



Phytoplankton structure and dynamics in Lake Sanabria and Valparaíso reservoir (NW Spain)

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Abstract

The aim of this work is to compare the composition and seasonality of the phytoplankton population in a natural oligotrophic lake (Lake Sanabria) and a mesotrophic reservoir (Valparaíso). Both ecosystems are located on the Tera river course (NW Spain), which runs along an area of ancient metamorphic and plutonic rocks. Some physical and chemical parameters, chlorophyll *a* and phytoplankton biovolume were studied from monthly samples collected at different depths during the periods 1987–1989 (Lake Sanabria) and 1991–1992 (Valparaíso). Phytoplankton biovolume and chlorophyll *a* concentration were about five times higher in Valparaíso than in Lake Sanabria. Species composition (and main phytoplankton groups) were different. Valparaíso was highly dominated by diatoms and Lake Sanabria by cryptophytes and small chlorophytes. In spite of the fact that both sites were nitrogen limited, heterocystous cyanophytes (*Anabaena* sp.) were detected only in Valparaíso. The relationships between phytoplankton structure and trophic level, hydrological conditions and nitrate content are discussed.

Introduction

Differences in phytoplankton biomass and composition have been found between lakes of different trophic status (Duthie & Hart, 1987; Kalff & Knoechel, 1978; Kalff et al., 1975; Olsén & Willén, 1980; Petrova, 1987; Priddle & Happey-Wood, 1983). Biomass in nutrient-rich lakes is several times greater than in nutrient-poor waters (Kalff et al., 1975). Nutrient-rich lakes of temperate areas are usually dominated by diatoms and blue-green algae (Moustaka-Gouni & Tsekos, 1989; Olsén & Willén, 1980; Petrova, 1987; Priddle & Happey-Wood, 1983), whereas the commonest phytoplankton organisms in poor environments are nanoplanktonic species (frequently chlorophytes) (Krienitz et al., 1997; Priddle & Happey-Wood, 1983) and flagellates (Eloranta, 1995; Ilmavirta, 1983, 1990; Sheath & Hellebust, 1978).

Lake Sanabria is the largest natural freshwater lake in Spain. It has been studied since 1986, and a study of its phytoplankton was carried out in detail during the period 1987–89. This research has demonstrated the oligotrophic character of the lake (De Hoyos, 1996). Valparaíso reservoir has only been surveyed during

a short period, but the levels of some limnological parameters suggest that it is a mesotrophic ecosystem.

In this paper we make a comparison between Lake Sanabria phytoplankton composition and dynamics and another lacustrine system of a higher trophic level, in order to investigate phytoplankton species that could serve as indicators of a trophic level increase in Lake Sanabria. Valparaíso reservoir was chosen for this study as it was the nearest ecosystem that had a comparable thermic and hydrological regime but a different trophic status.

Study sites

Lake Sanabria and Valparaíso reservoir are located in the NW part of Spain, in the Sanabria region, an area geologically situated on the paleozoic Iberian system. The Alpine orogeny raised the Cabrera and Segundera mountains, and there exists a large group of lakes, ponds and mires originated during Würm glaciation (Vega & Aldasoro, 1994; Vega et al., 1991). All this region is characterized by ancient metamorphic and plutonic rocks which determines the low conductivity

and pH of all lacustrine ecosystems of Segundera and Cabrera mountains (Vega et al., 1991).

The area is of the Mediterranean-mountain climate type, with annual mean temperature of about 10°C (monthly mean temperature interval; 3.7–18.6°C) and a total cumulative annual rainfall mean of about 1400 mm (monthly mean rainfall interval; 19.8–198.4 mm) (De Hoyos, 1996).

Lake Sanabria occupies a glacial depression of the Tera river valley, a river that starts in Cabrera and Segundera mountains. This lake is in the protection zone of Lake Sanabria Natural Park, an area supporting a low population (about 200 inhabitants) except during the summer, when it rises sharply due to the high influx of tourists. The lake shows a low water retention time, with a mean value of 0.76 years (from 1942 to 1993) (De Hoyos, 1996). Such high water renewal rate is related to abundant rainfall and high D_a/V ratio (D_a , drainage area; V , lake volume), with a value of 1.36 m^{-1} . In Lake Sanabria mean pH is 6.1 and mean conductivity $14.19 \mu\text{S/cm}$ (De Hoyos, 1996). Lake Sanabria shows a water colour level slightly lower than the limit generally accepted to consider a lake as dystrophic (50 mg Pt/l), but indicates the presence of dissolved organic matter, probably coming from the mires and forests located in the catchment area (De Hoyos, 1996).

Valparaíso is an artificial reservoir of Tera river (about 40 km away from Lake Sanabria), filled in 1988 and it is the second of a cascade series of three dams constructed between 1965 and 1994. There are several small towns in the area but sewage discharges are of little importance. Valparaíso is only used for electricity production, so there are no marked water level variations (less than 2 m) (Fraile, 1994). Its water retention time was 0.50 years in 1991 (Fraile, 1994), very similar to Lake Sanabria values in the study period. Conductivity and pH are a little higher than in Lake Sanabria (mean conductivity, $24.13 \mu\text{S/cm}$; mean pH, 6.5) (Negro et al., 1994).

Table 1 shows some characteristic parameters of the studied systems.

Materials and methods

This work is based on data obtained from samplings carried out from May 1987 to December 1989 in Lake Sanabria (De Hoyos, 1996), and from May 1991 to April 1992 in Valparaíso (Negro et al., 1994). In both cases there was one sampling station situ-

Table 1. Main general features of Lake Sanabria and Valparaíso reservoir

		Lake Sanabria	Valparaíso reservoir
Altitude	(m)	1000 ^(a)	833 ^(b)
Maximal depth	(m)	51 ^(a)	67 ^(b)
Area	(km ²)	3.46 ^(a)	12.33 ^(b)
Volume	(Hm ³)	93.3 ^(a)	168.5 ^(b)
Drainage area	(km ²)	127.3 ^(a)	798 ^(b)
Water retention time	(years)	0.76 ^(a)	0.5 ^(c)

^(a)De Hoyos, 1996.

^(b)Bengoechea, 1991.

^(c)Fraile, 1994.

ated above the deepest point and visited monthly. Temperature and oxygen profiles were recorded in situ (2.5-m depth intervals). Water transparency was determined with a Secchi disc. Some direct measurements of light intensity made with a Li-Cor radiometer at different depths in Lake Sanabria, permitted to calculate the light extinction coefficient (ϵ) and the following $Z_{\text{eu}}-S_{\text{d}}$ relationship (Z_{eu} , euphotic zone, according to Moss, 1980; S_{d} , Secchi depth): $Z_{\text{eu}}=1.92 S_{\text{d}}$. This equation was also applied to calculate Z_{eu} in Valparaíso. Nitrate-nitrogen, nitrite-nitrogen, ammonium-nitrogen, soluble reactive phosphorus (SRP), total phosphorus (TP), soluble reactive silica (SRSi) and chlorophyll *a* were analyzed by standard methods (APHA, 1989; Grasshoff et al., 1983). The depths sampled were always the same in Lake Sanabria during the study period (0, 2.5, 5, 10, 15, 20, 25, 35, and 45 m) but samples were taken at five variable depths in Valparaíso (two included in the epilimnion, one in the metalimnion and two in the hypolimnion). Phytoplankton samples were preserved in Lugol's solution, and counted using the Utermöhl method (Sournia, 1978). Species cell volume was calculated from direct measurements of several individuals of the population, and then applying the most suitable geometric formula in each case.

