Arch. Hydrobiol. | 126 | 4 | 469–486 | Stuttgart, Februar 1993

Long-term periodicity of *Planktothrix agardhii*, *Pseudanabaena galeata* and *Geitlerinema* sp. in a shallow hypertrophic lagoon, the Albufera of Valencia (Spain)

By Susana Romo and M. Rosa Miracle[1]

University of Valencia

With 5 figures and 5 tables in the text

Abstract

A long-term phytoplankton study was carried out in a shallow hypertrophic lagoon, the Albufera of Valencia (Spain), between 1980 and 1988. The lake serves as a reservoir for surrounding rice cultivation, with two seasonal periods of water retention to keep ricefields flooded. Three persistent species, *Planktothrix agardhii, Pseudanabaena galeata* and *Geitlerinema* sp. maintained dominance throughout. Light intensity, N:P ratio and water residence times seem to be the environmental variables governing the population dynamics of these species. *P. agardhii* was dominant during spring, reaching its maximum numbers under high nutrient concentrations and increasing light intensity, temperature and water stagnation. The periodicity progressed towards *Geitlerinema* sp. dominance in summer, with low water renewal rates and phosphate depletion, and then to *Ps. galeata* in November–December during the second period of water stability. The cyanophyta succession pattern apparently differs from that observed in other European shallow eutrophic lakes.

Introduction

Long-term phytoplankton studies on shallow hypertrophic lakes and on the ecology of the filamentous blue-green algae which usually dominate them are few (Gibson & Fitzsimons 1982; Loogman & Van Liere 1986; Moed & Hoogveld 1982; Berger 1987; Klapwijk 1988). In these nutrient rich systems, severe restriction of light has often been shown to select in favour of filamentous blue-green algae (Reynolds & Walsby 1975; Mur et al. 1977; Zevenboom & Mur 1980; Van Liere & Mur 1980; Reynolds 1984). Several laboratory and field studies (Gibson & Fitzsimons 1982; Berger 1984; Berger & Sweers 1988; Nicklisch & Kohl 1989; Nicklisch et al. 1991) have been made to ascertain the factors controlling the growth performance of *Planktothrix agardhii* (Gom.) Anagn. Kom. and other more slender cyanophytes such as *Limnothrix redekei* (Van Goor) Meffert. The sequence of dominance may de-

---

[1] Address of the authors: Area de Ecología, Facultad de Biología, Universidad de Valencia, 46100 Burjassot, Valencia, España.

0003-9136/93/0126-0469 $ 4.50

pend on various factors such as the different trichome diameter, which is a determinant of reproduction rates (Foy 1980); light-dark photoperiods (Foy et al. 1976; Nicklisch et al. 1981); nutrient requirements (Zevenboom 1980; Wernicke & Nicklisch 1986) and temperature (Jones 1977; Meffert 1989). The influence of the zooplankton on these filamentous blue-green algae has been considered to be negligible (Lyche 1984; Davidowicz et al. 1988).

Only two studies of Spanish shallow hypertrophic ecosystems have been reported (Rojo 1990; Lopez et al. 1991), even though such lakes constitute almost 40 % of the total number of water bodies in the country (Alvarez-Cobelas et al. 1991). Despite the fact that the Albufera of Valencia is the largest Spanish oligohaline coastal lake, few studies concerning its phytoplankton have been published (Pardo 1942; Blanco 1974; Garcia et al. 1984). Since the first descriptions, the phytoplankton has been altered markedly from a mesotrophic to a hypertrophic character (Romo 1991), as a consequence of the increasing pollution (Dafauce 1975; Soria et al. 1987).

The present paper describes the long-term population dynamics and ecology of the three main filamentous blue-green algae species in the Albufera of Valencia, from 1980 to 1988.

Material and methods

Study area

The Albufera of Valencia is a shallow hypertrophic lagoon, located in the Natural Park of the Albufera and Devesa, near the city of Valencia (39° 20′ N,

Table 1. Morphometric features and basic data of the Albufera of Valencia Lake. Meteorological data correspond to the period 1980 – 88.

Mean area	21 km^2
Maximum area	24 km^2
Minimum area	19 km^2
Length	7 km
Breadth	6 km
Perimeter	29 km
Mean depth	1 m
Maximum depth	2 m*
Mean volume	22 Hm^3
Maximum volume	41 Hm^3
Minimum volume	17 Hm^3
Ricefields area	160 km^2
Annual water renewal rate	10 y^{-1}
Mean annual precipitation	435 mm
Mean annual evaporation	901 mm
Air temperature	6 – 30 °C
Mean wind velocity	6 km/h
Daily average sunshine	7 h
Mean solar radiation	353 cal cm^{-2} d^{-1}

* up to 3 m in some dredging points.

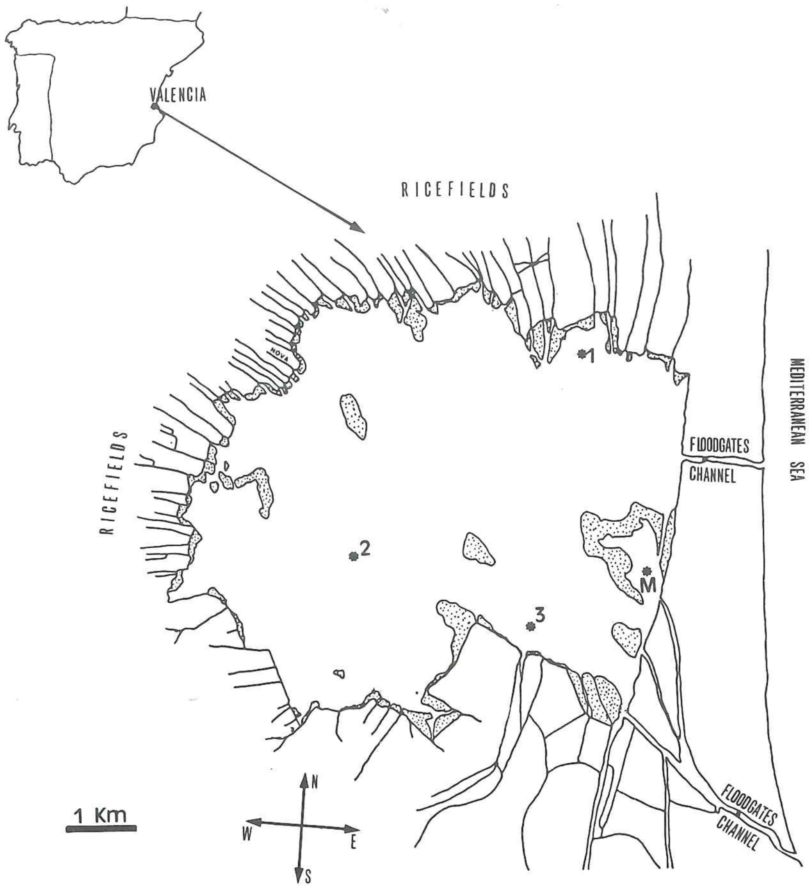

Fig. 1. Map of the Albufera of Valencia showing location, sampling sites and outlet channels.

