Hydrobiologia **273**: 37–56, 1994.

Population dynamics and ecology of subdominant phytoplankton species in a shallow hypertrophic lake (Albufera of Valencia, Spain)

S. Romo & M. R. Miracle
Area de Ecología, Facultad de Ciencias Biológicas, Universidad de Valencia, 46100-Burjasot, Valencia, Spain

Received 24 June 1992; in revised form 26 January 1993; accepted 23 March 1993

Key words: ricefields area, phytoplankton, subdominant species, long-term study, population dynamics, ecology

Abstract

Long-term population dynamics and ecology of the abundant but non-dominant phytoplankton species of the shallow hypertrophic lake the Albufera of Valencia (Spain) are described for the period 1980–88. The lake is used as a reservoir for the surrounding ricefield cultivation. It is continuously dominated by three filamentous blue-green algae, *Planktothrix agardhii*, *Pseudanabaena galeata* and *Geitlerinema* sp. Horizontal differences of the phytoplankton were less important than annual and seasonal variations. An annual increasing trend was observed for *Planktolyngbya subtilis*, *Planktolyngbya contorta*, *Cylindrospermopsis raciborskii*, *Microcystis incerta*, *Nitzschia palea* var. *tenuirostris* and *Rhodomonas lacustris* var. *nannoplanctica*, whereas *Anabaenopsis elenkinii*, *Scenedesmus acuminatus*, *Scenedesmus quadricauda* and *Cyclotella meneghiniana* showed an opposite trend. This pattern seems related to the increase of nitrogen and phosphorus loading in the lake and certain hydrological changes occurred in the latter years of the study. Seasonal pattern of the subdominant species showed the presence of *Cyclotella meneghiniana*, *Scenedesmus* species and *Chlamydomonas* spp. in spring, during moderate water renovation rates and phosphate availability. Periodicity shifted to blue-green algae and *Nitzschia* species in summer and early autumn, during reduced phosphate levels and initial low but later high water renewal. Autumn and winter species, such as *Monoraphidium contortum*, *Nitzschia gracilis*, *Rhodomonas lacustris* var. *nannoplanctica* and *Cryptomonas erosa*, were mainly related to light intensity and temperature. Although the lake has a typical hypertrophic phytoplankton assemblage, the general seasonal variation of the species is similar to that often described in temperate lakes. Diatom species composition differs to that cited in other shallow hypertrophic lakes of Europe.

Introduction

The Albufera of Valencia is a shallow, hypertrophic lake dominated since the late 1970's by filamentous blue-green algae (Romo, 1991). This algal group has focussed the few long-term phytoplankton studies carried out in these systems (Gibson & Fitzsimons, 1982; Berger, 1984; Loogman & Van Liere, 1986; Berger & Sweers, 1988; Romo & Miracle, 1993). Several laboratory and field studies have been made to ascertain the factors controlling the growth performance of the dominant filamentous blue-green algae, such as *Planktothrix agardhii* (Gom.) Anagn. Kom. and other more slender cyanophytes, e.g. *Limnothrix redekei* (Van Goor) Meffert (Gibson & Fitzsimons, 1982; Berger & Sweers, 1988; Nicklisch & Kohl, 1989; Nicklish *et al.*, 1991). However, the dynamics and ecology of the abundant but non-dominant species of shallow hypertrophic lakes have been often overlooked and seldom reported (Fott, 1975; Moed & Hoogveld, 1982; Alvarez-Cobelas & Rojo, 1990). The aim of this article is to describe the long-term periodicity and ecology of the subdominant species in the Albufera of Valencia, for the period 1980–88. Analyses relating algae population dynamics to environmental features will be used, since these are regarded as a suitable method for highlighting relationships that deserve further research (Trimbae & Harris, 1983).

Description of study site

The Albufera of Valencia is a shallow, hypertrophic, oligohaline lagoon located in the National Park of the Albufera, Spain (39° 20′ N, 0° 20′ W). It is an exposed polymictic lake, with a mean depth of 1 m, a mean area of 21 km^2 and a length and breadth of approximately 6 km. Detailed description of its morphometric and limnological features are shown in Serra *et al.* (1984); Soria *et al.* (1987) and Romo & Miracle (1993). Since the last century, the lagoon has functioned as a reservoir for the demands of the surrounding rice cultivation. Water level of the lagoon is regulated by sluice gates situated at the outlet channels (Fig. 1). The hydrological cycle of the lake has been described in Romo & Miracle (1993) and can be summarized as follows: there are two periods of water retention to keep rice-fields flooded, from mid-April to August and from November to December. Rice is grown from May to August. From September to October, the floodgates are opened to empty the fields for rice ripening and harvest. Then, in November, the sluices are closed and the level of the lagoon is raised to flood the paddy fields for winter protection and organic matter degradation. From 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 opening of the sluices, Jan–Mar and Sep–Oct, lake water renewal is high.

Material and methods

Samples were collected between July 1980 and January 1989. No samples were taken in 1984. They were taken seasonally between 1980 and 1983 and approximately monthly from 1985 onwards. 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 northeast corner (station 1), in the centre (station 2) and in the south-east (station 3). 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 y^{-1}) than the central point (approx. 7 times y^{-1}). This latter has also the lowest nutrient concentrations. In 1987, point 1 was not sampled because of problems of access, due to a severe reduction in depth as a consequence of sediment accumulation carried from the main inlet situated at the front.

Samples were taken by filling bottles 30 cm below the water surface. The number of individuals were counted by the iodine-sedimentation method (Uthermöhl, 1958), using an Olympus inverted microscope. Cells, trichomes and colonies were used as counting units. The estimated counting error was less than 6% (Lund *et al.*, 1958). The length and width of a representative number of the main species (100–20) were measured for each sample under × 1000 magnification, the measuring precision being 0.8 μm. The

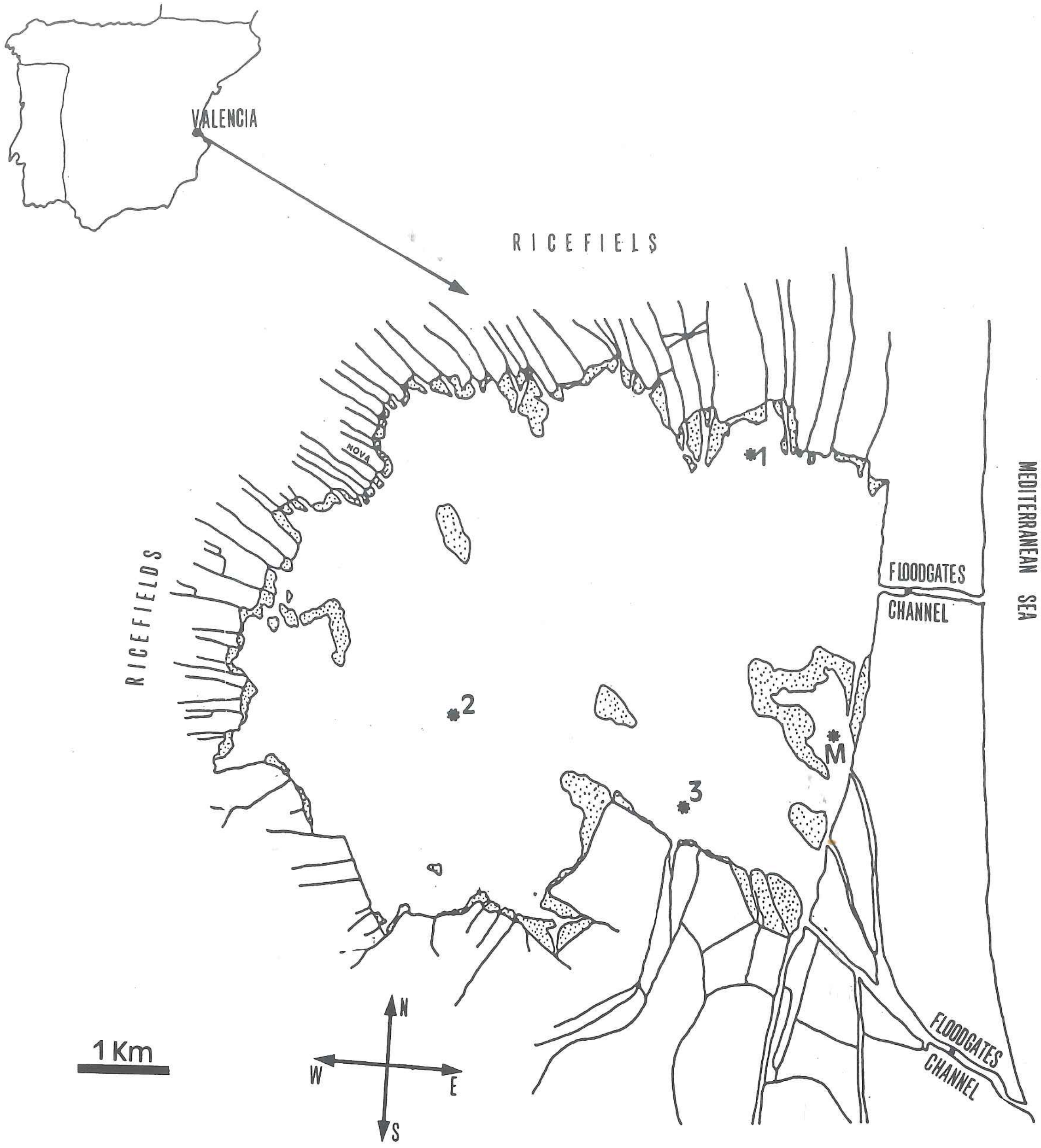


Fig. 1. Map of the Albufera of Valencia showing location, sampling sites and outlet channels.