Results and discussion

Main physical and chemical aspects and trophic status

Both ecosystems are of monomictic type. The stratification period extended in Lake Sanabria from March or April (it depends on the year) to November, and was

Table 2. Annual mean (integrated mean of water column) and range of variation of the main physical, chemical, and phytoplankton parameters in Lake Sanabria and Valparaíso reservoir

		Lake Sanabria		Valparaíso reservoir	
		Mean	Range	Mean	Range
Secchi disc depth	(m)	6.82	5.0–9.10	3.18	2.50–4.0
Euphotic zone	(m)	13.0		6.08	
Oxygen	(mg/l)	8.70	3–10.7	7.07	0–11.4
SRP	($\mu\text{g/l}$)	6.18	0–34	1.59	0.1–12.5
TP	($\mu\text{g/l}$)	8.20	2.6–46.5	9.68	3.8–27.1
NO_3^- -N	($\mu\text{g/l}$)	59.30	0.5–165	20.42	0–83
NO_2^- -N	($\mu\text{g/l}$)	0.11	0–2.5	0.79	0–13
NH_4^+ -N	($\mu\text{g/l}$)	1.20	0–20	0.07	0–1900
SRSi	(mg/l)	1.48	0.9–1.94	0.42	0–2
Chlorophyll <i>a</i>	($\mu\text{g/l}$)	1.89	0–6	7.82	0.9–26.68
Biovolume	(mm^3/m^3)	184.65	38–1020	1254.69	19.30–5861.37

slightly shorter in Valparaíso (from May to October). In spite of longer stratification period, dissolved oxygen concentration was higher in Lake Sanabria (Table 2), where there was no anoxia during all the study period. Oxygen level was very low on the bottom of Valparaíso in July, August and October, and total anoxia was detected in September from 45 to 50 m depth. In a study carried out during the same period as the presented one, Fraile (1994) calculated that the stock of undecomposed organic matter in the bottom of Valparaíso, coming from the vegetation and soil of the original river valley, was responsible for a 20% of the summer consumption of oxygen; the remaining 80% corresponded to the oxidation of sedimented phytoplankton biomass (Fraile, 1994).

Mean Secchi depth in Lake Sanabria was about twice the value of Valparaíso (Table 2). Mean Z_{eu} was 13 m in Lake Sanabria (max. 17.4 m) and 6.08 m in Valparaíso (max. 7.68 m).

A comparison of average concentration of some chemical variables is presented in Table 2. Lake Sanabria showed a slightly higher concentration of SRP, NO_3^- -N and SRSi but a lower of TP than Valparaíso.

Lake Sanabria was nitrogen limited (De Hoyos, 1996) and Valparaíso probably had the same nitrogen-supply pattern. Nitrate concentration always decreased in the epilimnion during the summer in both sites, to even lower than $10 \mu\text{g NO}_3^-$ -N/l. Mineralization process led to maximum nitrate concentration in the hypolimnion in July 1991 in Valparaíso ($83 \mu\text{g NO}_3^-$ -N/l) and at the end of the stratification period in Lake Sanabria (more than $150 \mu\text{g NO}_3^-$ -N/l).

In contrast to nitrate, the SRP amount increased during the summer in Valparaíso and at the end of the stratification period in Lake Sanabria (in the epilimnion and along the whole water column).

Phytoplankton biovolume was several times higher in Valparaíso than in Lake Sanabria (Figure 1, Table 2). Annual biovolume mean was 1254.69 and 184.65 mm^3/m^3 in Valparaíso and Lake Sanabria, respectively. The higher phytoplankton volume in Valparaíso led to a lower SRP, nitrate and SiRP concentrations.

Chlorophyll *a* concentrations were related to biovolume values. Valparaíso showed a higher chlorophyll *a* content (mean, $7.82 \mu\text{g/l}$; max., $26.68 \mu\text{g/l}$) than Lake Sanabria (mean, $1.89 \mu\text{g/l}$; max., $6 \mu\text{g/l}$).

The OECD classification (OECD, 1982), based on annual TP mean, euphotic annual chlorophyll *a* mean, annual chlorophyll *a* maximum, and annual Secchi depth mean, was used to describe the trophic status of the ecosystems. According to the magnitude of these parameters, Lake Sanabria can be classified as an oligotrophic lake and Valparaíso as a mesotrophic one (Table 3).

Annual phytoplankton dynamics and species composition

The annual evolution of phytoplankton volume and the dominating phytoplankton groups were different in the two places. In Lake Sanabria maximum cell volume was recorded in the euphotic zone from May to November (Figure 1). As regards the annual biovolume mean, cryptophytes were the most abundant algae in Lake Sanabria (Figure 2, Table 4).

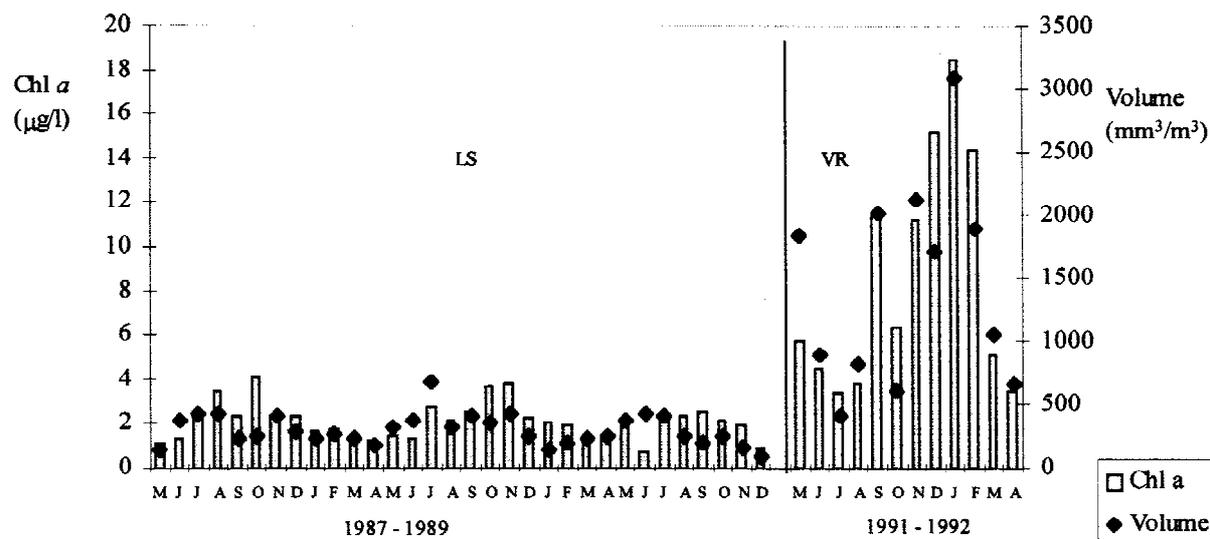


Figure 1. Seasonal changes in chlorophyll *a* concentration and phytoplankton volume. LS, Lake Sanabria (mean, 0–15 m); VR, Valparaíso reservoir (mean, 0–10 m).

Table 3. OECD limits for oligotrophy and mesotrophy, and values recorded from Lake Sanabria and Valparaíso reservoir

		Oligotrophy	Lake Sanabria	Mesotrophy	Valparaíso reservoir
TP annual mean	($\mu\text{g/l}$)	<10.0	8.20	10.0–35.0	9.68
Chl <i>a</i> annual mean	($\mu\text{g/l}$)	<2.5	1.89	2.5–8.0	8.5
Chl <i>a</i> max.	($\mu\text{g/l}$)	<8.0	6	8.0–25.0	26.68
Secchi disc mean	(m)	>6.0	6.82	6.0–3.0	3.18

Table 4. Annual mean volume (integrated mean of water column) of each phytoplankton group in Lake Sanabria and Valparaíso reservoir

	Lake Sanabria	Valparaíso reservoir
Cyanophyta	14.12	33.21
Chlorophyta	42.62	235.51
Bacillariophyceae	32.63	717.36
Raphidophyta		71.01
Euglenophyta		9.43
Cryptophyta	45.97	123.32
Pyrrhophyta	30.21	41.26
Chrysophyceae	15.16	17.31
Xanthophyceae	3.95	6.28

Flagellates dominate phytoplankton biomass in oligotrophic and humic lakes of Northern Europe and North America (Eloranta, 1962, 1989, 1995; Ilmavirta, 1983, 1990; Nygaard, 1978; Sheath & Hellebust, 1978),

mainly due to chrysophytes, a group of minor importance in Lake Sanabria. Cryptophytes can be dominant under oligotrophy, dystrophy or eutrophy (Ilmavirta, 1980; Wojciechowska & Krupa, 1992; Wojciechowska et al., 1996), since they have a wide ecological spectrum (Ilmavirta, 1980). Small chlorophytes and diatoms followed cryptophytes in biovolume contribution in Lake Sanabria.