0° 20′ W). It is an exposed polymictic lake. Its main morphometric features are shown in Table 1.

Originally, the lagoon was an extensive gulf which later became separated from the Mediterranean Sea by a sand bar (Rosello 1972). This sand bar is nowadays crossed by three channels, connecting the lagoon to the sea. The southernmost of them, crosses an extensive zone of ricefields before flowing into the sea. Water level of the lagoon is regulated by sluice gates situated at the channels (Fig. 1).

Since the last century, the lagoon has functioned as a reservoir for the demands of the surrounding rice cultivation. The hydrological cycle of the lake can be briefly described as follows (Fig. 2): from April to September the sluices are almost closed to allow a slow flow during rice cultivation in the flooded ricefields. From September to October, the floodgates are opened to empty the fields for rice ripening and harvest. Then, in November, the sluices are closed again and the level of the lagoon is raised to flood the paddy fields for winter protection and organic matter degradation. From

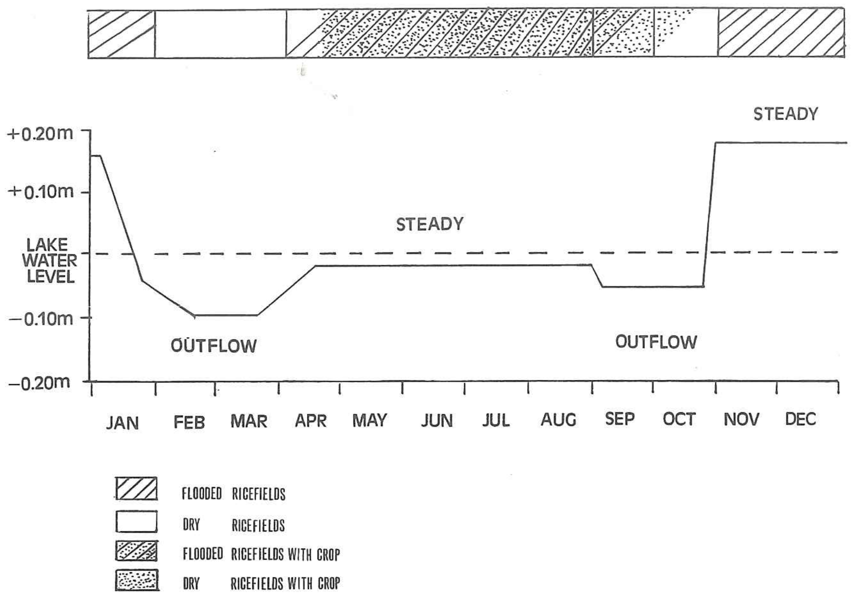

Fig. 2. General annual pattern of water-level fluctuations in the lake of the Albufera of Valencia, mainly influenced by rice cultivation in the surrounding area. Vertical axis values correspond to water-level differences respect the lake average depth.

Table 2. Limnological features of the Albufera of Valencia Lake.

	Average	Range	Units
pH	8.7	8 – 10	–
Temperature	19	6 – 31	°C
Dissolved oxygen	12	5 – 17	mg/l
Conductivity	1780	770 –3300	μS/cm
Chloride	9.5	4.5 – 19.4	meq/l
Alkalinity	2.5	1.0 – 4.7	meq/l
Secchi disk	0.21	0.11 – 0.40	m
Dissolved inorganic nitrogen	112	0.8 – 402	μM
Soluble reactive phosphorus	3.12	0.01 – 24	μM
Soluble reactive silicon	101	0.05 – 270	μM
Chlorophyll a	300	80 – 830	mg/m^3
Phytoplankton productivity	0.3	0.4 – 1.8	$gC\ m^{-3}\ h^{-1}$

January to March, the sluice gates are opened again and the fields are drained for tilling and sowing. This latter is completed by the end of April or early May, being preceeded by land fertilization. During the periods of low water level (Jan–Mar and Sep–Oct) water renewal is high, producing an outflow and decrease of the total phytoplankton abundance (Romo 1991). The cycle may be varied by opening of the sluices for weeding in early summer, heavy rainfall (frequently in autumn) or occasional maintenance to clear outlet channels blocked by the accumulation of sediments (mainly in summer).

Physico-chemical characteristics of the lake between 1980 and 1985 are described in Serra et al. (1984); Miracle et al. (1987) and Soria et al. (1987). Data collected since 1986 have yet to be published. Nutrient inputs and balance for 1988 are described in Vicente et al. (1990). These limnological investigations have confirmed the oligohaline hypertrophic nature of the lake (Table 2). The ratio N:P in the lake varied according to the algal growth and water renewal, linked by rice cultivation and lake fertilization. It increased from June to October during rice growth and harvest, and decreased from then to May after rice cultivation. According to Redfield (1958) and Forsberg et al. (1978), phosphate might be considered to be one of the possible factors limiting phytoplankton growth in the lagoon, because mean seasonal nutrient values exceeded $N:P > 30$. Taxonomy and physiology of the main cyanophyta species and phytoplankton composition are described in Romo (1991) and Romo et al. (in press). Zooplankton species composition and ecology are described in Alfonso & Miracle (1990) and Oltra & Miracle (1992).

Methods

One hundred and fourteen sample collections were performed between July 1980 and January 1989. No samples were taken in 1984. In 1980–81, only one sampling point was adopted (station M), situated on the eastern part of the lake (Fig. 1). From 1982 to 1989, the lake was sampled at three sites: in the north-east corner (station 1), in the centre (station 2) and in the south-east (station 3) (Fig. 1). These three sampling sites experience different water retention times and nutrient loadings. The northern zone receives industrial and urban sewage water, with high concentrations of phosphate and ammonia, while the lake inlets from the south catchment areas mainly receive agricultural water, enriched with high concentrations of nitrogen (Soria et al. 1987). The northern and southern points, due to their location near the main inflows and the lake outlet channels, have higher theoretical water renewal rates (approx. 20 and 35 times/year) than the central point (approx. 7 times/year). Because differences in phytoplankton composition between sites were found to be rather small (Romo 1991), only the average value of the three sampling points will be further considered in the analyses of the samples taken between 1982 and 1989.

Phytoplankton samples were taken each season between 1980 and 1983, and monthly from then onwards. They were collected by filling bottles 30 cm below the water surface. The number of trichomes were counted by the iodine-sedimentation method (Utermöhl 1958), using an Olympus inverted microscope. A sample volume between 1 and 3 ml was normally used. At least 1000 individuals of the most abundant species and 100 fields were counted. The estimated counting error was less than 6% (Lund et al. 1958). The length and width of 50–100 trichomes of every species were measured for each sample under 1000× magnifications, the measuring precision being 0.8 μm. The biomass of the phytoplankton was calculated multiplying the number of individuals by the volume of the algae estimated according to Rott (1981).