fresh biomass of the phytoplankton was calculated according to Rott (1981). Oscillatorial species were identified using the recent taxonomic criteria specified in Anagnostidis & Komárek (1988). The taxonomic descriptions are detailed in Romo (1991), and the taxonomy and ecology of *Geitlerinema amphibium* (Ag. ex Gom.) Anagn. in Romo *et al.* (1993).

Simultaneously with the collection of phytoplankton samples, some physico-chemical parameters of the lake were measured. Environmental data from 1980 to 1985 are described in Serra *et al.* (1984); Miracle *et al.* (1987) and Soria *et al.* (1987). Data collected from 1986 to 1988 have yet to be published.

Statistical tests were made according to Sokal & Rohlf (1981), using the SPSS package (Nie *et al.*, 1984). A stepwise multiple linear regression analysis of each species abundance against some environmental variables (temperature, underwater light climate, nitrate, nitrite, ammonia, total dissolved nitrogen, dissolved phosphate and for diatoms also dissolved silica) was performed. Data were normalized when necessary by means of a logarithmic transformation.

Results

Abundant species and horizontal pattern

A total of 131 phytoplankton species were identified in the lake from 1980 to 1988. The species having a high density, biomass and occurrence during the study period were selected to establish their algal periodicity in the Albufera of Valencia (Table 1). Phytoplankton was almost continuously dominated by three filamentous blue-green species, *Planktothrix agardhii*, *Pseudanabaena galeata* and *Geitlerinema* sp., that represented approximately half of the algal relative abundance and more than 70% of the biomass for 1980–88. Their periodicity and ecology in the lake has been described in Romo & Miracle (1993). After the three major algae, the species that contributed the most to the phytoplankton density was *Planktolyngbya subtilis* although its small trichome volume (29 μm^3) considerably reduced the importance of its relative biomass (Table 1). Other abundant filamentous cyanophytes were *Planktolyngbya contorta*, *Cylindrospermopsis raciborskii*, *Jaaginema* cf. *metaphyticum*, *Anabaenopsis elenkinii* and *Geitlerinema amphibium* (Table 1).

In general, the other species apart from Cyanophyta represented less than 1% of the total phytoplankton relative abundance and biomass for 1982–88, with the exception of the diatom *Cyclotella meneghiniana* (Table 1). Similarly as was described by Shoeman & Archibald (1980) in the Albufera, and in other shallow hypertrophic lakes (Rojo, 1990; Kiss & Padisak, 1990), the populations of *C. meneghiniana* during the present study were constituted by individuals of different sizes corresponding to distinct growth phases (diameter size 8–12 μm and (4–) 5–7 μm). This centric diatom was almost permanently present in the lake (Table 1), amounted to 56% (points 1 and 3) and 38% (point 2) to the total diatoms density. Nevertheless, the genus *Nitzschia* was the most important in number of species, representing 50% of the total diatoms identified in the Albufera (Table 1).

Chlorophyta consisted mainly of *Scenedesmus* and *Monoraphidium* species, the former with 20 taxa represented 29% of the total identified Chlorophyta (Table 1). The most abundant and frequent algae were *Scenedesmus acuminatus*, *Scenedesmus quadricauda*, *Monoraphidium contortum* and *Chlamydomonas* spp. These species amounted to 40% of the total density of Chlorophyta for the period 1982-88. The highest mean density corresponded to *Scenedesmus acuminatus* (Table 1).

The most relevant Cryptophyta were *Cryptomonas erosa* and *Rhodomonas lacustris* var. *nannoplanctica*. They amounted to 90–95% of total Cryptophyta density for 1982–88. The greatest mean density corresponded to *Rhodomonas lacustris* var. *nannoplanctica* (Table 1). They were almost permanently present in the lake, appearing in 70–90% of the total samples. It is interesting to note that prior to Javornicky's (1976) taxonomic criteria for *Rhodomonas* species, *Rh. lacustris* var. *nannoplanctica* was classified as *Rhodomonas minuta* Skuja var. *nannoplanctica* Skuja.

Horizontal differences in the annual and seasonal pattern were small except in the case of *Planktolyngbya subtilis*, *Cylindrospermopsis raciborskii*, *Chlamydomonas* spp., *Cyclotella meneghiniana* and the coccal cyanophytes (Fig. 2). *Planktolyngbya subtilis* and *Cylindrospermopsis raciborskii* had at point 1 much lower frequency

