There was a good correspondence between the concentrations of Chl-*b* and *c* on the one hand (Fig. 7) and the algal group composition of both ice-free periods studied on the other (Felip *et al.* 1999b). Chrysophytes and dinoflagellates were the dominant algae during spring and autumn overturn periods; chryptophytes were associated with the deep layers, while the chlorococcal chlorophytes appeared during the stratification periods and during the 1997 autumn overturn.

Since the pheopigment index is the ratio of Chl-*a* to both pheophytin-*a* and pheophorbides, a low index may be related to an increase in pheophytin-*a* (mainly a degradation product of Chl-*a*: Moss, 1967), or to an increase in pheophorbides (grazing products of zooplankton: Moss 1967) or both. In both years, the zooplankton maximum coincided with the minimum in the pheopigment index, indicating that pheophorbide was probably contributing most to the decrease in the index. On the other hand, the low values of the index in the deeper layers of the lake were most probably related to the degradation of Chl-*a* down the water column.

An evaluation of the importance of macrozooplankton in Lake Redó lies outside the scope of this paper. However, because macrozooplankton biomass exhibits high concentrations in certain periods, coupled with a high degree of seasonal variation, we have presented it here in terms of carbon. *D. pulicaria* was found mainly under ice, while *D. cyaneus* was only found during open-water periods. Because of such important seasonal changes, it is important that life cycle studies in alpine lakes be based on samples covering the entire year. The interannual differences in *Daphnia* species growth coincided with differences in respirat ion rates estimated from oxygen consumption, and both *D. pulicaria* peaks also coincided with higher NH_4^+ and DOC concentrations. The 1996 peak also coincided with higher DON, PON, SRP and SNRP concentrations, indicating the potential influence of macrozooplankton on the nutrient cycle of the lake ecosystem. *Daphnia* species are known to have an important influence on nutrient recycling (Hessen 1992).

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