Simultaneously with the sample collection, temperature, oxygen and conductivity were measured in situ using a YSI salinometer and an oxymeter. Samples were also taken to determine pH and redox in situ and some chemical analyses according to the methods described by Golterman et al. (1978) and Strickland & Parsons (1978). Irradiance profiles were determined with a quantometer (Crump. Sci. Ins. mod. 550) during 1982 and 1983, and a Secchi-disk extinction depth was measured on every sampling occasion. Data were used to calculate the vertical attenuation coefficient (Wetzel & Likens 1979) and the underwater light climate as defined by Riley (1957). The ratio

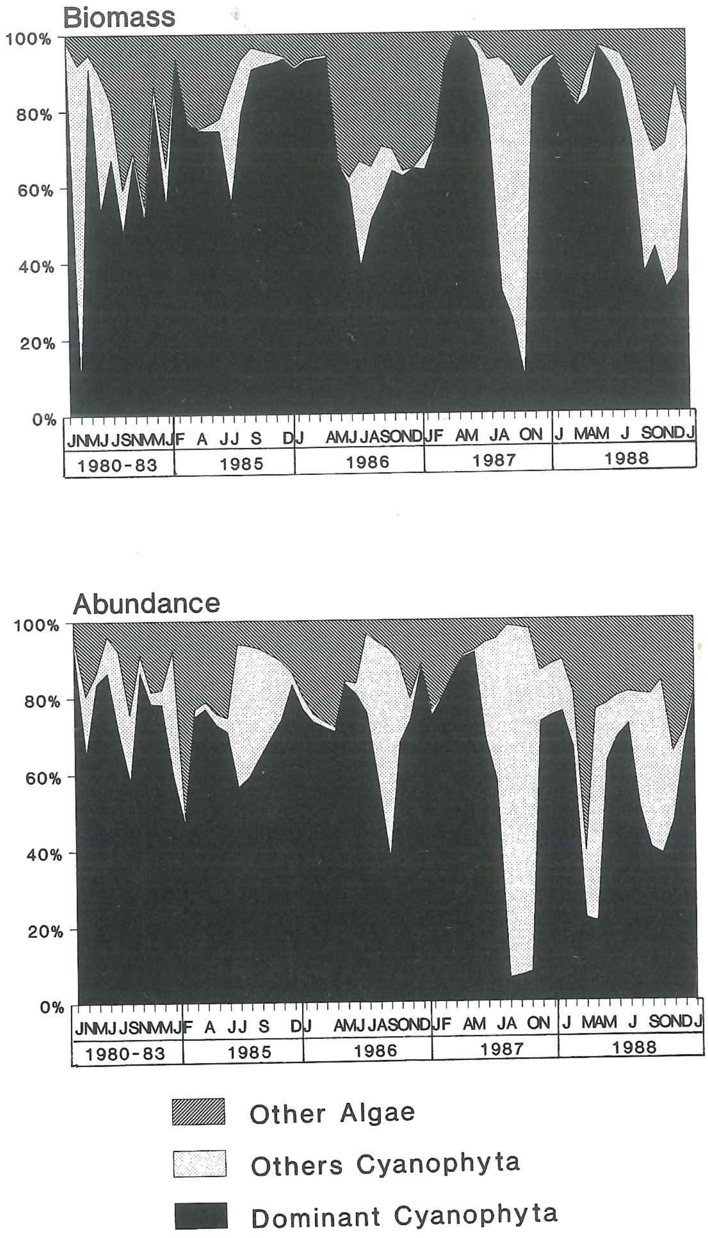

Fig. 3. Relative abundance (ind/ml) and fresh weight (mg/l) of the three main blue-green algae species (*Planktothrix agardhii*, *Ps. galeata* and *Geitlerinema* sp.), other cyanophytes and other algae belonging to several taxonomic group, in the Albufera of Valencia between 1980 and 1988. Data correspond to the average values from three sampling sites.

euphotic to mixed zone (Zeu : Zm) was calculated assuming the euphotic depth to be 1 % of subsurface irradiance (Reynolds 1984) and the mixed zone to be the mean depth of the lake on the sampling dates.

Statistical tests were made according to Sokal & Rohlf (1979) using the SPSS package (Nie et al. 1984). A correlation analysis of the species abundance against some environmental variables (temperature, alkalinity, underwater light climate, nitrate, ammonia, total dissolved nitrogen, dissolved phosphate and the N : P ratio) was performed. The abiotic variables with high correlation coefficients were then entered in a stepwise multiple linear regression analysis. Data were normalized where necessary by means of a logarithmic transformation.

Results

The phytoplankton in the Albufera of Valencia between 1980 and 1988 was continuously dominated by three filamentous blue-green algae, *Planktothrix agardhii* (Gom.) Anagn. Kom., *Pseudanabaena galeata* Böcher and *Geitlerinema* sp. (Fig. 3). These three species were each present in more than 75 %

Table 3. Abundance and biomass percentages of *Planktothrix agardhii* (1), *Geitlerinema* sp. (2) and *Pseudanabaena galeata* (3) in the phytoplankton of the Albufera of Valencia between 1980 and 1988.

Abundance (%)	1980–81			1982–83			1985			1986			1987			1988		
	(1)	(2)	(3)	(2)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)
January	–	–	–	–	–	–	–	–	–	57	0	20	48	1	27	12	1	38
February	–	–	–	–	–	–	32	9	7	–	–	–	69	0	9	–	–	–
March	–	–	–	2	0	77	–	–	–	–	–	–	–	–	–	27	0	3
April	–	–	–	–	–	–	14	63	0	65	0	8	84	0	6	27	0	2
May	30	0	53	12	59	8	–	–	–	75	0	12	69	0	22	66	0	5
June	–	–	–	–	–	–	6	57	9	24	1	56	–	–	–	–	–	–
July	70*	20	3	3	62	2	4	51	1	22	49	6	8	40	9	28	5	42
August	–	–	–	–	–	–	–	–	–	12	39	7	1	4	1	–	–	–
September	–	–	–	0	54	4	40	15	10	12	21	3	–	–	–	1	39	3
October	–	–	–	–	–	–	–	–	–	9	51	6	1	6	1	1	30	9
November	0	58	7	0	43	43	–	–	–	24	47	2	9	10	54	1	6	44
December	–	–	–	–	–	–	57	26	0	38	38	13	–	–	–	1	0	73
Biomass (%)																		
January	–	–	–	–	–	–	–	–	–	87	0	4	62	0	2	81	0	12
February	–	–	–	–	–	–	88	1	2	–	–	–	71	0	1	–	–	–
March	–	–	–	10	0	41	–	–	–	–	–	–	–	–	–	79	0	0
April	–	–	–	–	–	–	57	17	0	91	0	3	99	0	0	83	0	1
May	83	0	8	60	18	4	–	–	–	65	0	1	98	0	1	95	0	1
June	–	–	–	–	–	–	43	28	4	51	0	9	–	–	–	–	–	–
July	94*	2	0	12	48	2	29	26	1	35	3	1	58	15	5	67	1	19
August	–	–	–	–	–	–	–	–	–	40	9	2	24	6	2	–	–	–
September	–	–	–	0	44	4	87	2	1	48	8	1	–	–	–	7	27	2
October	–	–	–	–	–	–	–	–	–	46	14	3	4	5	1	7	28	7
November	0	6	1	2	33	33	–	–	–	55	7	1	58	3	24	6	2	24
December	–	–	–	–	–	–	91	3	0	60	3	2	–	–	–	7	0	30

* Data for July 1980. For July 1981: abundance (1) = 1 %, (2) = 82 %, (3) = 3 %; biomass (1) = 10 %, (2) = 42 %, (3) = 2 %.

of the samples from the lake. *Geitlerinema* sp. achieved the highest mean abundance (7 × 10^4 ind/ml) over the whole period between 1982 and 1988, while *P. agardhii* and *Ps. galeata* each averaged approximately half this value (4 × 10^4 ind/ml). However, the relatively larger *Planktothrix agardhii* represented 68 % of the total phytoplankton biomass for the complete period 1982 – 88.