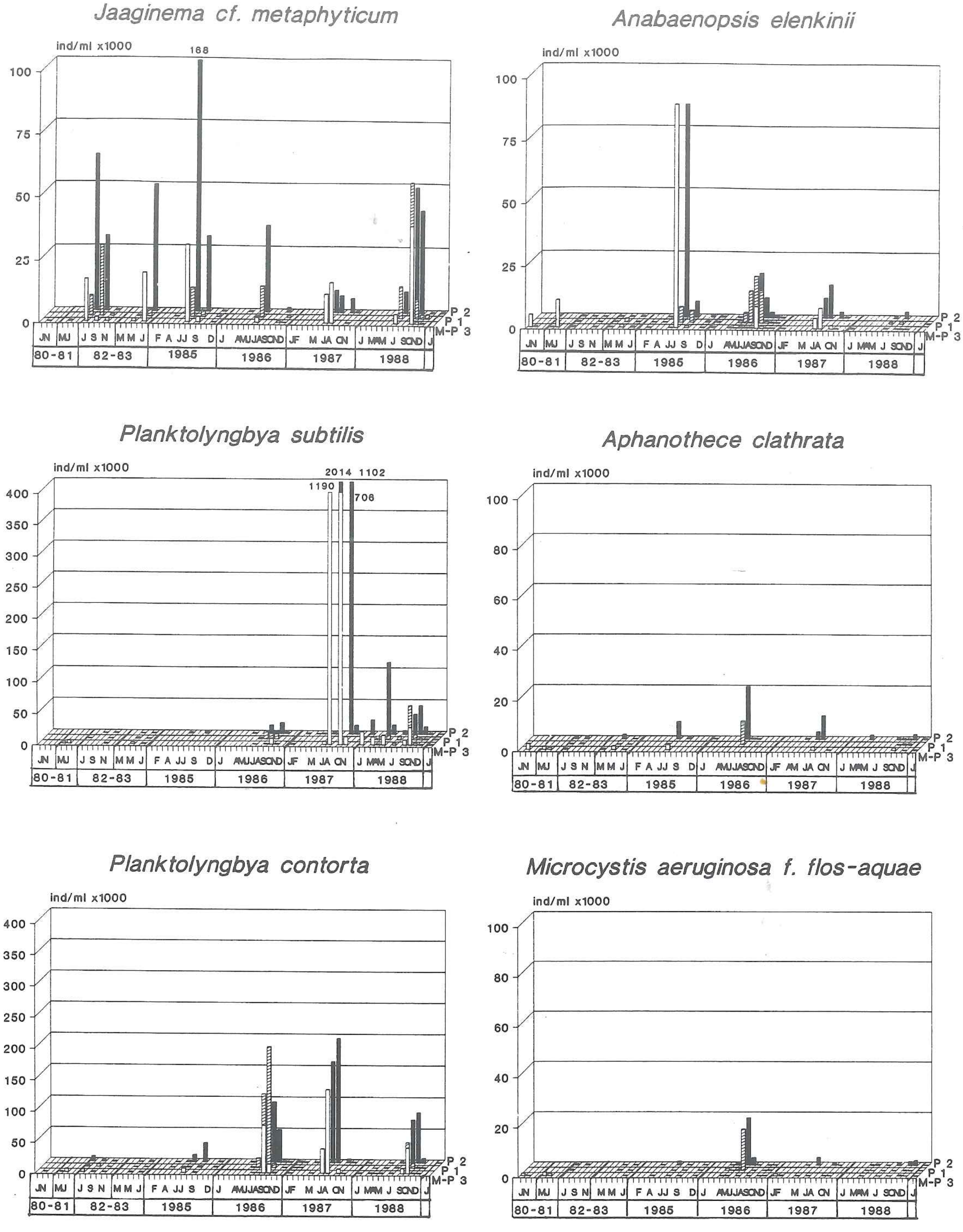
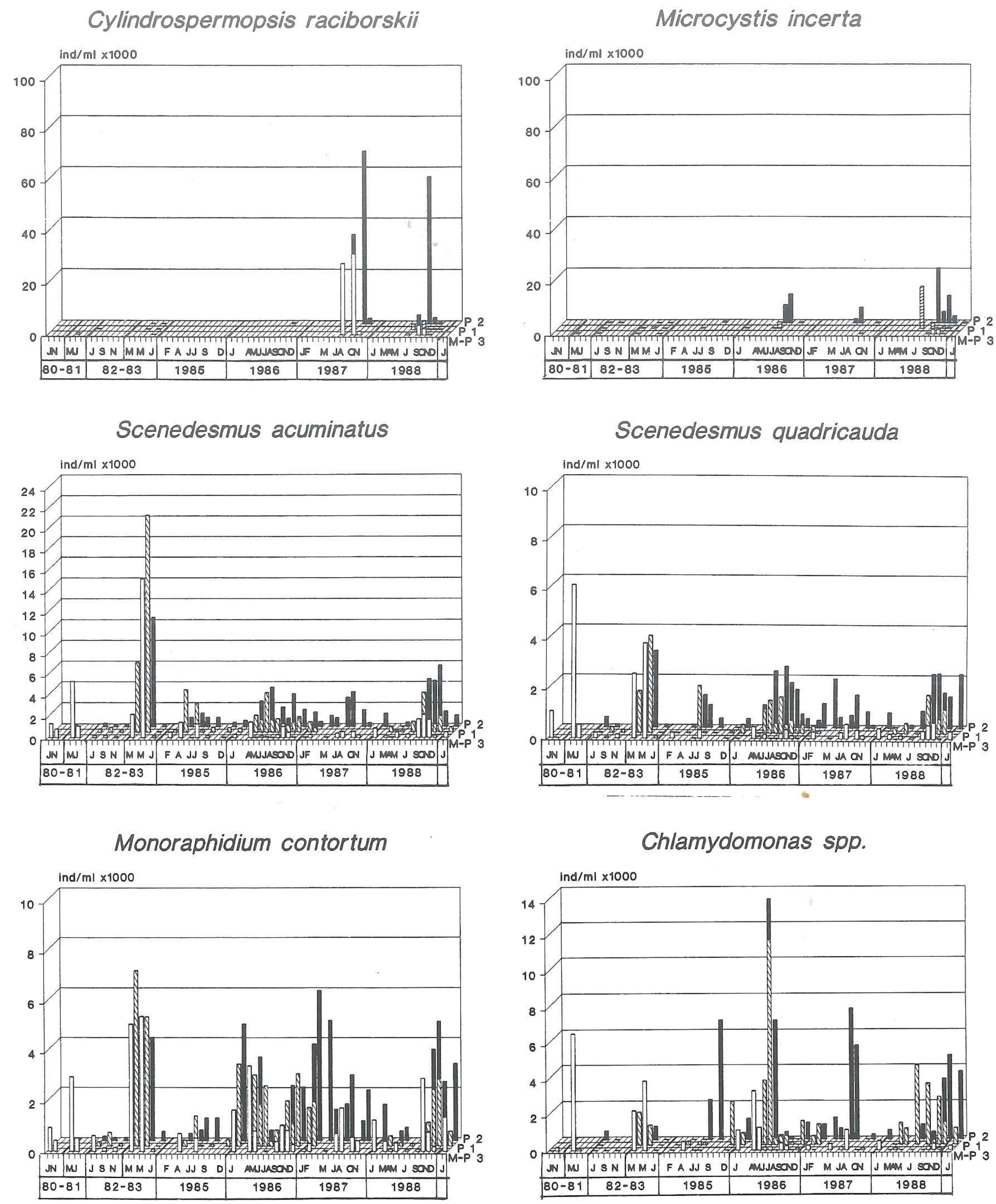


Fig. 2. For caption see p. 44.



Cylindrospermopsis raciborskii

Microcystis incerta

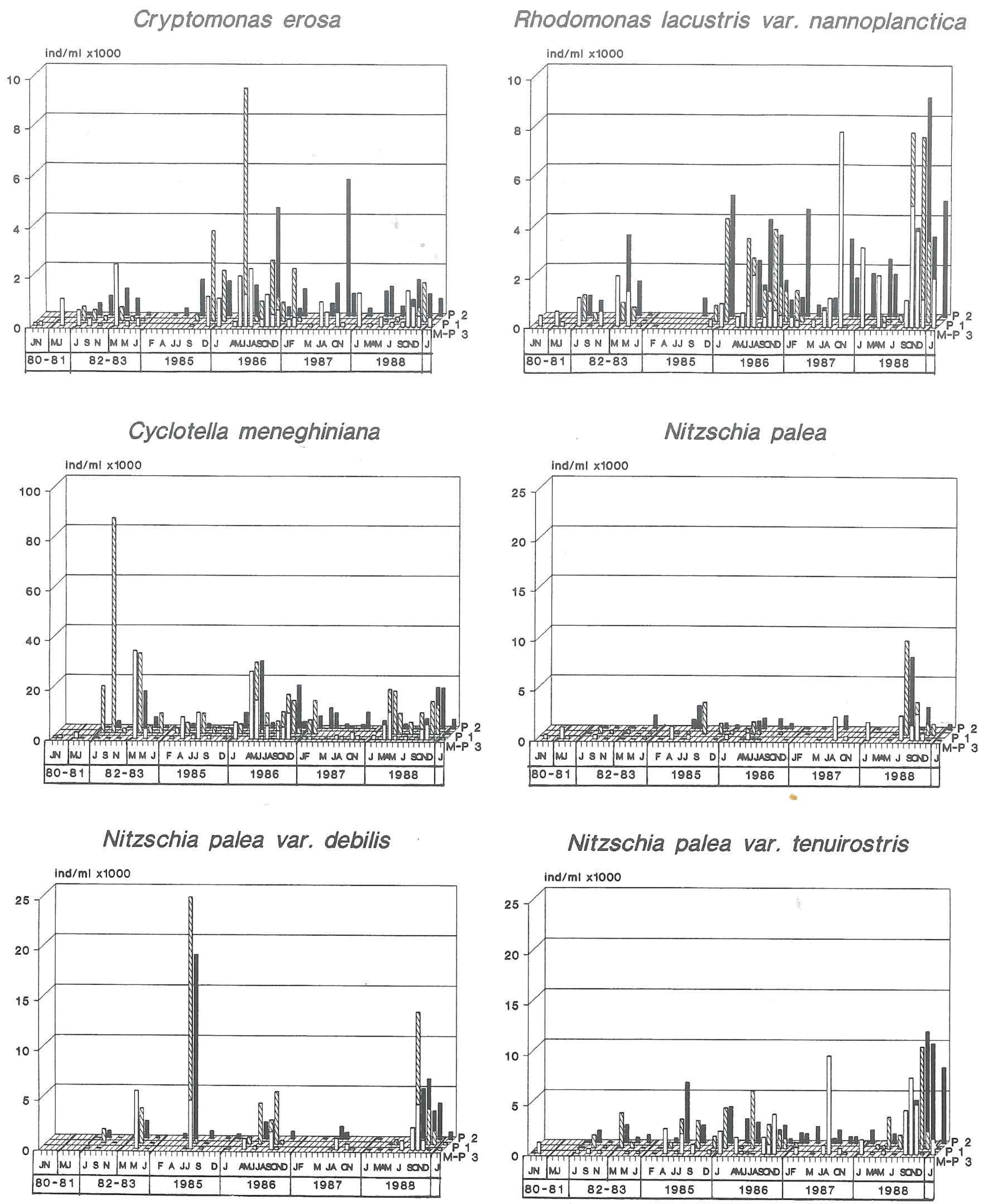
Scenedesmus acuminatus

Scenedesmus quadricauda

Monoraphidium contortum

Chlamydomonas spp.

Fig. 2. (Continued). For caption see p. 44.