It is necessary to emphasize that coccal cyanophytes represented 20% of Lake Sanabria phytoplankton volume at times of their highest growth. If we consider the total biovolume of each species (including mucilages of colonial species), phytoplankton was dominated here by cyanophytes and chlorococcales.

Valparaíso showed maximum biovolume during the winter (Figure 1). In summer there was a drastic reduction of biovolume in all of the groups except in the raphidophycean species *Gonyostomum semen*, that had its maximum development at the end of the stratification period. Diatoms dominated the phytoplankton population almost the rest of the year (Fig-

ure 2) and this group had the highest annual mean biovolume; chlorophytes and cryptophytes occupied second and third place, respectively (Table 4). A 42% of chlorophyte volume corresponded to desmids.

Regarding species composition and dominating species, we have found several differences between Lake Sanabria and Valparaíso. Table 5 shows the most important species of each group.

Cyanophyta

The dominant cyanophytes in both ecosystems were coccal species (Chroococcales), but some of the taxa were only important in Lake Sanabria: *Aphanocapsa elachista*, *Coelosphaerium kützingianum*, *Merismopedia tenuissima* and *Microcystis* sp. *Aphanothece clathrata* showed a rather high development in both places. Species found in Lake Sanabria, such as *Microcystis* sp., are generally related to eutrophic conditions. Nevertheless here it was found with *Merismopedia tenuissima* and *Aphanothece clathrata*, both typical of oligotrophic waters (Bozniak & Kennedy, 1968; Ilmavirta, 1980; Rosén, 1981; Round, 1957). An *Anabaena* species appeared in Valparaíso, but heterocystous cyanophytes were not observed in Lake Sanabria.

A strong correlation was found between cyanophytes and water retention time in Lake Sanabria, because the stability of environmental conditions probably favoured cyanophytes (De Hoyos, 1996), as seems to occur in other ecosystems (Barbosa et al., 1995; Reynolds & Walsby, 1975). Water retention time in Valparaíso during the study period permitted an elevated cyanophyte cell number during the summer and all the winter, especially of *Aphanothece clathrata*, although its biovolume contribution did not exceed 1%. The relation between Z_{eu} and Z_m might determine the vertical distribution of cyanophytes in Lake Sanabria (De Hoyos et al., in press). In Valparaíso the appearance and maximum development of *Anabaena* sp. coincided with the summer nitrate depletion (Figure 3). The N_2 fixation ability of *Anabaena* sp. permitted its growth when nitrate was too low for other species. The summer nitrate depletion in Lake Sanabria did not lead to the growth of *Anabaena* sp. in any of the 3 years of the study, which is likely related to the low SRP concentration during that period (De Hoyos & Comin, 1999).

Chlorococcales

The dominating chlorophytes were chlorococcacean species in both sites (Table 5), and their contribu-

tion to total biovolume was very high (Table 4). The most abundant chlorophytes in Lake Sanabria were *Quadricoccus laevis*, *Chlorella* cf. *vulgaris*, *Crucigenia tetrapedia*, and *Crucigenia quadrata*. The first one was not observed in Valparaíso. *Planktosphaeria gelatinosa*, absent in Lake Sanabria, was the most important chlorophyte in Valparaíso, followed by *Crucigenia tetrapedia* and *Oocystis lacustris*. Some species, such as *Monoraphidium komarkovae*, *M. contortum*, *Sphaerocystis schroeteri*, *Botryococcus neglectus* and *Oocystis submarina*, are adapted to oligotrophy and mesotrophy (Komárek & Fott, 1983; Komárek & Marvan, 1992; Reynolds, 1988; Rosén, 1981; Willén, 1992). Other coccal chlorophytes present in Lake Sanabria and/or Valparaíso, such as *Crucigenia quadrata*, *C. tetrapedia*, *Scenedesmus* spp., *Pediastrum* spp., *Dictyosphaerium pulchellum*, *D. ehrenbergianum*, *Coelastrum microporum* or *Tetraedrum minimum*, are considered as eutrophic species (Komárek & Fott, 1983; Rosén, 1981; Willén, 1992). *Ankistrodesmus falcatus* and *Chlorella vulgaris* have been reported in a wide range of nutrient status (Priddle & Happey-Wood, 1983).

In spite of the high number of coccal green-algae cells in Lake Sanabria, the volume of this group was higher in Valparaíso, mainly because of the growth of *Planktosphaeria gelatinosa*. This species has been found in oligotrophic environments (Krienitz et al., 1997; Padišák et al., 1998). It can be often abundant for a short period in late summer (Krienitz et al., 1997).

Most chlorococcacean species in Lake Sanabria and Valparaíso had a small cellular size (and a large cell surface-volume ratio), which favour the nutrient uptake in poor-nutrient environments. Nevertheless, small chlorophytes may constitute the major fraction of phytoplankton population not only in oligotrophic but in eutrophic environments (Priddle & Happey-Wood, 1983; Szlag-Wasielewska, 1998). These algae show in general an opportunistic behavior, responding fast to changes in nutritional supplies because of their short reproduction time (Krienitz et al., 1997).

Desmidiaceae

Desmid population was more important in Valparaíso than in Lake Sanabria (Tables 4 and 5). The main desmid volume contribution in both ecosystems corresponded to the genus *Staurastrum*. *Staurastrum mandfeldtii* var. *annulatum*, the most relevant species in Valparaíso prefers eutrophy (Coesel & Kooijman-Van Blokland, 1994; Negro & De Hoyos, unpub-

Table 5. Species composition of phytoplankton community in Lake Sanabria (LS) and Valparaíso reservoir (VR). *Less than 0.5% of mean volume contribution; **more than 0.5% of mean volume contribution