Annual and seasonal periodicity

P. agardhii was the dominant species in the phytoplankton of the Albufera between January and May (amounting to 50 – 80 % of total phytoplankton

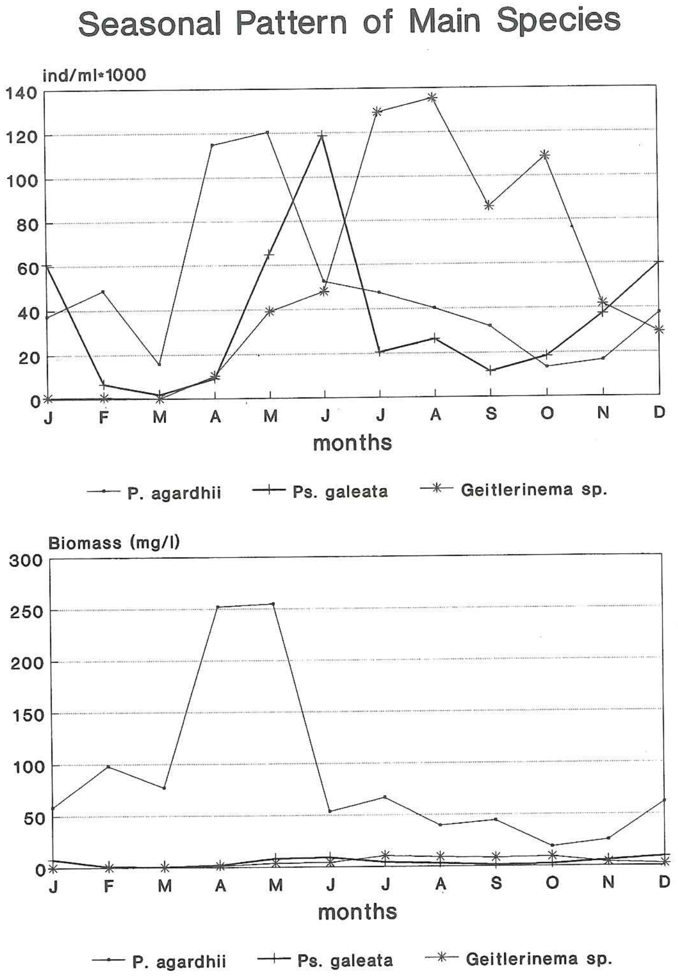

Fig. 4. Eight year monthly mean standing crops (trichomes/ml) and fresh weight (mg/l) of *Planktothrix agardhii*, *Pseudanabaena galeata* and *Geitlerinema* sp.

abundance during these months), while *Geitlerinema* sp. and *Ps. galeata* were dominant in the phytoplankton (40–70 %) during summer and autumn (Table 3). However, expressed as biomass, *P. agardhii* was the predominant alga during almost the entire study period (Fig. 4).

Maximal populations of *P. agardhii* were attained during April or May (Fig. 5), coincidental with the onset of water level stabilisation after the closing of the sluices (Fig. 2). Nutrient concentrations were high, owing to the fertilization of the ricefields. In 1986 and 1987, *P. agardhii* peaks reached between $2.6-3 \times 10^5$ ind/ml and 460–740 mg/l of fresh weight. In 1988, its annual population maximum in May was lower (0.6×10^5 ind/ml and 150 mg/l), as a consequence of the algal loss when the floodgates were opened in April due to high rainfall. In 1986–1988, *P. agardhii* standing crops amounted to 65–80 % of total abundance and 90–99 % of total phytoplankton biomass. After the annual peaks, the population decreased ten-fold during summer and autumn, when it represented generally less than 25 % of the total algal abundance but up to 60 % of the total biomass (Table 3).

P. agardhii crops seems dependent on the population loss produced in the early period of high water renewal rates (January–March) and on the density levels attained in the previous months. Thus, for example, the high *P. agardhii* numbers registered during April and May of 1986 and 1987 (Fig. 5), were preceeded by densities of about 10^4 ind/ml during November and December. These were maintained between January and March, with a ten-fold increase in April or May. In contrast, in the spring of 1988 a smaller autumn inoculum in the final months of 1987, followed by the phytoplankton flushing out in April, led to a much smaller spring population maximum of this species that year.

In 1985, the periodicity of *P. agardhii* was different. It was dominant in the phytoplankton in September and December, and *Geitlerinema* sp. was more abundant in spring (Fig. 5, Table 3). *P. agardhii* growth in 1985 was sustained under the special conditions of reduced water renewal in September, which resulted from the restricted flows due to this year dry weather. Furthermore, the N : P ratio decreased from a mean value of $N:P>30$ in summer months to $N:P = 9$ in September.

After the spring growth of *P. agardhii* the dominance in the algal assemblage shifted to *Geitlerinema* sp. between July and October, and to *Ps. galeata* mainly during November and December, after rice harvest and closure of the sluices (Fig. 5).

Maximum populations of *Geitlerinema* sp. occurred mainly in July between 1980 and 1988, reaching values of about $1.5-2.5 \times 10^5$ ind/ml or 11–20 mg/l of fresh weight. It developed under conditions of water hydrological stability (see Fig. 2) and nutrient depletion. Other filamentous cyanophyta, such as *Planktolyngbya contorta* (in August 1986) and *Planktolyngbya subtilis* (in August–October 1987), became important in the summer phyto-