Cryptomonas erosa

Rhodomonas lacustris var. nannoplanctica

Cyclotella meneghiniana

Nitzschia palea

Nitzschia palea var. debilis

Nitzschia palea var. tenuirostris

Fig. 2. (Continued). For caption see p. 44.

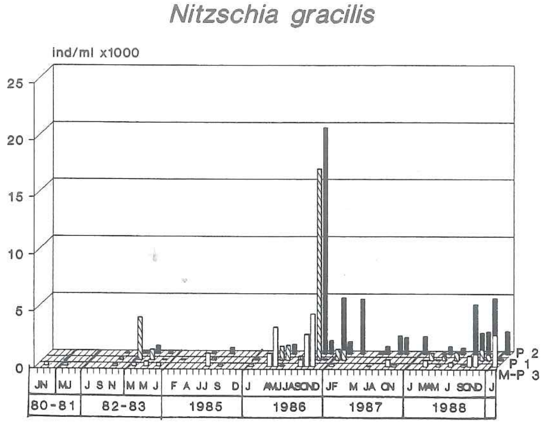


Fig. 2. Periodicity and horizontal changes in the abundance of the main phytoplankton species of the Albufera of Valencia, between 1980 and 1988. On the abscise only the sampled dates are indicated with the initial of the corresponding month. Sampling points are shown as: M, P1, P2 and P3 (see text).

values than in the other sampling points (Table 1), due to the lack of data at this station in 1987, when these species reached their maximum development (Fig. 2). In contrast, at point 1 the average density and biomass of *Cyclotella meneghiniana* for 1982–88 was double that at the other stations (Table 1), due to an important increase of small forms in 1982 (Fig. 2). Its relative frequences of density and biomass were in generalhigher at the stations of greater turbulence (points 1 and 3). This also applied to the three *Nitzschia palea* forms. The coccal blue-green species showed a higher density at point 2, which is the zone with the lowest renewal time. Among them, *Aphanothece clathrata* was the one having the highest occurrence in the lake, while *Microcystis incerta* had the highest mean density at point 2 for 1982–88 (Table 1).

Table 1. Percentage of occurrence (Occur), relative frequencies of biomass (B) and density (A), mean biomass (MB, mg·l^{-1}) and mean density (MA, ind·μl^{-1}) of the phytoplankton species identified in the Albufera of Valencia for 1982–88. Codes for the relative frequencies of biomass and density: $>10\%$ equals 5; [10–1%] equals 4;]1–0.1%] equals 3;]0.1–0.01%] equals 2; $<0.01\%$ equals 1; (–) No present.

	Station 1 (Zone North)					Station 2 (Zone Center)					Station 3 (Zone South)				
	Occur	B	A	MB	MA	Occur	B	A	MB	MA	Occur	B	A	MB	MA
CYANOPHYCEAE															
Planktothrix agardhii (Gom.) Anagn. Kom	100	5	5	77.49	40.69	100	5	5	133	61.20	97	5	5	26.60	16.40
Pseudanabaena galeata Böcher	97	4	5	7.41	47.49	100	4	5	8.44	62.20	92	4	4	2.21	14.60
Geitlerinema sp.	76	4	5	5.71	62.02	76	4	5	10.30	106	79	4	5	4.40	42.50
Planktolyngbya subtilis (Lemm.) Anagn. Kom.	52	2	4	0.13	6.86	71	4	5	2.87	127	56	4	5	1.94	91.90
Planktolyngbya contorta (Lemm.) Anagn. Kom.	67	3	4	0.22	16.37	82	3	4	0.35	26.38	67	3	4	0.18	12.40
Cylindrospermopsis raciborskii (Wol.) Seen. Raju	15	2	2	0.31	1.16	21	3	4	4.99	21.00	18	3	4	1.89	9.63
Jaaginema cf. *metaphyticum* Kom.	52	3	4	0.25	8.54	55	3	4	0.67	23.88	44	3	4	0.24	8.13
Anabaenopsis elenkinii Miller	70	4	3	1.73	2.84	71	3	4	2.47	5.96	77	4	4	1.00	3.90
Geitlerinema amphibium (Ag. ex Gom.) Anagn.	36	3	4	1.70	8.19	55	3	4	2.25	10.74	41	3	4	0.76	3.81
Aphanothece clathrata W. & G. S. West	21	4	3	9.30	1.50	47	4	3	10.60	2.74	23	4	3	2.55	0.71
Microcystys aeruginosa f. flos-aquae (Wit.) Elenk.	21	4	3	6.42	2.72	37	4	3	14.40	2.34	10	4	2	4.50	0.32
Microcystis incerta (Lemm.) Starmach	33	3	3	2.86	2.13	37	4	3	7.20	4.70	18	3	2	1.18	0.63
Oscillatoria lanceaeformis Kalbe	36	3	4	0.35	7.44	61	2	3	0.25	4.89	38	3	3	0.15	2.83

Table 1. (Continued)

	Station 1 (Zone North)					Station 2 (Zone Center)					Station 3 (Zone South)				
	Occur	B	A	MB	MA	Occur	B	A	MB	MA	Occur	B	A	MB	MA
Merismopedia tenuissima Lemm.	67	2	3	0.09	2.39	76	2	3	0.16	4.29	54	2	3	0.06	1.21
Merismopedia punctacta Meyer	21	1	2	0.05	0.40	37	2	2	0.39	0.80	31	2	2	0.04	0.33
Chroococcus limneticus var. subsalsus Lemm.	15	1	2	0.05	0.75	53	2	3	0.10	1.45	41	2	2	0.03	0.33
Synechocystis cf. *pevaleckii* Erceg.	18	1	2	0.03	0.52	24	1	2	0.05	1.24	10	1	2	0.01	0.24
Marssoniella elegans Lemm.	3	1	1	0.08	0.31	5	1	1	0.13	0.42	–	–	–	–	–
Spirulina albida Kolkwitz	12	1	2	0.05	0.76	3	1	1	0.01	0.18	3	1	1	0.01	0.18
Anabaena cf. *laxa* Rabehn.	–	–	–	–	–	3	1	1	0.17	0.30	5	3	2	2.16	1.39
Anabaena sp.	6	2	1	0.67	0.31	8	2	1	0.26	0.20	10	2	1	0.08	0.09
Komvophoron schmidlei (Jaag) Anagn. Kom.	3	–	1	–	0.16	3	–	1	–	0.36	–	–	–	–	–
Romeria elegans Wol.	6	1	2	0.02	0.13	–	–	–	–	–	5	1	2	0.04	1.69
BACILLARIOPHYCEAE															
Cyclotella meneghiniana Kütz.	97	4	4	5.06	11.27	100	4	3	2.25	5.41	100	4	4	2.48	4.86
Nitzschia palea (Kütz.) W. Smith	67	3	3	0.44	1.15	63	3	3	0.43	0.92	67	3	3	0.26	0.62
Nitzschia palea var. *tenuirostris* Grun.	88	3	3	0.41	1.86	89	3	3	0.51	2.25	87	3	3	0.27	1.51
Nitzschia palea var. *debilis* (Kütz.) Grun.	58	3	3	0.26	3.30	58	2	3	0.15	0.22	62	3	3	0.08	1.10
Nitzschia gracilis Hantz.	73	3	3	0.71	1.44	76	3	3	1.10	2.07	62	3	3	0.51	0.93
Cyclotella comta (Ehr.) Kütz.	70	4	3	2.33	0.92	58	3	2	1.59	0.46	44	3	2	0.55	0.24
Cyclotella sp.	24	2	2	0.08	0.57	53	2	3	0.14	1.00	28	2	2	0.05	0.25
Nitzschia intermedia Hantz.	70	3	3	0.50	0.55	71	3	3	0.66	0.69	56	4	3	1.25	0.55
Nitzschia longissima (Bréb.) Ralfs.	55	3	3	0.32	0.90	61	3	3	0.44	1.24	74	3	3	0.16	0.44
Nitzschia acicularis W. Smith	48	2	3	0.15	0.75	50	2	3	0.13	0.78	51	2	2	0.05	0.27
Nitzschia closterium (Ehr.) W. Smith	3	1	1	0.08	0.47	–	–	–	–	–	8	1	1	0.01	0.07
Nitzschia pusilla Kütz.	45	2	3	0.10	2.24	37	2	3	0.07	1.57	38	2	2	0.02	0.36
Nitzschia dissipata (Kütz.) Grun.	15	2	2	0.13	0.19	16	2	2	0.39	0.51	10	2	2	0.20	0.39
Nitzschia sp.	6	–	2	–	0.44	5	–	1	–	0.63	3	–	1	–	0.07
Nitzschia subcapillata Hustedt	3	2	–	0.61	–	5	2	1	0.54	0.90	8	2	2	0.37	0.45
Navicula cryptocephala Kütz.	3	1	1	0.08	0.04	–	–	–	–	–	5	2	1	0.14	0.16
Navicula sp.	6	1	1	0.01	0.05	–	–	–	–	–	18	2	2	0.03	0.14
Cocconeis placentula Ehr.	–	–	–	–	–	–	–	–	–	–	3	–	1	–	0.06
Synedra ulna (Nitz.) Ehr.	–	–	–	–	–	3	1	1	0.07	0.42	3	1	1	0.01	0.03
Acanthoceras zachariasi (Brun.) Simonsen	–	–	–	–	–	–	–	–	–	–	3	2	2	1.13	0.83
Amphora sp.	–	–	–	–	–	–	–	–	–	–	3	1	1	0.12	0.05
Pinnularia sp.	–	–	–	–	–	–	–	–	–	–	3	2	1	0.21	0.13
CRYPTOPHYCEAE															
Cryptomonas erosa Ehr.	82	3	3	0.71	1.14	92	3	3	0.50	0.93	85	3	3	0.34	0.71
Rhodomonas lacustris var. *nannoplanctica* (Skuja) Jav.	73	2	3	0.09	1.82	87	2	3	0.11	2.14	90	3	3	0.05	1.21
Crytomonas erosa var. *reflexa* Marsson	15	2	2	0.31	0.60	16	2	2	0.15	0.30	5	1	1	0.07	0.18
Crytomonas marsonii Skuja	27	2	2	0.17	0.37	26	2	2	0.12	0.34	28	2	2	0.05	0.17
Crytomonas ovata Ehr.	3	1	1	0.06	0.16	13	1	1	0.09	0.26	10	2	2	0.10	0.18
Rhodomonas lacustris Pascher Ruttner	24	1	2	0.04	0.40	32	2	2	0.06	0.49	28	2	2	0.03	0.36
Cryptomonas sp.	–	–	–	–	–	–	–	–	–	–	5	1	1	0.02	0.21
CHLOROPHYCEAE															
Scenedesmus acuminatus (Lagerh.) Chod.	100	4	3	1.25	1.83	97	3	3	1.00	1.96	95	3	3	0.44	0.97
Scenedesmus quadricauda (Turp.) Bréb. Chod.	79	2	3	0.06	0.70	95	2	3	0.12	1.03	77	3	3	0.10	0.44
Chlamydomonas spp.	76	3	3	0.50	1.67	74	3	3	0.61	2.34	56	3	3	0.19	0.77
Monoraphidium contortum (Thur.) Kom. Legn.	91	2	3	0.04	1.41	95	2	3	0.06	1.90	85	2	3	0.04	0.98
Monoraphidium griffithii (Berk.) Kom. Legn.	33	2	3	0.05	0.63	39	2	2	0.10	0.84	46	2	3	0.06	0.45
Monoraphidium komarkovae Nyg.	9	1	2	0.09	0.98	11	1	2	0.05	0.63	8	1	2	0.04	0.70
Monoraphidium tortile (W. & G.S.) Kom. Legn.	12	1	2	0.01	0.32	16	1	1	0.01	0.24	10	1	2	0.01	0.28
Monoraphidium arcuatum (Kors.) Hind.	64	2	3	0.04	0.35	63	2	2	0.04	0.51	54	2	2	0.01	0.12