	LS	VR		LS	VR
CYANOPHYTA					
<i>Anabaena</i> sp.		*	<i>Microcystis</i> sp.		*
<i>Aphanocapsa elachista</i> W. & G. S. West	**		<i>Oscillatoria acutissima</i> Kuff.		*
<i>Aphanothece clathrata</i> W. & G. S. West	*	**	<i>O. chalybea</i> Mertens		*
<i>Aphanothece</i> sp.	*		<i>O. irrigua</i> Kütz.		*
<i>Chroococcus minutus</i> (Kütz.) Näg.		*	<i>O. lacustris</i> (Kleb.) Geitler	*	*
<i>Ch. turgidus</i> (Kütz.) Näg.		*	<i>O. subbrevis</i> Schmidle		*
<i>Coelosphaerium kützingianum</i> Näg.	**	*	<i>Pseudanabaena cf. catenata</i> Lauterborn	*	*
<i>Merismopedia glauca</i> (Ehr.) Näg.	*	*	<i>Rabdoderma lineare</i> Smidle et Lauterborn	*	
<i>M. tenuissima</i> Lemmerm.	**		<i>Synechococcus</i> sp.	**	*
CHLOROPHYTA (without Zygnematales)					
<i>Ankistrodesmus falcatus</i> (Corda) Ralfs	*	*	<i>Monoraphidium contortum</i> (Thur.) Kom.-Legn.	*	*
<i>A. fasciculatus</i> (Lundb.) Kom.-Legn.	*		<i>M. komarkovae</i> Nyg.	**	*
<i>A. fusiformis</i> Corda	*	*	<i>M. tortile</i> (W. & G. S. West) Kom.-Legn.		*
<i>A. gelifactum</i> (Chod.) Bourr.	*		cf. <i>Neochloris minuta</i> Arce & Bold	*	*
<i>Ankyra lanceolata</i> (Kors.) Fott		*	<i>Oocystis lacustris</i> Chod.	*	**
<i>Asterococcus limneticus</i> G. M. Smith	*	*	<i>O. naegeli</i> A. Br.	*	
<i>Botryococcus neglectus</i> (W. & G. S. West) Kom. & Marvan	**	*	<i>O. rhomboidea</i> Fott	*	
<i>Chlamydomonas botryopara</i> Rodhe & Skuja	*		<i>O. submarina</i> Lagerh.	**	*
<i>Chlamydomonas</i> sp.	*		<i>Pandorina morum</i> (O. F. Müll.) Bory	*	
<i>Chlorella cf. vulgaris</i> Beij.	**		<i>Pediastrum duplex</i> Meyen		*
<i>Closteriopsis acicularis</i> (G. M. Smith) Belch. & Swale		*	<i>P. privum</i> (Printz) E. H. Hegew	*	*
<i>Coelastrum microporum</i> Näg.	*		<i>P. tetras</i> (Ehr.) Ralfs	*	*
<i>C. pulchrum</i> Schmidle		*	<i>Pedinomonas minutissima</i> Skuja	**	*
<i>Crucigenia quadrata</i> Morr.	**	*	<i>Planktosphaeria gelatinosa</i> G. M. Smith		**
<i>C. tetrapedia</i> (Kirchn.) W. & G. S. West	**	*	<i>Pseudosphaerocystis lacustris</i> (Lemmerm.) Nováková	*	*
<i>Crucigeniella pulchra</i> (W. & G. S. West) Kom.	*	*	<i>Quadricoccus laevis</i> Fott	**	
<i>Dictyosphaerium pulchellum</i> Wood	*	*	<i>Quadrigula closterioides</i> (Bohl.) Printz	*	*
<i>D. sphagnale</i> Hinddák	*		<i>Q. pfitzeri</i> (Schröd.) G. M. Smith	*	*
<i>D. subsolitarium</i> Van Goor	*	*	<i>Radiococcus cf. bavaricus</i> (Skuja) Kom.	**	
<i>Dimorphococcus lunatus</i> A. Br.		*	<i>Scenedesmus acuminatus</i> (Lagerh.) Chod.		*
<i>Elakatothrix gelatinosa</i> Wille	*	*	<i>Sc. acutus</i> Meyen	*	
<i>Gloeococcus alsius</i> (Skuja) Fott & Nováková		*	<i>Sc. disciformis</i> (Chod.) Fott & Kom.		*
<i>Gonium pectorale</i> O. F. Müller		*	<i>Sc. magnus</i> Meyen	*	
<i>G. sociale</i> (Dujard.) Warm.	*		<i>Sc. ovalternus</i> Chod.	*	*
<i>Gyromitus cordiformis</i> Skuja	**	**	<i>Sc. sooi</i> Hortob	*	
<i>Kirchneriella contorta</i> (Schmidle) Bohl.	*		<i>Scenedesmus</i> spp.	*	*
<i>K. microscopica</i> Nyg.	*	*	<i>Sphaerocystis schroeteri</i> Chod.	**	*
<i>Lobococcus</i> sp.		*	<i>Tetraedron caudatum</i> (Corda) Hansg.		*
<i>Monomastix astigmata</i> Skuja	*	*	<i>T. minimum</i> (A. Br.) Hansg.	*	*
ZYGNEMATALES					
<i>Arthrodesmus incus</i> var. <i>ralfssii</i> W. & G. S. West	*	*	<i>Mougeotia</i> sp.	*	*
<i>Closterium acutum</i> var. <i>variabile</i> (Lemmerm.) W. Krieg.	*	**	<i>Sphaerosoma granulatum</i> Roy & Biss.	*	*
<i>Cl. cornu</i> Ehr. ex Ralfs		*	<i>S. vertebratum</i> (Bréb.) Ralfs	*	
<i>Cl. diana</i> Ehr. ex Ralfs	*	*	<i>Spondylosium planum</i> (Wolle) W. & G. S. West	*	*
<i>Cl. incurvum</i> Bréb.	*		<i>S. pygmaeum</i> (Cooke) West.	*	*
<i>Cl. intermedium</i> Ralfs		*	<i>Spyrogyra</i> sp.	*	*

Continued on p. 31

Table 5. Continued

	LS	VR		LS	VR
<i>Cl. parvulum</i> Nägeli		*	<i>Staurastrum anatinum</i> Cooke & Wills	**	*
<i>Cl. setaceum</i> Ehr. ex Ralfs		*	<i>St. arctiscon</i> (Ehr.) Lund	*	
<i>Cosmarium contractum</i> Kirchn.		*	<i>St. brachiatum</i> Ralfs	*	*
<i>C. contractum</i> var. <i>minutum</i> (Delp.) W. & G. S. West		*	<i>St. denticulatum</i> (Näg.) Arch.	**	*
<i>C. humile</i> (Gay) Nordstedt in De Toni		*	<i>St. manfeldtii</i> var. <i>annulatum</i> W. & G. S. West		**
<i>C. margaritifera</i> Menegh. ex Ralfs		*	<i>St. paradoxum</i> var. <i>longipes</i> Nordst.		*
<i>C. punctulatum</i> Bréb.		*	<i>St. teliferum</i> Ralfs		*
<i>C. subarctoum</i> (Lagerh.) Raciborski		*	<i>St. tohopekaligense</i> Wolle	*	*
<i>Cosmarium</i> sp.	*		<i>Staurodesmus extensus</i> (Anderson) Teiling		*
<i>Cosmocladium constrictum</i> Arch. ex Joshua	*	*	<i>Std. glabrus</i> (Ehr.) Teiling	*	*
<i>Euastrum ansatum</i> Ehr. ex Ralfs		*	<i>Std. jaculiferus</i> (West.) Teiling	**	*
<i>Hyalotheca dissilens</i> (Sm.) Bréb.		*	<i>Xanthidium antilopaeum</i> (Bréb.) Kütz	*	
BACILLARIOPHYCEAE					
<i>Achnantes lanceolata</i> Bréb.	*		<i>F. crotonensis</i> Kitton		*
<i>A. minutissima</i> Kütz.		*	<i>Frustulia rhomboides</i> (Ehr.) De Toni	*	*
<i>Anomoeoneis seriens</i> (Bréb.) C.	*		<i>Gomphonema acuminatum</i> Ehr.	*	
<i>A. vitrea</i> (Grün.) Ross	*		<i>G. constrictum</i> Ehr.	*	
<i>Asterionella formosa</i> Hassall		**	<i>G. gracile</i> Ehr.	*	
<i>Aulacoseira distans</i> (Ehr.) Simonsen	**	*	<i>Meridion circulare</i> Agardh	*	
<i>A. granulata</i> (Ehr.) Simonsen	*	*	<i>Navicula cari</i> Ehr.	*	
<i>A. granulata</i> var. <i>angustissima</i> (O. Müll.) Simonsen	*	*	<i>N. cryptocephala</i> Kütz.	*	*
<i>Cyclotella glomerata</i> Bachmann	**	*	<i>N. subtilissima</i> Cleve		*
<i>C. stelligera</i> Cleve & Grunow	*	*	<i>Nitzschia</i> spp.	*	*
<i>Cymbella ventricosa</i> Kütz.	*	*	<i>Pinnularia brebissonii</i> (Kütz.) Rabh.	*	
<i>Diatoma mesodon</i> (Ehr.) Kütz.	*		<i>P. gibba</i> Ehr.	*	*
<i>Eunotia lunaris</i> Bréb.		*	<i>P. subcapitata</i> Greg.	*	
<i>E. pectinalis</i> (Dillwyn) Rabenh.	*	*	<i>P. viridis</i> (Nitz.) Ehr.		*
<i>E. praerupta</i> Ehr.	*		<i>Rhizosolenia longiseta</i> Zach.	**	*
<i>E. valida</i> Hustedt	*		<i>Stauroneis phoenicenteron</i> (Nitzs.) Ehr.	*	
<i>Fragilaria arcus</i> (Ehr.) Cleve	*	*	<i>Surirella linearis</i> W. Smith	*	
<i>F. brevistriata</i> Grunow	*	*	<i>Synedra ulna</i> (Nitzs.) Ehr.	*	
<i>F. capucina</i> Desm.	*		<i>Tabellaria fenestrata</i> (Lyng.) Kütz.	*	**
<i>F. construens</i> f. <i>binodis</i> (Ehr.) Hustedt		*	<i>T. flocculosa</i> (Roth) Kütz.	**	*
RAPHIDOPHYTA					
<i>Gonyostomum semen</i> (Ehr.) Diesing		**			
EUGLENOPHYTA					
<i>Astasia hypolimnica</i> Skuja		*	<i>Trachelomonas curta</i> Da Cunha em. Delf.		*
<i>Euglena</i> spp.	*	*	<i>T. hispida</i> (Perty) Stein in Defl.	*	*
<i>Phacus</i> spp.		*	<i>T. volvocina</i> Ehr.	*	*
<i>Rhabdomonas incurva</i> Fres.		*	<i>Trachelomonas</i> sp.		*
CRYPTOPHYTA					
<i>Cryptomonas</i> spp.	**	**	<i>Rhodomonas minuta</i> Skuja	**	**
<i>Katablepharis ovalis</i> Skuja	**	**			
PYRRHOPHYTA					
<i>Amphidinium elenkinii</i> Skvorcov	*	*	<i>Gymnodinium</i> spp.	**	*
<i>Amphidinium</i> sp.		*	<i>Katodinium schilleri</i> (Wolosz.) Loebli.	*	