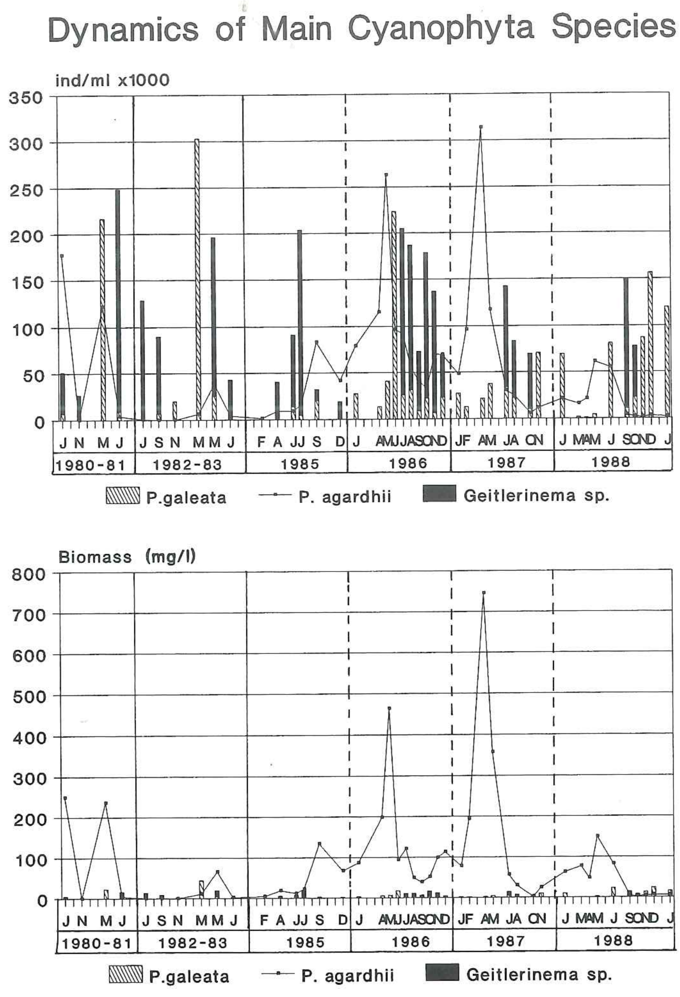

Fig. 5. Abundance (trichomes/ml) and biomass (mg/l) of the main filamentous blue-green algae, *Pseudanabaena galeata*, *Planktothrix agardhii* and *Geitlerinema* sp., in the Albufera of Valencia for 1980–88. Data correspond to the average values from three sampling sites. Only sampled months are shown.

plankton (Romo & Miracle, in press). In 1986, a second population increase of *Geitlerinema* sp. was attained in late October, 1986, after the re-establishing of water stability, reaching similar values to those of July (Fig. 5). In 1987, however, a second increase of this species was prevented as a consequence of the accumulation of sediments in the outlet channels of the lake which produced a prolonged lake water retention until October and the maintenance of a *Pl. subtilis* bloom.

From 1980 to 1985, when *P. agardhii* growth was weaker *Ps. galeata* showed some development early in the season. However, from 1986 onwards it showed its maximum increase after *P. agardhii* vernal peak (1986) or more frequently in autumn (1987 and 1988) (Fig. 5). Its maximal populations ranged between 0.7–3 × 10^5 ind/ml and 10–44 mg/l of fresh weight. In 1988, the rainy autumn of the previous year and the bad weather in spring delayed the sequence with a major presence of *Ps. galeata* over the year.

Relationships with the environmental parameters

Correlation and stepwise multiple linear analyses were undertaken to reveal relationships between the blue-green algae species and the environmental variables. Temperature, alkalinity and dissolved phosphate and nitrogen differentiated between these species (Table 4).

Table 4. Partial correlation between *Planktothrix agardhii* (PA), *Pseudanabaena galeata* (PS) and *Geitlerinema* sp. (GEIT) populations density and environmental factors. Thinner (*Geitlerinema* sp. and *Ps. galeata* populations together). Temp (temperature), Alk (alkalinity), Light (underwater light climate), NOX (Nitrate + Nitrite), N (dissolved inorganic nitrogen), P (dissolved inorganic phosphate), N:P (nitrogen-phosphate ratio). Relationships significant at $P < 0.05$ are underlined.

	PA	GEIT	PS	Thinner
Temp	−0.28	$\underline{0.32}$	−0.09	$\underline{0.35}$
Alk	$\underline{-0.51}$	0.17	$\underline{-0.42}$	−0.03
Light	−0.24	0.18	−0.08	0.28
NOX	$\underline{-0.34}$	−0.01	−0.27	−0.18
NH_4	$\underline{-0.42}$	−0.14	$\underline{-0.51}$	−0.31
N	$\underline{-0.44}$	−0.01	$\underline{-0.38}$	−0.25
P	−0.05	$\underline{-0.32}$	$\underline{-0.48}$	$\underline{-0.41}$
N:P	$\underline{-0.48}$	−0.06	−0.21	−0.07

Table 5. Values of the physico-chemical parameters during annual maximum populations of *Planktothrix agardhii*, *Geitlerinema* sp. and *Pseudanabaena galeata* between 1980 and 1988.

	Temp (°C)	Alk meq/l	pH	I (%)	N μM	P μM	N:P
A. Average values of the abiotic variables during maximum populations							
P. agardhii	21	1.77	9.3	16	73.01	5.37	14
Geitlerinema sp.	26	2.59	8.99	19	80.33	0.18	450
Ps. galeata	15	1.58	9.17	20	56.39	3.25	17
B. Range of abiotic variables during maximum populations							
P. agardhii	18–25	1.0–2.4	8.6–10.4	11–21	3.1–162	0.3 –24	10–1500
Geitlerinema sp.	19–30	1.1–4.7	8.3– 9.6	14–22	1.1–228	i–0.35	24–5600
Ps. galeata	13–23	1.0–2.5	8.4–10.4	13–25	6.6–151	0.15–12	14–370

Temp (temperature), Alk (Alkalinity), I (underwater light climate, percentage of subsurface intensity), P (dissolved inorganic phosphate), N (dissolved inorganic nitrogen). i = indetectable levels.

The population dynamics of *P. agardhii* showed significant negative correlations with alkalinity, dissolved nitrogen and the N : P ratio (Table 4), this latter being selected in the stepwise regression ($r = 0.48$, $F_{1,26} = 7.67$, $p < 0.05$). Unlike the other cyanophytes, the annual maxima of this alga were attained typically under the seasonally highest phosphate levels (Table 5). A mean value of N : P = 14 coincided with the annual peaks of *P. agardhii* in the Albufera, i.e. within the optimum range of N : P = 7–14 claimed to apply to this cyanophyte (Van Liere & Mur 1980; Zevenboom 1980; Ahlgren 1985), but it is slightly higher than the ratios N : P = 8–11 registered during its maximum development in other hypertrophic lakes (e.g. Berger 1975; Rojo 1990).

In contrast to the other two major species of the lake, *P. agardhii* developed under the poorest underwater light intensity (Table 5). Moreover, the Zs : Zm ratio (Secchi-disk depth : mixed depth) during the months of its maximum growth was at its lowest (April–May Zs : Zm = 0.23, summer Zs : Zm = 0.26 and November–December Zs : Zm = 0.32). The mean temperature during its maximum crops (21 °C) was within the optimum range cited for this species in hypertrophic lakes (Berger & Sweers 1988).

The *Geitlerinema* sp. populations were related to water temperature (positive coefficient) and phosphate (negative coefficient) in the stepwise regression analysis ($r = 0.71$, $F_{2,26} = 13.47$, $p < 0.01$). In comparison with the other members of the Oscillatoriales studied, this species developed under the highest mean temperatures and the lowest phosphate concentrations (Table 5).