Table 1. (Continued)

	Station 1 (Zone North)					Station 2 (Zone Center)					Station 3 (Zone South)				
	Occur	B	A	MB	MA	Occur	B	A	MB	MA	Occur	B	A	MB	MA
Monoraphidium circinale (Nyg.) Nyg.	33	2	3	0.06	1.48	29	1	2	0.04	0.90	18	1	2	0.02	0.26
Monoraphidium minutun (Nag.) Kom. Legn.	67	1	3	0.01	0.41	71	1	3	0.02	0.66	62	1	2	0.01	0.18
Tetraedrom minimum(A. Br.) Hansg.	67	2	2	0.04	0.28	74	2	2	0.04	0.40	51	2	3	0.03	0.31
Tetraedrom incus (Teil.) G. M. Smith	12	1	2	0.07	0.28	32	2	2	0.08	0.38	10	2	2	0.06	0.20
Tetraedrom cf. *trigonum* (Nag.) Hansg.	3	2	2	1.65	2.16	3	2	1	1.70	0.66	3	1	1	0.02	0.06
Lagerheimia genevensis (Chod.) Chod.	21	1	2	0.02	0.30	21	1	2	0.04	0.50	28	2	2	0.02	0.22
Lagerheimia marssonii Lemm.	12	1	2	0.02	0.28	–	–	–	–	–	5	1	1	0.01	0.14
Oocystis spp.	42	2	3	0.17	0.51	42	2	2	0.21	0.72	41	2	2	0.06	0.22
Actinastrum hantzschii Lagerh.	82	2	3	0.04	0.69	82	2	3	0.03	0.73	67	2	3	0.03	0.52
Actinastrum sp.	–	–	–	–	–	3	1	1	0.01	0.42	3	1	2	0.02	1.40
Chlamydomonas leiostraca (Stre.) Ettl.	36	2	3	0.01	0.64	26	2	2	0.08	0.52	15	2	2	0.03	0.21
Chlorogonium elongatum Dangeard	64	3	3	0.02	0.86	63	2	2	0.16	0.53	44	2	2	0.04	0.17
Chlorogonium gracile Matwienko	12	1	2	0.04	0.54	11	1	2	0.03	0.50	5	1	2	0.03	0.47
Pediastrum boryanum (Turp.) Menegh.	15	2	1	0.17	0.11	16	2	2	0.21	0.25	10	2	1	0.33	0.12
Pediastrum duplex Meyen	3	1	1	0.24	0.17	–	–	–	–	–	–	–	–	–	–
Scenedesmus acutus Meyen	76	3	3	0.18	0.55	63	2	3	0.28	0.66	49	3	2	0.14	0.31
Scenedesmus longispina Chod.	12	1	2	0.07	0.28	8	1	1	0.03	0.21	5	2	2	0.13	0.57
Scenedesmus quadrispina Chod.	18	1	2	0.05	0.26	11	1	2	0.04	0.57	10	1	2	0.03	0.29
Scenedesmus ecornis (Ehr.) Chod.	42	1	2	0.02	0.36	61	1	2	0.02	0.44	46	1	2	0.01	0.22
Scenedesmus spinosus Chod.	39	2	2	0.04	0.42	58	1	2	0.02	0.36	49	2	2	0.01	0.16
Scenedesmus pecsensis Uherk.	18	1	1	0.01	0.10	21	1	2	0.04	0.44	15	1	2	0.01	0.16
Scenedesmus obliquus (Turp.) Kütz.	30	2	3	0.20	0.80	68	2	3	0.20	0.77	41	3	3	0.14	0.59
Scenedermus antillarum Comas	21	2	2	0.17	0.41	34	2	2	0.44	0.81	21	2	2	0.11	0.22
Scenedesmus incrassatulus Bohl.	–	–	–	–	–	8	1	1	0.03	0.21	–	–	–	–	–
Scenedesmus intermedius Chod.	15	1	2	0.03	0.17	13	1	1	0.03	0.26	5	2	1	0.09	0.11
Scenedesmus costato-granulatus Skuja	6	1	2	0.03	0.43	5	1	2	0.01	0.94	3	1	1	0.00	0.12
Scenedesmus sooi var. *tiszae* Hortob	21	1	2	0.05	0.24	16	1	1	0.04	0.20	33	2	2	0.03	0.16
Scenedesmus lefevrii var. *manguinii* Lef. Bourr.	12	1	2	0.05	0.35	8	1	2	0.10	0.58	8	2	2	0.08	0.23
Scenedesmus cf. *brevispina* (Smith) Chod.	6	1	2	0.12	0.49	13	1	2	0.05	0.58	10	2	2	0.15	0.51
Scenedesmus cf. *sempervirens* Chod.	–	–	–	–	–	–	–	–	–	–	3	1	1	0.00	0.05
Scenedesmus cf. *dispar* (Bréb.) Rabehn	–	–	–	–	–	8	1	1	0.04	0.34	8	2	2	0.07	0.37
Scenedesmus opoliensis Richt.	6	1	1	0.08	0.14	3	1	–	0.12	–	–	–	–	–	–
Scenedesmus bicaudatus Dedus.	–	–	–	–	–	3	–	1	–	0.62	–	–	–	–	–
Schroederia setigera (Schrod.) Lemm.	39	2	2	0.13	0.41	58	2	2	0.04	0.33	41	3	2	0.12	0.27
Closteriopsis acicularis (Smith) Bel. Swale	61	2	3	0.07	0.45	76	2	3	0.08	0.62	64	2	3	0.03	0.25
Chlorella vulgaris Beijer.	21	2	3	0.23	1.47	21	2	2	0.31	1.51	13	2	2	0.11	0.69
Tetrastrum staurogeniaeforme (Schrod.) Lemm.	6	1	1	0.01	0.13	18	1	2	0.03	0.28	13	1	1	0.01	0.12
Dyctiosphaerium pulchellum Wood	58	3	3	0.36	0.86	58	2	2	0.16	0.60	44	3	3	0.16	0.37
Coelastrum microporum Nag.	36	3	3	0.42	0.58	42	2	2	0.19	0.59	36	3	2	0.14	0.41
Coelastrum astroideum De-Not	18	3	2	1.00	0.95	21	2	2	0.21	0.38	18	2	2	0.09	0.24
Golenkinia radiata Chod.	12	2	2	0.13	0.87	8	1	1	0.07	0.32	8	1	1	0.03	0.12
Chloromonas spp.	39	2	3	0.20	1.09	45	2	2	0.06	0.86	8	1	2	0.03	0.36
Pyramimonas sp.	–	–	–	–	–	3	2	1	1.63	0.51	–	–	–	–	–
Treubaria cf. *triappendiculata* Bern.	3	1	1	0.03	0.37	3	1	1	0.01	0.21	8	2	1	0.09	0.12
Didymogenes palatina Schmidle	21	1	2	0.04	0.36	32	1	2	0.03	0.33	8	1	2	0.02	0.23
Didymogenes anomala (G. M. Smith) Hind.	6	1	1	0.01	0.13	3	1	1	0.03	0.35	–	–	–	–	–
Didymocystis f. *planctonica* Kors.	21	1	2	0.03	0.17	26	1	2	0.04	0.29	21	1	2	0.01	0.20
Nephroclamys subsolitaria (G. S. West) Kors.	18	1	2	0.05	0.42	34	1	2	0.05	0.47	23	2	2	0.03	0.20
Phacotus cf. *lenticularis* (Ehr.) Stein	12	1	1	0.08	0.13	3	2	1	0.68	0.51	5	2	1	0.17	0.12
Spermatozopsis exultans Korsch.	–	–	–	–	–	5	1	1	0.01	0.27	8	1	1	0.00	0.06
Pteromonas angulosa (Carter) Lemm.	–	–	–	–	–	3	1	1	0.08	0.12	–	–	–	–	–
Choricystis chodatii (Jaag.) Fott	18	2	2	0.07	1.05	8	1	2	0.06	0.71	18	3	3	0.30	3.70
Choricystis minor (Skuja) Fott	39	1	3	0.02	1.51	39	1	3	0.01	1.45	26	1	3	0.01	0.64
Diplostauron sp.	6	1	1	0.04	0.24	11	1	1	0.03	0.34	5	1	1	0.01	0.16
Kirchneriella sp.	18	1	2	0.02	0.60	34	1	2	0.03	0.65	8	1	2	0.02	0.60