Continued on p. 32

Table 5. Continued

	LS	VR		LS	VR
<i>Ceratium hirundinella</i> (O. F. Müll.) Dujard.	**	*	<i>Peridinium cinctum</i> Ehr.	**	*
<i>Gymnodinium uberrimum</i> (Allman) Kofoid & Swezy	**	**	<i>P. umbonatum</i> Stein	**	*
CHRYSOPHYCEAE					
<i>Bitrichia ochridana</i> (Fott) Bourrelly	*	*	<i>Mallomonas</i> spp.	**	*
<i>Crhysostephanosphaera globulifera</i> Scherffel		*	<i>Monosiga</i> sp.		*
<i>Dinobryon bavaricum</i> Imhof		*	<i>Ochromonas</i> spp.	**	*
<i>Dinobryon</i> spp.	*	*	<i>Pseudopedinella</i> cf. <i>erkensis</i> Skuja	**	*
<i>Kephyrion rubri-claustri</i> W. Conrad	*		cf. <i>Syncrypta volvox</i> Ehr.	*	
<i>Mallomonas akrokomos</i> Ruttner	*		<i>Synura</i> spp.	*	*
XANTHOPHYCEAE					
<i>Isthmochloron trispinatum</i> (W. & G. S. West) Skuja		*	<i>Nephrوديella lunaris</i> Pascher	**	**

lished), whereas *Staurastrum anatinum*, more abundant in Lake Sanabria, is frequent in oligotrophic waters (Tassigny, 1973). *Closterium acutum* var. *variabile*, abundant in Valparaíso, has been reported as an important species in mesotrophic and eutrophic environments (Coesel & Kooijman-van Blokland, 1994; Tassigny, 1973), but it can also be found in nutrient-poor lakes (Willén, 1992).

The higher volume of desmids in Valparaíso could be related to the organic matter content of the reservoir after filling. Duthie (1965) reported that the maximum peak of desmids coincided with the maximum dissolved organic matter. Nevertheless, the distribution of desmids in Lake Sanabria, parallel to cyanophytes, coincided with periods of low water renewal (De Hoyos, 1996), when water colour (and hence dissolved organic matter) was low too.

Bacillariophyceae

Species composition and diatom abundance is one of the most relevant phytoplankton differences between Lake Sanabria and Valparaíso. In the former, the major diatoms were centric species (Table 5): *Aulacoseira distans*, *Cyclotella glomerata* and *Cyclotella stelligera*. *Aulacoseira distans* and *Aulacoseira granulata* were abundant in Valparaíso, but the pennate taxa *Tabellaria fenestrata* and *Asterionella formosa* dominated the diatom population and were responsible for the winter biovolume maximum. *A. formosa* was almost absent in Lake Sanabria. *Tabellaria fenestrata* and *Asterionella formosa* are frequent algae (and often found together) in oligo-mesotrophic or mesotrophic

environments (Duthie & Hart, 1987; Eloranta, 1995; Howard, 1968; Petrova, 1987; Rosén, 1981), or they become dominant species when nutrient supply increases (Lachavanne, 1980; Olsén & Willén, 1980). *A. formosa* and *T. fenestrata* can also grow under more extreme nutrient supply such as oligotrophy (Bozniak & Kennedy, 1968; Ilmavirta, 1975; Spaulding et al., 1993; Tassigny, 1973) or hypereutrophy (Alhonen & Mantere-Alhonen, 1988). Bozniak & Kennedy (1968) reported a relationship between the increase in *Asterionella formosa* number and increase in nitrate level. *Aulacoseira granulata*, which showed a higher volume in Valparaíso, prefers eutrophic conditions (Lund, 1962; Moustaka-Gouni & Tsekos, 1989; Rosén, 1981), and is rare or absent in oligotrophic lakes (Lund, 1962). The most abundant diatom in Lake Sanabria, *Aulacoseira distans*, is a good indicator of oligotrophy (Ilmavirta, 1975; Ilmavirta, 1980; Rosén, 1981). *Rhizosolenia longiseta*, quite numerous in this lake, is also related to oligotrophy (Ilmavirta, 1975) or oligo-mesotrophy (Rosén, 1981). Other characteristic diatoms in Lake Sanabria, such as *Cyclotella glomerata* and *C. stelligera*, are typical phytoplankton components in oligotrophic lakes (Hutchinson, 1967; Moore, 1971, 1978; Reynolds, 1996; Sheath & Steinman, 1982), although *C. glomerata* also grows in nutrient-rich environments (Kalff et al., 1975).

Diatoms were inversely related to SRSi and to SRP in both sites due to the nutrient assimilation, although the inverse relation to SRP concentration may support the idea that this algae are good SRP competitors (Sommer, 1988; Tilman et al., 1986).