Ps. galeata populations were related to alkalinity, dissolved nitrogen and phosphate (negative coefficient), this latter being selected by the stepwise regression ($r = 0.48$, $F_{1,26} = 7.90$, $p < 0.01$). *Ps. galeata* has a high capacity to store intracellular phosphate under starting nutrient deficiency in culture (Romo et al., in press). Maximum development of this alga took place under nutrient concentrations lower than those of *P. agardhii* (Table 5). There are no references to the nutrient requirements of this cyanophyte, although the relation N : P = 17 observed during its annual peaks is higher than the optimum growth value of N : P = 9 cited for *Pseudanabaena catenata* in laboratory (Healey & Hendzel 1979).

Geitlerinema sp. and *Ps. galeata* abundance grouped together, showed significant relationships with light (positive coefficient) and phosphate (negative coefficient) ($r = 0.56$, $F_{2,25} = 5.79$, $p < 0.01$). Their populations mainly distinguished for developing under higher underwater light intensity and temperatures, and lower orthophosphate levels than those of *P. agardhii.*

Discussion

In the Albufera of Valencia, interannual variations of the three main blue-green algae species were much less pronounced than seasonal changes. The cyanophyte seasonality was quite consistent during the study period. *P. agardhii* dominated during winter and spring, while *Geitlerinema* sp. and *Ps. galeata* were relatively more abundant during summer and autumn. The factors regulating this pattern seem mainly related to underwater light climate, nutrients (especially phosphate concentrations) and water residence times.

Differential resource requirements for these major species were observed. *P. agardhii* seemed the most oligophotic of them. Its peaks in the Albufera almost resemble a monoalgal culture. This agrees with the observations of Zevenboom et al. (1982) and Berger (1984) in which the organism created a selfshading light climate selecting for its own growth.

In summer, increased underwater light intensity and photoperiods in the Albufera enhanced growth of *Ps. galeata* and *Geitlerinema* sp. relative to that of *P. agardhii*. This latter is better adapted to low light intensities (Foy & Gibson 1982; Berger 1989) and short light-dark cycles (Foy et al. 1976; Nicklisch & Kohl 1989). On the other hand, the euphotic depth in the Albufera (0.65 m, Miracle et al. 1987) is higher than the threshold of 0.50 m cited in the *P. agardhii* dominated-lakes (Berger 1984). The development of *Geitlerinema* sp. during summer months, under reduced phosphate concentrations could suggest that this species has lower phosphate requirements than *Ps. galeata*. However, this observation needs experimental appraisals. Despite the fact that *Geitlerinema* sp. lacks intracellular gas-vesicles, contrasting to *P. agardhii* and *Ps. galeata* (Anagnostidis & Komarek 1988; Anagnostidis 1989), the polymictic features of the Albufera and the east wind stirring in summer, allowed a good development of this non-vacuolated filamentous species during prolonged summer stagnation.

The low N : P values found in the Albufera at the time of maximal growth of *P. agardhii*, with relatively high phosphate concentrations agree with the nutrient requirements claimed for this species (Van Liere & Mur 1980; Zevenboom 1980; Ahlgren 1985; Nicklisch et al. 1991). In contrast, in summer the reduction of nutrient levels, especially phosphate, and the prevailing light conditions favoured the development of the other major cyanophyte species.

During November and December, the environmental conditions in the Albufera also seemed not to favour the growth of *P. agardhii*. Although, solar irradiance decreases towards the end of the year, the raising of lake level for ricefield management and a general reduction in algal abundance (Romo 1991) led to better light penetration (Soria et al. 1987). The N : P ratio is high during this period because the drying of ricefield in September resulting in an important input of nutrients, especially nitrogen, into the lake (Soria et al. 1987). Moreover, the long generation times of *P. agardhii* (Ahlgren 1978; Van Liere 1979; Foy 1980), seem unsuited for its development under frequent autumn rainflushing. The maximum theoretical water residence in the Albufera at this time is lower than that required for *P. agardhii* to attain a persistent bloom

(Berger & Sweers 1988; Olli 1989). *P. agardhii* was only dominant during the final months of the year in 1985, when unusual conditions of reduced post-summer water replacement and a decrease in the N:P ratio were observed. The major presence of *Ps. galeata* over 1988 was probably related to the maintenance of a high density from the end 1987, to having higher reproduction rates than *P. agardhii* (Romo 1991) and to being able to better recover from periods of high flushing.

Finally, it is interesting to note that the periodicity observed for the main blue-green algae in the Albufera and El Porcal, another shallow Spanish hypertrophic lake (Alvarez-Cobelas et al. 1987; Rojo 1990), is opposite to the periodic sequence described between *P. agardhii* and *Limnothrix redekei* in several other shallow European lakes (e.g. Berger 1975; Gibson & Fitzsimons 1982; Moed & Hoogveld 1982; Hickel 1988; Chorus & Wesseler 1988). It is possible to compare these two sequences because of the taxonomic proximity and the similar growth rates between *Ps. galeata* and *Geitlerinema* sp. and *L. redekei* (Anagnostidis & Komarek 1988; Anagnostidis 1989; Romo 1991).

In the two Spanish lakes, maximal increase of *P. agardhii* occurred in spring, while in the other European lakes it takes place in summer or autumn, the spring phytoplankton being dominated by *L. redekei.* It is argued that this is dependent upon the higher respiration rates of *L. redekei* in summer (Foy et al. 1976; Foy & Smith 1980); selective zooplankton predation (Gibson & Fitzsimons 1982); a lower capacity of *L. redekei* to use trace elements (Moed et al. 1988) and differential nutrient requirements (Nicklisch et al. 1981). However, competition experiments carried out with these two species (Nicklisch & Kohl 1989; Nicklisch et al. 1991) showed that the conditions generally prevailing in many of these lakes during summer (e.g. high temperatures, long photoperiod) can only favour the dominance of *L. redekei* or the coexistence between both species. These experimental results clearly support the species sequence found in the two Spanish hypertrophic lakes. The possible reasons for this seasonal divergence could be the higher solar radiation and temperatures obtaining at our latitude, and a more pronounced phosphorus limitation during summer. For instance, the shallow hypertrophic lakes of Holland have a maximum subsurface light intensity during summer months at midday, of about 1800 μE m^{-2} s^{-1} (Van Liere & Mur 1980). In the Albufera and El Porcal (Rojo 1990) this value can be reached in March, which in both cases is in accordance with the growth period of *P. agardhii* but the seasons are different. Moreover, the spring temperature in the Albufera at the time of *P. agardhii* peaks is similar to summer temperatures for most of the lakes in Northern and Central Europe (Stewart & Gibson 1987; Berger & Sweers 1988). In this way, the seasonal sequence described between *P. agardhii* and *Pseudanabaena catenata* in some eutrophic lakes of Argentina (latitude 34° 53′ S, 57° 49′ W) (So-

LARI 1987), is similar to that observed in Spain. However, further reports and studies are required in order to clarify this point.