Table 1. (Continued)

	Station 1 (Zone North)					Station 2 (Zone Center)					Station 3 (Zone South)				
	Occur	B	A	MB	MA	Occur	B	A	MB	MA	Occur	B	A	MB	MA
Crucigeniella sp.	6	1	1	0.02	0.26	16	1	2	0.02	0.33	5	1	1	0.03	0.13
Platymonas sp.	3	2	1	1.02	0.39	3	1	1	0.13	0.18	3	1	1	0.07	0.06
Sphaerellopsis sp.	18	2	2	0.40	0.21	–	–	–	–	–	10	2	1	0.11	0.07
Carteria sp.	3	1	1	0.06	0.08	3	1	1	0.34	0.42	10	2	1	0.10	0.12
Phyllocardium sp.	9	1	2	0.03	0.56	13	1	2	0.06	0.58	10	1	2	0.01	0.18
Chlamydonephris sp.	12	1	2	0.05	0.19	16	1	1	0.05	0.19	15	2	2	0.05	0.29
Pyramichlamys sp.	–	–	–	–	–	–	–	–	–	–	3	1	1	0.02	0.12
DESMIDIACEAE															
Closterium cf. *acutum* Bréb.	3	1	1	0.27	0.11	5	2	1	0.51	0.36	3	1	1	0.07	0.07
EUGLENOPHYCEAE															
Euglena proxima Dangeard	30	3	2	1.59	0.42	11	2	1	0.41	0.20	23	3	2	0.24	0.13
Euglena agilis var. *pisciformis* Carter	30	3	3	1.77	1.71	8	2	2	0.90	0.81	21	3	2	0.51	0.68
Euglena sp.	24	3	2	0.89	0.36	16	2	2	0.31	0.29	21	2	2	0.11	0.09
Trachelomonas volvocina Ehr.	36	3	3	0.43	0.41	21	2	2	0.21	0.24	26	3	3	0.48	0.78
Trachelomonas hispida Stein	30	3	1	0.61	0.12	8	2	1	0.25	0.15	21	2	2	0.20	0.09
Phacus sp.	33	3	2	0.74	0.42	24	2	2	0.35	0.23	28	3	2	0.26	0.21
DINOPHYCEAE															
Gymnodinium cf. *lacustre* Schiller	45	3	2	0.36	0.38	71	3	2	0.34	0.47	49	3	2	0.20	0.19
Other algae	18	1	2	0.03	0.59	18	1	2	0.06	0.63	21	1	2	0.01	0.22

Annual periodicity

The lake showed a pronounced algal periodicity during the years 1980–88, with seasonality of the abundant species remaining almost similar from year to year (Fig. 2). Nevertheless, two hydrological events influenced nutrient and phytoplankton dynamics during the last two years. In 1987, the usual post-summer water renewal (from September to October) for harvest of the ricefields, was disturbed by the blocking of the outlet channels with sediments. The prolonged water retention enhanced the growth of several species but especially that of *Planktolyngbya subtilis* (Fig. 2). It attained the highest standing crop recorded for any species in the study (2×10^6 ind ml^{-1}), dominating the phytoplankton assemblage (represented 80% of the total algal density). At this time, water drainage from the ricefields into the lake resulted in an increment of nitrogen loading, shifting the concentration from 36 μM in late August to 154 μM in October, while orthophosphate dropped to undetectable values as a consequence of the algal growth. In 1988, a rainy spring delayed the general species periodicity towards the end of the year.

Some species such as *Planktolyngbya subtilis*, *Planktolyngbya contorta*, *Cylindrospermopsis raciborskii*, *Microcystis incerta*, *Nitzschia palea* var. *tenuirostris* and *Rhodomonas lacustris* var. *nannoplanctica* showed an annual trend of increasing throughout the study period, whereas *Anabaenopsis elenkinii*, *Scenedesmus acuminatus*, *Scenedesmus quadricauda* and *Cyclotella meneghiniana* showed the opposite trend (Fig. 2).

Therefore, maximum populations of *A. elenkinii* took place during the years of the lowest nitrogen levels, in 1985 and 1986 (summer values $N:P < 30$, $N = 1–3$ μM), having its populations density an inverse relationship with this nutrient (Table 2). *Scenedesmus acuminatus* and *Sc. quadricauda* had after their maximum increases of May

Table 2. Multiple linear regression analyses between the populations density of main phytoplankton species of the Albufera of Valencia and the environmental variables, for each of the sampling points and the average values of them. T (temperature), I (underwater light climate), N (dissolved inorganic nitrogen), P (dissolved inorganic phosphate), Si (dissolved silica), NOX (nitrate + nitrite), NR (ammonia). Significant $P < 0.05$. A = species favoured by high values of the variable, B = favoured by low values.