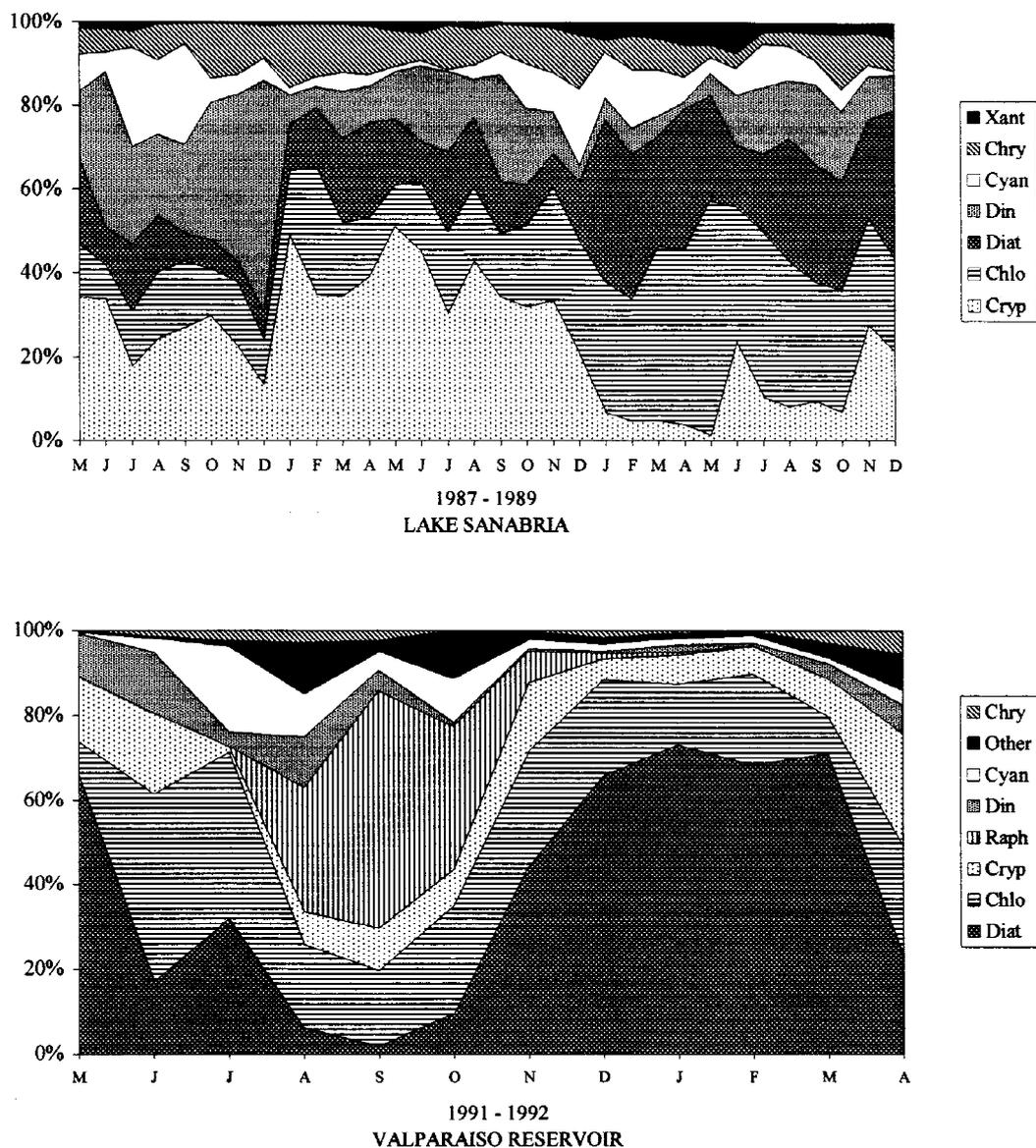


Figure 2. Phytoplankton volume dynamics in Lake Sanabria and Valparaíso reservoir. Xant, xantophytes; Chry, chrysophytes; Cyan, cyanophytes; Din, dinoflagellates; Diat, diatoms; Chlo, chlorophytes; Crypt, cryptophytes; Raph, raphidophytes.

Raphidophyta

Gonyostomum semen, the only species belonging to Raphidophyta we found, was present exclusively in Valparaíso. Although it has also been reported in some ecosystems of Segundera mountains (Negro et al., in press), it was nonetheless absent in Lake Sanabria during all the study period. *G. semen* appeared in Valparaíso during thermal stratification, concentrating in the epilimnion, and representing the major fraction of total biovolume of summer phytoplankton (Figure 2).

Its maximum occurred in September (10 m depth), leading to the highest chlorophyll *a* peak (Figure 4). Such annual distribution and the relation between *G. semen* and chlorophyll *a* has been reported in other ecosystems (Cronberg et al., 1988; Le Cohu et al., 1989; Lepistö et al., 1994; Van Den Avyle et al., 1982). *G. semen*, a quite frequent species in Nordic countries (Cronberg et al., 1988; Lepistö et al., 1994), is generally associated with rich humic lakes (Eloranta, 1995; Rosén, 1981) and is favoured by moderate phosphor-

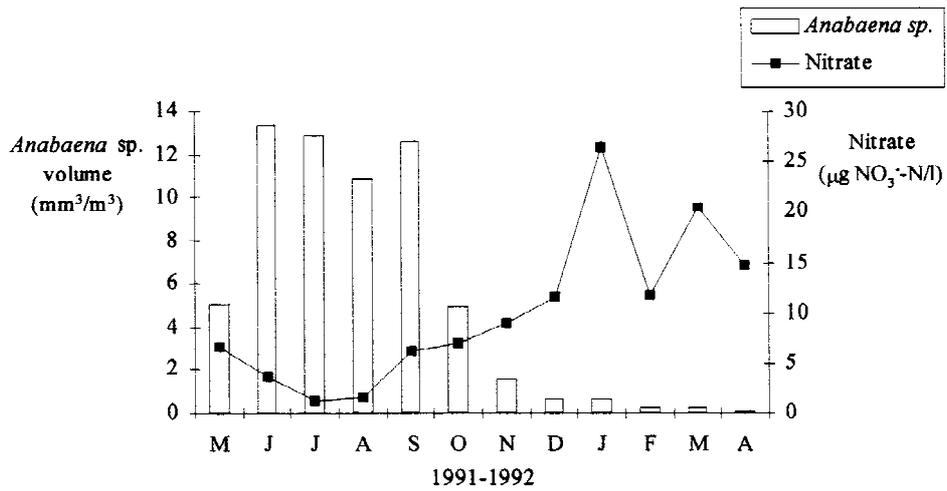


Figure 3. Epilimnion dynamics (mean, 0–10 m) of nitrate concentration and *Anabaena sp.* volume in Valparaíso reservoir.

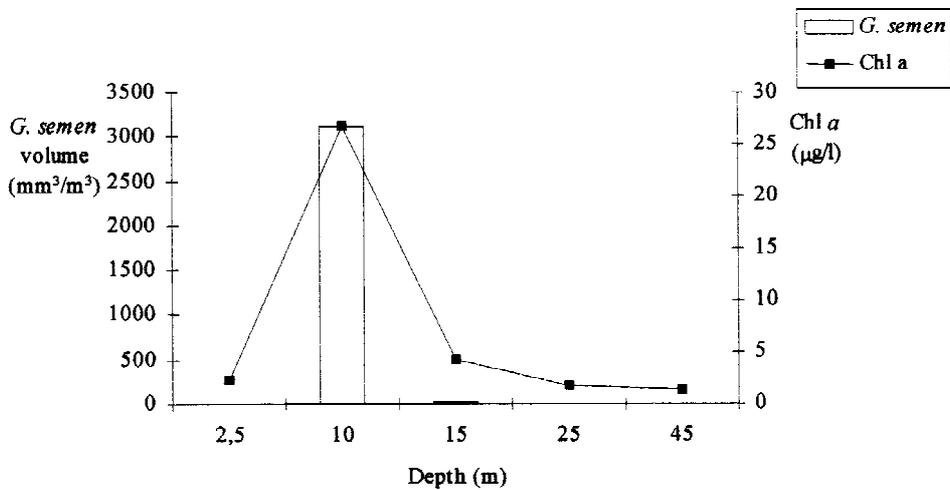


Figure 4. Depth variations of *Gonyostomum semen* volume and chlorophyll *a* concentration in September 1991 in Valparaíso reservoir.

ous concentration, but not with increased eutrophy (Rosén, 1981). In fact, high phytoplankton volume in lakes with *G. semen* is not an indicator of eutrophy (Eloranta, 1995).

Rest of phytoplankton groups

There were little differences within the remaining phytoplankton groups between Lake Sanabria and Valparaíso.

Species composition of cryptophytes and dinoflagellates was almost the same in both sites (Table 5). The major fraction of cryptophyte volume in Lake Sanabria corresponded to *Cryptomonas* species and to *Rhodomonas minuta* in Valparaíso. The highest presence of cryptophytes was detected in Lake Sanabria

during the periods of high water supply (and water colour), suggesting a relationship between cryptophytes and humic matter. The unarmoured dinoflagellates were the most relevant species regarding volume contribution in both sites. Among armoured species, *Ceratium hirundinella* only showed a relatively important contribution in Lake Sanabria.

Chrysophytes had a low importance in both places. This might be related to the key role played by nitrogen in this sites as compared to other lakes where chrysophytes are abundant and where phosphorus is the major nutrient controlling phytoplankton growth (De Hoyos et al., 1998). Species number and volume of chrysophytes were higher in Lake Sanabria than in Valparaíso (Tables 4 and 5). Chrysophytes are

frequently dominant in oligotrophic lakes (Duthie & Hart, 1987; Eloranta, 1989, 1995; Ilmavirta, 1980; Moore, 1978, 1971; Nygaard, 1978; Rosén, 1981). Nevertheless, Kristiansen (1986) pointed out that chrysophytes are not good oligotrophy indicators (especially scaled chrysophytes), as they can reach high numbers in eutrophic ecosystems.