Acknowledgements

The authors wish to thank to Dr. CHRIS GIBSON for his comments on the manuscript and DONALD SAVAGE for kindly correcting the English. The authors are also thankfull for the sampling facilities given by the City Council of Valencia. This research was performed under a grant held by SUSANA ROMO from the Spanish Ministry of Education and Science.

References

AHLGREN, G. (1978): Growth of *Oscillatoria agardhii* GOM. in chemostat culture. II. Dependence of growth constants on temperature. – Mitt. int. Ver. Limnol., **21:** 88–102.

– (1985): Growth of *Oscillatoria agardhii* in chemostat culture. 3. Simultaneous limitation of nitrogen and phosphorus. – Br. phycol. J., **20:** 249–261.

ALFONSO, M. T. & MIRACLE, M. R. (1990): Distribución espacial de las comunidades zooplanctónicas de la Albufera de Valencia. – Scientia gerundensis, **16:** 11–25.

ALVAREZ-COBELAS, M., RUBIO, A., ARAUZO, M., ALARCON, P. & ALARIO, V. (1987): Morfometría y composición química de una laguna de gravera. – Limnética, **3:** 91–95.

ALVAREZ-COBELAS, A., MUÑOZ, P. & RUBRO, A. (1991): La eutrofización de las aguas continentales españolas. – Ed. Henkel Ibérica. Madrid. 339 pp.

ANAGNOSTIDIS, K. & KOMAREK, J. (1988): Modern approach to the classification system of cyanophytes. 3 Oscillatoriales. – Arch. Hydrobiol./Suppl. 80, Algological Studies, **50–53:** 327–472.

ANAGNOSTIDIS, K. (1989): *Geitlerinema,* a new genus of oscillatorialean cyanophytes. – Pl. Syst. Evol., **164:** 33–46.

BERGER, C. (1975): Occurrence of *Oscillatoria agardhii* GOM. in some shallow eutrophic lakes. – Verh. Int. Ver. Limnol., **19:** 2689–2697.

– (1984): Consistent blooming of *Oscillatoria agardhii* GOM. in shallow hypertrophic lakes. – Verh. Internat. Verein. Limnol., **22:** 910–916.

– (1987): Habitat en ecologie van *Oscillatoria agardhii* GOMONT. – PhD Thesis. Lelystad (The Netherlands). 233 pp.

– (1989): In situ primary production, biomass and light regime in the Wolderwijd, the most stable *Oscillatoria agardhii* lake in the Netherlands. – Hydrobiologia, **185:** 233–244.

BERGER, C. & SWEERS, H. E. (1988): The Ijsselmeer and its phytoplankton with special attention to the suitability of the lake as a habitat for *Oscillatoria agarchii* GOM. – J. Plankton Res., **10:** 579–599.

BLANCO, C. (1974): Estudio de la contaminación de la Albufera de Valencia y de los efectos de dicha contaminación sobre la fauna y flora del lago. – PhD Thesis. University of Valencia (Spain). 193 pp.

CHORUS, I. & WESSELER, E. (1988): Response of the phytoplankton community to therapy measures in a highly eutrophic urban lake (Schlachtensee, Berlin). – Verh. Int. Ver. Limnol., **23:** 719–728.

DAFAUCE, C. (1975): La Albufera de Valencia. Un estudio piloto. Ed. Monografías ICONA, Madrid, **4:** 1–127.

Davidowicz, P., Gliwicz, Z. M. & Gulati, R. D. (1988): Can *Daphnia* prevent a blue-green algal bloom in hypertrophic lakes? A laboratory test. – Limnologica (Berlin), **19** (1): 21–26.

Forsberg, C., Ryding, S. O., Claesson, A. & Forsberg, A. (1978): Water chemical analysis or algal assay? Sewage effluent and polluted lake water studies. – Mitt. int. Ver. Limnol., **21:** 352–363.

Foy, R. H. (1980): The influence of surface to volume ratio on the growth rates of planktonic blue-green algae. – Br. phycol. J., **15:** 279–289.

Foy, R. H. & Smith, R. V. (1980): The role of carbohydrate accumulation in the growth of planktonic *Oscillatoria* species. – Br. phycol. J., **15:** 139–150.

Foy, R. H. & Gibson, C. E. (1982): Photosynthetic characteristics of planktonic blue-green algae: the response of twenty strains grown under high and low light. – Br. phycol. J., **17:** 169–182.

Foy, R. H., Gibson, C. E. & Smith, R. V. (1976): The influence of daylength, light intensity and temperature on the growth rates of planktonic blue-green algae. – Br. phycol. J., **11:** 151–163.

Garcia, M. P., Vicente, E. & Miracle, M. R. (1984): Sucesión estacional del fitoplancton de la Albufera de Valencia. – Anales de Biología, **2** (Sección especial): 91–100.

Gibson, C. E. & Fitzsimons, A. G. (1982): Periodicity and morphology of planktonic blue-green algae in an unstratified lake (Lough Neagh, Northern Ireland). – Int. Rev. Hydrobiol., **67:** 459–476.

Golterman, H. L., Clymo, R. S. & Ohnstad, M. (1978): Methods for physical and chemical analysis of fresh waters. – IBP Handbook **8:** 214 pp.

Healey, F. P. & Hendzel, L. L. (1979): Indicators of phosphorus and nitrogen deficiency in live algae in culture. – J. Fish. Res. Board Canada, **36:** 1364–1369.

Hickel, B. (1988): Unexpected disappearance of cyanophyte blooms in Plußsee (North Germany). – Arch. Hydrobiol./Suppl. 80, 1–4, Algological Studies, **50–53:** 545–554.

Jones, R. I. (1977): Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinego bay, Lough Neagh) III. Interspecific competition in relation to irradiance and temperature. – J. Ecol., **65:** 579–586.

Klapwijk, S. P. (1988): Eutrophication of surface waters in the dutch polder Landscape. – PhD Thesis. University of Delf (The Netherlands). 227 pp.

Loogman, J. G. & Van Liere, L. (1986): Restoration of shallow lake ecosystems with emphasis on loosdrecht lakes. – Hydrobiological Bull., Vol. 20 (1–2).

Lopez, T., Toja, J. & Nestor, A. (1991): Limnological comparation of two peridunar ponds in the Doñana National Park (Spain). – Arch. Hydrobiol., **120:** 357–378.

Lund, J. W. G., Kipling, C. & Le Cren, E. D. (1958): The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. – Hydrobiologia, **11:** 143–170.

Lyche, A. (1984): Eksperimentelle studier av beitbarhet og assimilerbarhet av 6 planktonalger for *Daphnia longispina.* Nordisk Limnologsymposium: Interaksjoner mellom trofiske nivaer i ferskvann. p. 49–62.

Meffert, M. E. (1989): In situ and in vitro photosynthesis of *Limnothrix redekei* (Cyanophyta). – Arch. Hydrobiol., **116:** 401–414.

Miracle, M. R., Soria, J. M., Vicente, E. & Romo, S. (1987): Relaciones entre la luz, los pigmentos fotointéticos y el fitoplancton en la Albufera de Valencia, laguna litoral hipertrófica. – Limnética, **3:** 25–34.