		T (°C)	I (%)	NOX μM	NR μM	N μM	P μM	Si μM			T (°C)	I (%)	NOX μM	NR μM	N μM	P μM	Si μM
Jaaginema cf. *metaphyticum*	MEAN	A							*Nitzschia palea* var. *tenuirostris*	MEAN							
	PTO 1			A						PTO 1							
	PTO 2	A								PTO 2							
	PTO 3	A								PTO 3		B					
Anabaenopsis elenkinii	MEAN	A		B					*Nitzschia palea* var. *debilis*	MEAN							
	PTO 1	A		B	B					PTO 1					B		
	PTO 2	A		B						PTO 2							
	PTO 3	A			B					PTO 3					B		
Aphanothece clathrata	MEAN								*Nitzschia gracilis*	MEAN	B	B					
	PTO 1									PTO 1							
	PTO 2									PTO 2	B	B					
	PTO 3									PTO 3	B			A			
Microcystis aeruginosa f. flos-aquae	MEAN								*Cryptomonas erosa*	MEAN		B					
	PTO 1									PTO 1							
	PTO 1									PTO 1							
	PTO 2									PTO 2		B					
	PTO 3									PTO 3			B				
Microcystis incerta	MEAN						A		*Rhodomonas lacustris* var. *nannoplanctica*	MEAN		B					
	PTO 1		A							PTO 1							
	PTO 2	A					A			PTO 2	B	B			A	A	
	PTO 3	A	B			B	A			PTO 3							
Planktolyngbya subtilis	MEAN			A					*Monoraphidium contortum*	MEAN	B	B					
	PTO 1									PTO 1	B				B		
	PTO 2			A	B					PTO 2	B	B					
	PTO 3				B					PTO 3		B					
Planktolyngbya contorta	MEAN	A	B	A					*Scenedesmus acuminatus*	MEAN		B	B			A	
	PTO 1			B	B					PTO 1			B				
	PTO 2	A	B	A	B	A				PTO 2		B	B	B		A	
	PTO 3	A	B	A			B			PTO 3		B					
Cylindrospermopsis raciborskii	MEAN								*Scenedesmus quadricauda*	MEAN		B			B	A	
	PTO 1									PTO 1		A	B	B		A	
	PTO 2				B					PTO 2		B					
	PTO 3				B		B			PTO 3		B			B		
Cyclotella meneghiniana	MEAN	B	B					B	*Chlamydomonas* spp.	MEAN							
	PTO 1	B	B					B		PTO 1			B				
	PTO 2	B	B		B	B	A	B		PTO 2							
	PTO 3		B		A					PTO 3		B					
Nitzschia palea	MEAN																
	PTO 1																
	PTO 2																
	PTO 3		B														

1981 and 1983, a decrease in their annual maximum to more of less constant levels of 2–4 × 10^3 ind ml^{-1} (Fig. 2). Similarly, the annual peaks of *Cyclotella meneghiniana* dropped approximate six-fold between 1982 and 1988 (from a mean value of 8.6 × 10^4 ind ml^{-1} in 1982 to 1.5 × 10^4 ind ml^{-1} in 1988). In contrast, *Nitzschia palea* var. *tenuirostris* showed an eight-fold rise for the same period (from an average of 1.2 × 10^3 ind ml^{-1} in 1982 to 9.6 × 10^3 ind ml^{-1} in 1988). However, the highest overall interannual increment was shown by *Rhodomonas lacustris* var. *nannoplanctica*, shifting from an average of 0.5 × 10^3 ind ml^{-1} in 1980 to 7 × 10^3 ind ml^{-1} in 1988 (Fig. 2).

Seasonal pattern

A general seasonal pattern is shown in Fig. 3. The abundant but non-dominant cyanophytes occurred mainly in summer and autumn. The trichomes of *Jaaginema* cf. *metaphyticum* identified in the Albufera corresponded rather well to the species description of Anagnostidis & Komarek (1988), although we could not confirm trichomes immobility (Romo, 1991). It has been described as a benthic or tycoplanktonic species found in diverse habitats (soil, sediment, epiphyte) (Koppe, 1924; Komárek, 1975) and in waters with high organic pollution (Alboal, 1988). Its presence in the Albufera mainly in July (Fig. 2), could

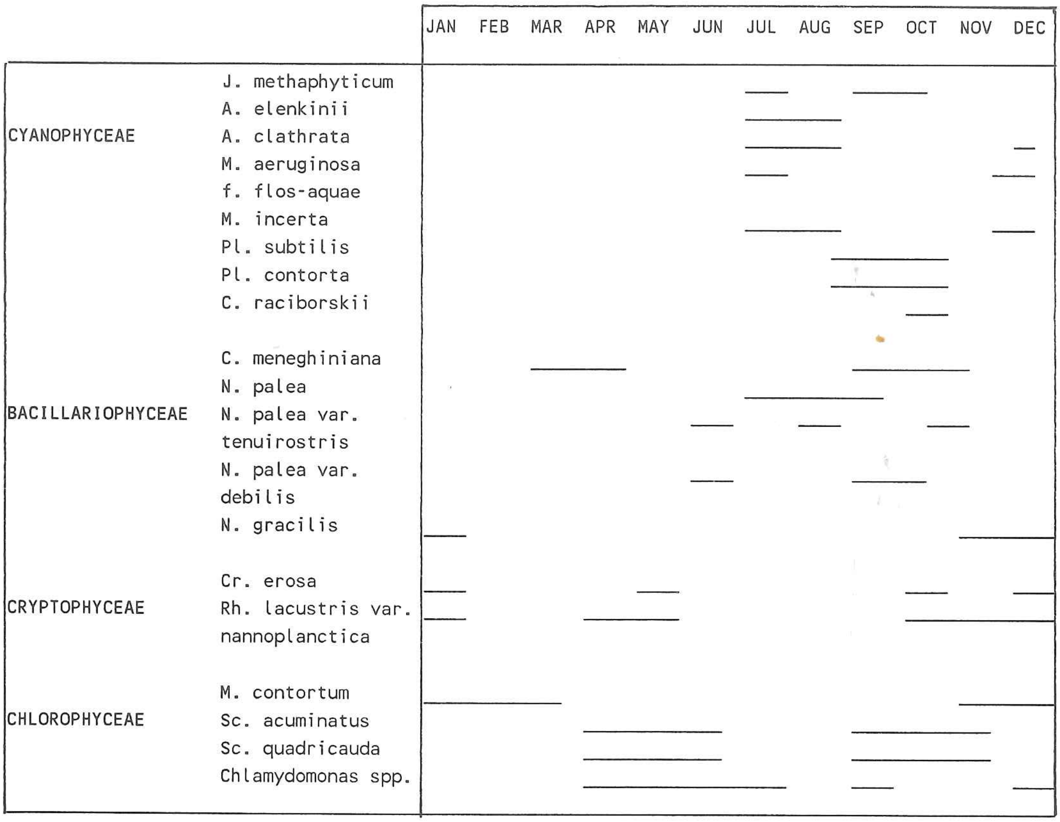


Fig. 3. Seasonal pattern of the subdominant phytoplankton species of the Albufera of Valencia, according to their annual maximum populations periods during 1980–88.

have been originated from an exogenous input from the surrounding ricefields, after their temporary drying for weeding and fertilization from late June to early July, developing afterwards its own populations in the lake. The shallowness of the lake and wind stirring in summer, could favour the suspension in the water column of this non-vacuolate algae. Its populations amounted to up 40% of the total phytoplankton abundance in July 1983.

Anabaenopsis elenkinii also developed in the Albufera during summer months (Figs 2–3). Its highest percentage within the total phytoplankton abundance (27%) was in July 1985. During the periods of its maximum standing crops the environmental conditions were characterized for high temperature, water stability and low nutrient concentrations, especially nitrate (Tables 2–3). These features agree with those described for this blue-green algae in another Spanish shallow hypertrophic lake (Rojo, 1990). It seems possible that this species fixed nitrogen in the lake, since its trichomes always showed the presence of 1 or 2 heterocytes. Moreover, its occurrence in summer could be related to the high light intensity requirement for nitrogen fixation (Zevenboom & Mur, 1980), although a direct relation with this parameter was not found (Table 2).

The three major coccal cyanophytes of the lake, *Aphanothece clathrata*, *Microcystis aeruginosa* f. *flos-aquae* and *Microcystis incerta* appeared during periods of water stability (summer and end-autumn), with higher abundance at the sampling point 2, which has the longest water residence (Figs 2–3). Nevertheless, these species differed from *Anabaenopsis elenkinii* for they were able to grow also in November–December, during the more moderate second period of water stability. The development of the coccal blue-green algae in the Albufera took place under higher phosphate levels and generally lower nitrogen concentrations than the filamentous cyanophytes, *Microcystis* species occurring at the lowest concentrations of nitrogen (Table 3). *Microcystis incerta* was the only coccal species showing some relationship with the abiotic parameters (Table 2). The main development of *M. incerta* in 1988, when the annual average of dissolved phosphate was 5–10 times higher than in the other years as a consequence of the wet weather (J. M. Soria, pers. comm.), could suggest a closer dependence of this algae on phosphorus than the other coccal species. However, this observation needs experimental appraisals. The big colonial size of these three coccal species ($4.5–1.4 \times 10^3\ \mu m^3$) accounted on some dates for an important percentage of the algal biomass, such as in November 1980 and January 1987, where *Aphanothece clathrata* and *Microcystis aeuroginosa* f. *flos-aquae* represented 83% and 65% of the total algal biomass, but only 4.9% and 6.6% of the total abundance, respectively. The maximum biomass (up 118 mg l^{-1}) corresponded to *Aphanothece clathrata* in July 1986 (amounted to 25% of total biomass).