Euglenophytes were found only occasionally in Lake Sanabria. The main species found in Valparaíso were *Trachelomonas hispida* and *T. volvocina*. Euglenophytes in general, and *Trachelomonas* species in particular, are associated with organic-matter rich environments and eutrophy (Ilmavirta, 1980; Rosén, 1981; Round, 1957; Wojciechowska & Krupa, 1992; Wojciechowska et al., 1996), but they often appear during a short period and do not dominate the phytoplankton population. In Valparaíso euglenophytes represented a 6% of the total biovolume in October, and were quite abundant during the rest of the autumn and summer.

Xanthophyceae was a minor group. *Nephrوديella lunaris* was the xanthophycean species found with a certain presence in both sites (Table 5).

Conclusions

The comparison of the oligotrophic Lake Sanabria and mesotrophic Valparaíso reservoir has shown some differences in phytoplankton volume and species composition. Valparaíso presented a higher biovolume and chlorophyll *a* concentration, related to its higher trophic status, and was dominated by diatoms, whereas the most important fraction of phytoplankton volume in Lake Sanabria corresponded to flagellates (cryptophytes).

The most characteristic species of each group found in the studied ecosystems are generally typical phytoplankton components in oligotrophic, mesotrophic, and humic lakes.

Cyanophytes were of a quite high importance in both places, but the dominating species were different. Nitrate shortage in the epilimnion limited the growth of phytoplankton in Valparaíso during the summer but favoured the growth of *Anabaena* sp. Because Lake Sanabria is also a nitrogen-limited ecosystem, it is likely that an increase in phosphorus concentration could lead to the appearance of heterocystous cyanophytes as occurred in Valparaíso, a hypothesis supported in previous studies on this lake.

The most relevant chlorophytes in Valparaíso were *Planktosphaeria gelatinosa*, *Staurastrum manfeldtii* var. *annulatum* and *Closterium acutum* var. *variabile*. In Lake Sanabria *Quadricoccus laevis* and some other coccal green algae (*Chlorella* cf. *vulgaris*, *Crucigenia quadrata*, *Crucigenia tetrapedia*) dominated the chlorophyte population.

Pennate taxa were the most abundant diatoms in Valparaíso (*T. fenestrata* and *A. formosa*) and central species in Lake Sanabria (*A. distans* and *C. glomerata*).

In Valparaíso we have found the raphidophycean algae *Gonyostomum semen*, also present in some mountain lakes in Segundera mountains, but absolutely absent in Lake Sanabria during the 3 years of study. The growth of *G. semen* in Valparaíso could be related to a high content of organic matter coming from the decomposition of vegetation of the recently filled Tera river valley. The higher presence of desmids and euglenophytes in Valparaíso could also be related to the organic matter content.

References

- Alhonen, P. & S. Mantere-Alhonen, 1988. Seasonal variation in the phytoplankton composition and biomass of two hypereutrophic lakes in southern Finland. Mem. Soc. Fauna Flora Fenn. 64: 57–64.
- APHA, 1989. Standard Methods for the Examination of Water, Sewage and Wastewater. 17th edn. American Public Health Association, Washington, DC, 1550 pp.
- Barbosa, F. A. R., C. E. M. Bicudo & V. L. De Moraes. 1995. Phytoplankton studies in Brazil: community structure variation and diversity. In Tundisi, G., C.E.M. Bicudo & T. Tundisi (eds), Limnology in Brazil. ABC/SBL, Rio de Janeiro.
- Bengochea, C. 1991. Valparaíso Dam-Tera river first filling experiences. Int. Commission Large Dams 64: 67–83.
- Bozniak, E. G. & L. L. Kennedy, 1968. Periodicity and ecology of the phytoplankton in an oligotrophic and eutrophic lake. Can. J. Bot. 46: 1259–1271.
- Coesel, P. & H. Kooijman-van Blokland, 1994. Distribution and seasonality of desmids in the Maarsveen Lakes area. Neth. J. aquat. Ecol. 28: 19–24.
- Cronberg, G., G. Lindmark & S. Björk, 1988. Mass development of the flagellate *Gonyostomum semen* (Raphidophyta) in Swedish forest lakes – an effect of acidification? Hydrobiologia 161: 217–236.
- De Hoyos, C., 1996. Limnología del Lago de Sanabria. Variabilidad interanual del fitoplancton. Tesis doctoral. Universidad de Salamanca, 438 pp.
- De Hoyos, C., J. J. Aldasoro, M. Toro & F. A. Comín, 1998. Specific composition and ecology of chrysophyte flagellates in Lake Sanabria (NW. Spain). Hydrobiol. 369/370 (Dev. Hydrobiol. 129): 287–295.
- De Hoyos, C. & F. A. Comín, 1999. The importance of inter-annual variability for management. Hydrobiologia 395/396 (Dev. Hydrobiol. 136): 281–291.