Moed, J. R. & Hoogveld, H. L. (1982): The algal periodicity in Tjeukemeer during 1968–1978. – Hydrobiologia, **95:** 223–234.

Moed, J. R., Hoogveld, H. L. & De Haan, H. (1988): A study of factors regulating the succession of Cyanobacteria in lake Tjeukemeer, The Netherlands. – Verh. int. Ver. Limnol., **23:** 1894–1897.

Mur, L. R., Gons, H. J. & Van Liere, L. (1977): Some experiments on the competition between green algae and blue-green bacteria in light-limited environments. – FEMS Microbiol. Letters, **1:** 335–338.

Nicklisch, A., Conrad, B. & Kohl, J. G. (1981): Growth kinetics of *Oscillatoria redekei* Van Goor as a basis to understand its mass development in eutrophic lakes. – Verh. int. Ver. Limnol., **21:** 1427–1431.

Nicklisch, A. & Kohl, J. G. (1989): The influence of light on the primary production of two planktic blue-green algae. – Arch. Hydrobiol., **33:** 451–455.

Nicklisch, A., Roloff, B. & Ratsch, A. (1991): Competition experiments with two planktic blue-green algae (Oscillatoriaceae). – Verh. int. Ver. Limnol., **24:** 889–892.

Nie, N., Bent, H. & Hull, C. H. (1984): Statistical package for the Social Sciences. SPSS inc. Chicago, Illinois.

Olli, E. (1989): Simulated impacts of flow regulation on blue-green algae in a short retention time lake. – Arch. Hydrobiol. Beih. Ergebn. Limnol., **33:** 181–189.

Oltra, R. & Miracle, M. R. (1992): Seasonal succession of zooplankton populations in the hypertrophic lagoon Albufera of Valencia (Spain). – Arch. Hydrobiol., **124:** 187–204.

Pardo, L. (1942): La Albufera de Valencia. Estudio Limnográfico, biológico, económico y antropológico. – Bol. Inst. Forestal Invest. y Exper. **24:** 1–263.

Redfield, A. C. (1958): The biological control of chemical factors in the environment. – Amer. Sci., **46:** 205–221.

Reynolds, C. S. (1984): The ecology of freshwater phytoplankton. – Cambridge University Press. 384 pp.

Reynolds, C. S. & Walsby, A. E. (1975): Water blooms. – Biol. Rev., **50:** 437–481.

Riley, G. A. (1957): Phytoplankton of the North Central Sargasso Sea, 1950–52. – Limnol. Oceanogr., **2:** 252–270.

Rojo, C. (1990): Estructura de la comunidad fitoplanctonica de la laguna hipertrófica "El Porcal" (Madrid). – PhD Thesis. University of Valencia (Spain). 343 pp.

Romo, S. (1991): Estudio del fitoplancton de la Albufera de Valencia, una laguna hipertrófica y somera, entre 1980 y 1988. – PhD Thesis. University of Valencia (Spain). 295 pp.

Romo, S. & Miracle, M. R. (in press): Population dynamics and ecology of phytoplankton in a shallow hypertrophic lake. – Hydrobiologia.

Romo, S., Hernandez-Marine, M. & Miracle, M. R. (in press): Remarks on the morphology of *Pseudanabaena galeata* Böcher. – Arch. Hydrobiol., Algological Studies.

Rosello, V. M. (1972): Los rios Jucar y Turia en la génesis de la Albufera de Valencia. – Cuad. Geogr., **11:** 7–25.

Rott, E. (1981): Some results from phytoplankton counting intercalibrations. – Schweiz. Z. Hydrol., **43:** 34–62.

Serra, M., Miracle, M. R. & Vicente, E. (1984): Interrelaciones entre los principales parámetros limnológicos de la Albufera de Valencia. – Limnética, **1:** 9–19.

SOKAL, R. R. & ROHLF, F. J. (1979): Biometría. Principios y Métodos Estadísticos en la Investigación Biológica. Ed. Blume. Madrid. 832 pp.

SOLARI, L. C. (1987): Cyanophyta de ambientes lénticos del área platense. I. Variación estacional y floraciones. – Rev. del Museo de la Plata (Nueva Serie). Botánica, XIV **95:** 149–162.

SORIA, J. M., MIRACLE, M. R. & VICENTE, E. (1987): Aporte de nutrientes y eutrofización de la Albufera de Valencia. – Limnetica, **3** (2): 227–242.

STEWART, W. D. & GIBSON, C. E. (1987): A model for the heat budget of Lough Neagh. – In: Record of agricultural research. Vol. 35. Department of Agriculture. Northern Ireland. pp. 67–75.

STRICKLAND, J. D. & PARSONS, T. R. (1978): A practical handbook of sea water analysis. – Bull. Fish. Res. Bd. Can., **167:** 1–203.

UTERMÖHL, H. (1958): Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. – Mitt. int. Ver. Limnol., **9:** 1–38.

VAN LIERE, L. (1979): On *Oscillatoria agardhii* Gomont, experimental ecology and physiology of a nuisance bloom-forming cyanobacterium. – PhD Thesis. University of Amsterdam (The Netherlands). 100 pp.

VAN LIERE, L. & MUR, L. R. (1980): Occurrence of *Oscillatoria agardhii* and some related species, a survey. – In: BARICA, J. & MUR, L. R. (eds.): Hypertrophic ecosystems, Developments in Hydrobiology, Vol. **2:** 67–77, Dr. W. Junk Publ. The Hague.

VICENTE, E., MIRACLE, M. R. & SORIA, J. M. (1990): Global model for nutrient flux and biomass production in the Albufera of Valencia, Spain. – Rapp. Comm. Int. Medit., **32** (1).

WERNICKE, P. & NICKLISCH, A. (1986): Light/dark cycle and temperature. Their impact on phosphate-limited growth of *Oscillatoria redekei* VAN GOOR in semicontinuous culture. – Int. Revue. ges. Hydrobiol., **71:** 297–313.

WETZEL, R. G. & LIKENS, G. E. (1979): Limnological analyses. – W. B. Saunders Company. Philadelphia, P.A. 358 pp.

ZEVENBOOM, W. (1980): Growth and nutrient uptake kinetics of *Oscillatoria agardhii.* – PhD Thesis. University of Amsterdam (The Netherlands). 178 pp.

ZEVENBOOM, W. & MUR, L. R. (1980): N_2-fixing cyanobacteria: Why they do not become dominant in Dutch hypertrophic ecosystems? – In: BARICA, J. & MUR, L. R. (eds.): Hypertrophic ecosystems, Developments in Hydrobiology, Vol. **2:** 123–130, Dr. W. Junk Publ. The Hague.

ZEVENBOOM, W., BIJ DE VAATE, A. & MUR, L. R. (1982): Assessment of factors limiting growth rate of *Oscillatoria agarchii* in a hypertrophic lake, Lake Wolderwijd, 1978, by use of physiological indicators. – Limnol. Oceanogr., **27** (1): 39–52.

Submitted: 20 May 1992; accepted: 9 September 1992.