- De Hoyos, C., F. Comín, J. J. Aldasoro & J. C. Vega, 1999. Las cianofíceas en el Lago de Sanabria: significado y variabilidad estacional. In: Conservación de lagos y humedales de alta montaña de la Península Ibérica. Servicio de publicaciones de la Universidad Autónoma de Madrid (in press).
- Duthie, H. C., 1965. A study of the distribution and periodicity of some algae in a bog pool. *J. Ecol.* 53: 343–359.
- Duthie, H. C. & C. J. Hart, 1987. The phytoplankton of the subarctic Canadian Great Lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 25: 1–9.
- Eloranta, P., 1962. The phytoplankton of some subarctic lakes in Finnish Lapland. *Mem. Soc. Fauna Flora Fenn.* 62: 41–57.
- Eloranta, P., 1989. Scaled chrysophytes (Chrysophyceae and Synurophyceae) from national park lakes in southern and central Finland. *Nord. J. Bot.* 8: 671–681.
- Eloranta, P., 1995. Phytoplankton of the national park lakes in central and southern Finland. *Ann. Bot. Fenn.* 32: 193–209.
- Fraile, H., 1994. Limnología comparada del sistema de embalses del río Tera. Doctoral thesis. Departamento de Biología Vegetal y Ecología. Universidad del País Vasco, 231 pp.
- Grasshoff, K., M. Ehrhardt & K. Kremling, 1983. *Methods of Seawater Analysis*. Verlag Chemie, Weinheim; 419 pp.
- Howard, H. H., 1968. Phytoplankton studies of Adirondack mountain lakes. *Am. Midland Nat.* 80: 413–427.
- Hutchinson, G. E., 1967. *Treatise on Limnology*. Volume II. Introduction to Lake Biology and the Limnoplankton. New York, John Wiley & Sons, 1114 pp.
- Ilmavirta, V., 1975. Dynamics of phytoplanktonic production in the oligotrophic lake Pääjärvi, southern Finland. *Ann. Bot. Fenn.* 12: 45–54.
- Ilmavirta, V., 1980. Phytoplankton in 35 Finnish brown-water lakes of different trophic status. In Dokulil, M., H. Metz & D. Jewson (eds), *Shallow Lakes' Contributions to their Limnology*. Developments in Hydrobiology 3. Dr W. Junk Publishers, The Hague: 121–130.
- Ilmavirta, V., 1983. The role of flagellated phytoplankton in chains of small brown-water lakes in southern Finland. *Ann. Bot. Fenn.* 20: 187–195.
- Ilmavirta, V., 1990. Occurrence of phytoplankton species along nutrient, pH and color gradients in Eastern Finnish lakes. *Int. Ver. Theor. Limnol.* 24: 702–706.
- Kalff, J. & R. Knoechel, 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. *Ann. Rev. Ecol. Syst.* 9: 475–495.
- Kalff, J., H. J. Kling, S. H. Holmgren & H. E. Welch, 1975. Phytoplankton, phytoplankton growth and biomass cycles in an unpolluted and in a polluted polar lake. *Verh. int. Verein. Limnol.* 19: 487–495.
- Komárek, J. & B. Fott, 1983. Chlorophyceae (Grünalgen), Ordnung: Chlorococcales. In: Huber-Pestalozzi, G. (ed.), *Das Phytoplankton des Süßwassers: Systematik und Biologie*. 7 Teil. E. Schweizerbart schein Verlagsbuchhandlung, Stuttgart, 1044 pp.
- Komárek, J. & P. Marvan, 1992. morphological differences in natural populations of the genus *Botryococcus* (Chlorophyceae). *Arch. Protistenkd.* 141: 65–100.
- Krienitz, L., A. Hehmann & S. J. Casper, 1997. The unique phytoplankton community of a highly acidic bog lake in Germany. *Nova Hedwigia* 65 (1–4): 411–430.
- Kristiansen, J., 1986. Silica-scale bearing Chrysophytes as environmental indicators. *Br. Phycol. J.* 21: 425–436.
- Lachavanne, J. B., 1980. Les manifestations de l'eutrophisation des eaux dans un grand lac profond: le Léman (Suisse). *Schweiz. Z. Hydrol.* 42: 127–152.
- Le Cohu, R., J. Guitard, N. Comoy & J. Brabet, 1989. *Gonyostomum semen* (Raphidophycées), nuisance potentielle des grands réservoirs français? L'exemple du lac de Pareloup. *Arch. Hydrobiol.* 117: 225–236.
- Lepistö, L., S. Antikainen & J. Kivinen, 1994. The occurrence of *Gonyostomum semen* (Ehr.) Diesing in Finnish lakes. *Hydrobiologia* 273: 1–8.
- Lund, J. W. G., 1962. Phytoplankton from some lakes in Northern Saskatchewan and from Great Slave Lake. *Can. J. Bot.* 40: 1499–1514.
- Moore, J. W., 1971. Patterns of distribution of phytoplankton in Northern Canada. *Nova Hedwigia* 21: 923–1035.
- Moore, J. W., 1978. Distribution and abundance of phytoplankton in 153 lakes, rivers, and pools in the Northwest Territories. *Can. J. Bot.* 56: 1765–1773.
- Moss, B., 1980. *Ecology of Fresh Waters*. Blackwell, Oxford, 332 pp.
- Moustaka-Gouni, M. & I. Tsekos, 1989. The structure and dynamics of the phytoplankton assemblages in Lake Volvi, Greece. II. Phytoplankton biomass and environmental factors. *Arch. Hydrobiol.* 115: 575–588.
- Negro, A. I., C. De Hoyos, A. Del Río & R. Le Cohu, 1994. Comparación de las comunidades fitoplanctónicas en dos embalses de reciente creación: Riaño y Valparaíso (España). *Limnética* 10: 115–121.
- Negro, A. I., C. De Hoyos, J. J. Aldasoro & J. C. Vega. Comparación del fitoplancton de dos ecosistemas de montaña: Laguna y Turbera de La Clara (Sierra Segundera, Zamora). In: Conservación de Lagos y humedales de alta montaña de la Península Ibérica. Servicio de Publicaciones de la Universidad Autónoma de Madrid (in press).
- Nygaard, G., 1978. Freshwater phytoplankton from the Narssaq Area, South Greenland. *Bot. Tidssk.* 73: 3–4.
- OECD, 1982. *Eutrophication of waters. Monitoring, assessment and control*. Paris, 154 pp.
- Olsén, P. & E. Willén, 1980. Phytoplankton response to sewage reduction in Vättern, a large oligotrophic lake in Central Sweden. *Arch. Hydrobiol.* 89: 171–188.
- Padisák, J., L. Krienitz, W. Scheffler, R. Koschel, J. Kristiansen & I. Grigorszky, 1998. Phytoplankton succession in the oligotrophic Lake Stechlin (Germany) in 1994 and 1995. *Hydrobiologia* 369/370 (Dev. Hydrobiol. 129): 179–197.
- Petrova, N.A., 1987. The phytoplankton of Ladoga and Onega lakes and its recent successional changes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 25: 11–18.
- Priddle, J. & C. M. Happey-Wood, 1983. Significance of small species of chlorophyta in freshwater phytoplankton communities with special reference to five Welsh Lakes. *J. Ecol.* 71: 793–810.
- Reynolds, C. S., 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton. In Sandgren, C.D. (ed.), *Growth and Reproductive Strategies of Freshwater Phytoplankton*. Cambridge University Press, Cambridge: 388–426.
- Reynolds, C.S., 1996. Further remarks on phytoplankton ecology and trophic degree: community structure and dynamics in relation to the trophic spectrum. Unpublished manuscript.
- Reynolds, C. S. & A. E. Walsby, 1975. Water-blooms. *Biol. Rev.* 50: 437–481.
- Rosén, G., 1981. Phytoplankton indicators and their relations to certain chemical and physical factors. *Limnologica* (Berlin) 13: 2263–2290.
- Round, F. E., 1957. Studies on bottom-living algae in some lakes of the English Lake District. *J. Ecol.* 45: 649–664.

- Sheath, R. G. & J. A. Hellebust, 1978. Comparison of algae in the euplankton, tychoplankton, and periphyton of a tundra pond. *Can. J. Bot.* 56: 1472–1483.
- Sheath, R. G. & A. D. Steinman, 1982. A checklist of freshwater algae of the Northwest territories, Canada. *Can. J. Bot.* 60: 1964–1997.
- Sommer, U., 1988. Growth and survival strategies of planktonic diatoms. In Sandgren, C.D. (ed.), *Growth and Reproductive Strategies of Freshwater Phytoplankton*. Cambridge University Press, Cambridge: 227–260.
- Sournia, A., 1978. *Phytoplankton Manual*. UNESCO, 337 pp.
- Spaulding, S. A., J. V. Ward & J. Baron, 1993. Winter phytoplankton dynamics in a subalpine lake, Colorado, USA. *Arch. Hydrobiol.* 129: 179–198.
- Szelag-Wasielewska, E., 1998. Pico-, nano- and microphytoplankton in pelagial of small artificial reservoirs in Spring. *Int. Rev. Hydrobiol.* 83: 509–514.
- Tassigny, M., 1973. Observations des variations qualitatives des populations des Desmidiées dans quelques étangs mésotrophes et dystrophes. *Beih. Nova Hedwigia* 42: 283–316.
- Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham & F. A. Johnson. 1986. Green, bluegreen and diatom algae. Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. *Arch. Hydrobiol.* 106 (4): 473–485.
- Van Den Avyle, M. J., D. W. Allard, T. M. Dreier & W. J. Clark, 1982. Effects of diel phytoplankton migrations on chlorophyll *a* vertical profiles in a central Texas pond. *Texas J. Sci.* 34 (1): 69–78.
- Vega, J. C. & J. J. Aldasoro, 1994. Geología de Sanabria. In: *Monografías de la Red de Espacios Naturales de Castilla y León*. Consejería de Medio Ambiente y Ordenación del Territorio (Junta de Castilla y León), Valladolid, 79 pp.
- Vega, J. C., C. De Hoyos & J. J. Aldasoro, 1991. Estudio del sistema de lagunas de las sierras Segundera y Cabrera. In: *Monografías de la Red de Espacios Naturales de Castilla y León*. Consejería de Medio Ambiente y Ordenación del Territorio (Junta de Castilla y León), Valladolid, 47 pp.
- Willén, E., 1992. Planktonic Green Algae in an Acidification Gradient of Nutrient-poor Lakes. *Arch. Protistenkd* 141: 47–64.
- Wojciechowska, W. & D. Krupa, 1992. Many years' and seasonal changes in phytoplankton of lakes of Polesie National Park and its protection zone. *Ekol. Pol.* 40 (3): 317–332.
- Wojciechowska, W., W. Peczuła & A. Zykubek, 1996. Long-term changes in protected lakes (Sobibór Landscape Park, Eastern Poland). *Ekol. Pol.* 44 (1–2): 179–191.