Both *Planktolyngbya subtilis* and *Pl. contorta* showed a similar periodicity, although the latter developed earlier, from 1986 onwards (Fig. 2). They occurred mainly from late August to October (Fig. 3) at the time of ricefields drainage for harvest. During the rainy month of April 1988, *Pl. subtilis* populations were also important within the phytoplankton assemblage at point 2 (represented 71% of the total algal density). The two *Planktolyngbya* species were favoured by moderate water renewal, high nitrate but low phosphate levels, and temperatures above 19 °C (Tables 2–3). The relationship of *Pl. contorta* with low underwater light climate (Table 2) could be due to the alloctonous material carried out into the lake during drying of the ricefields. The development of *Cylindrospermopsis raciborskii* in 1987 was produced after the increases of *Planktolyngbya* species (Figs 2–3) with a N:P ratio higher than those of *Planktolyngbya*, but a lower mean temperature. These three cyanophytes occurred in the lake under very low phosphate concentrations (Table 3). Although, it is possible that *Cylindrospermopsis raciborskii* could be also present at the ricefields as a N_2-fixing species (Quesada, 1990), nitrogen fixation in the Albufera was unlikely because of the high nitrogen concentrations in the lake during its maximum populations and the frequent lacking of heterocytes in the trichomes.

Table 3. Values of the environmental variables during annual maximum populations of the subdominant species of the Albufera of Valencia, between 1980 and 1988. First line: average values; second line: range of the abiotic variables during maximum populations at the three sampling stations. Temp (temperature), I (underwater light climate, percentage of subsurface intensity), N (dissolved inorganic nitrogen), P (dissolved inorganic phosphate), SiO_2 (silica). i = (undetectable levels).

	Temp (°C)	pH	I (%)	N μM	P μM	N:P	SiO_2 μM	Si:P
J. methaphyticum	27	8.9	19	50	0.2	334		
	19–31	8–9.6	14–27	0.4–159	0.01–0.4	20–>1000		
A. elenkinii	27	8.8	17	26	0.4	70		
	25–28	7.6–10	14–24	1.2–79	0.01–1.3	1–600		
A. clathrata	21	9.4	18	30	1.5	20		
	7–28	8.8–10	14–25	4.3–61	0.08–7.5	20–500		
M. aeruginosa	23	9.7	19	12	1.4	8		
f. flos-aquae	7–28	9.5–10.4	13–27	0.8–39	0.07–7.5	2–560		
M. incerta	25	8.8	18	17	3.0	6		
	16–29	7.6–10	14–23	0.4–46	0.11–9.2	4–270		
Pl. subtilis	26	9.5	15	36	0.1	360		
	23–28	8.8–10	14–16	43–54	0.08–0.1	300–>1000		
Pl. contorta	25	8.6	17	38	0.3	140		
	19–28	7.6–10	14–24	0.5–79	0.08–0.8	2–600		
C. raciborski	20	8.9	19	103	0.01	>1000		
	17–25	8.7–9.4	16–20	0.4–255	i–0.01	>1000		
C. meneghiniana	15	8.9	14	240	11.1	22	37	3
	11–23	8.1–9.4	10–20	0.2–885	0.14–50.4	2–1000	0.2–127	1–150
N. palea	25	9.2	16	49	1.3	39	110	87
	18–29	8–10.4	9–23	1.0–150	0.01–9.2	5–>1000	27.7–207	70–>1000
N. palea var.	19	8.8	17	67	3.0	22	87	29
tenuirostris	8–28	7.9–9.8	9–24	3.9–219	0.01–16.4	4–>1000	27.7–187	20–>1000
N. palea var.	22	8.7	17	39	0.4	110	98	281
debilis	18–27	7.6–9.9	14–24	0.5–84	0.13–0.8	2–600	2.5–181	150–>1000
N. gracilis	11	8.8	17	167	1.7	98	124	73
	6–15	8–9.5	13–20	101–219	0.02–7.5	250–1000	94–189	60–>1000
Cr. *erosa*	17	8.8	18	106	5.9	18		
	7–26	7.6–9.8	14–38	1.5–415	0.01–32.7	0.4–>1000		
Rh. *lacustris* var.	18	8.6	18	71	2.4	30		
nannoplanctica	8–30	7.6–9.4	14–23	0.5–255	0.01–16.4	2–>1000		
M. contortum	15	9.0	16	56	3.7	15		
	8–19	8.3–10.4	10–20	6.6–134	0.01–25.2	4–>1000		
Sc. *acuminatus*	21	9.3	16	39	3.8	10		
	17–27	8.3–10.4	9–24	0.5–150	0.06–18.1	4–270		
Sc. *quadricauda*	23	8.9	17	16	1.0	17		
	17–28	7.6–10.4	11–27	0.5–66	0.06–4.7	2–500		
Chlamydomonas	19	9.5	17	81	5.6	14		
spp.	7–29	8.5–10.4	10–23	0.3–415	0.07–32.7	3–560		

Among diatoms a seasonal segregation was observed. *Cyclotella meneghiniana* was more abundant early in the year, whereas *Nitzschia* species appeared during summer and autumn. All of them developed under periods of high to moderate water renewal or changes in the lake water level. The highest percentage of *Cyclotella meneghiniana* within the algal abundance occurred in September 1982 (30% at point 1) and April 1988 (32% and 46% at points 1 and 3 resp.) coincidental with water renewal due to rainfall. In 1985 and 1987, *Nitzschia palea*, *N. palea* var. *tenuirostris* and *N. palea* var. *debilis* developed between June and August (Fig. 2), during changes in the lake water level as a consequence of blocking of the outlet channels with sediments and water flux received into the lake from the ricefields.

The periods of maximum populations for *N. palea* var. *tenuirostris* and *N. palea* var. *debilis* in general did not overlap (Figs 2–3). The three *N. palea* forms appear to differ in nutrient requirements. *N. palea* var. *tenuirostris* had its peaks during the highest nutrient levels and the lowest temperature, while *N. palea* var. *debilis* occurred at the lowest nutrient concentrations (Table 3). The inverse relationship of *N. palea* and *N. palea* var. *tenuirostris* with underwater light climate (Table 2) was probably due to the increase in water turbidity during the periods of water renovation. *N. palea* mainly occurred in summer, tolerating slightly higher temperatures and intermediate nutrient levels than the aforementioned *Nitzschia* (Table 3). In contrast to the other diatoms, *Nitzschia gracilis* had an autumn-winter distribution (Figs 2–3). It grew at temperatures below 15 °C, with an average nitrogen concentration 2–4 times higher than the above cited *Nitzschia*. In contrast to *Cyclotella meneghiniana*, no significant relationship between *Nitzschia* species density and silica were found (Table 2). The silicate to phosphate ratio for pennate diatoms in the Albufera (Si:P = 30-280) was much higher than that for *Cyclotella meneghiniana* (Si:P = 3). *C. meneghiniana* was the diatom with the highest nitrogen and phosphate levels, but the lowest silicate concentrations during its growth in the lake (Table 3).

Cryptomonas erosa and *Rhodomonas lacustris* var. *nannoplanctica* showed similar seasonality, although the maximum populations were not always concordant (Fig. 2). One or two annual increases were recorded, which occurred mainly between October and January. The abundance of both algae were inversely related to underwater light climate (Table 2). Both cryptophytes showed the highest percentage of the algal assemblage on one sampling date at point 3 (up to 9% of the algal density).

The *Monoraphidium contortum* growth period, as well as those of the other three more abundant and frequent *Monoraphidium* in the Albufera (*M. minutum*, *M. arcuatum* and *M. griffithii*), were attained during autumn and winter months (Fig. 2), under low temperatures (6–15 °C) and irradiance (Tables 2–3) and moderate to high turbulence, which allowed these species suspension in the water column.

The green-algae *Scenedesmus acuminatus* and *Sc. quadricauda* had similar annual and seasonal patterns, appearing mainly in spring and autumn (Fig. 2). *Sc. acuminatus* achieved its highest contribution to algal biomass and density in April 1985 (31% and 11% respectively). The maximum populations of these algae occurred under a wide range of nutrient levels, but better developed under low N:P ratios (Tables 2–3). In comparison, *Chlamydomonas* spp. prolonged its growth period from spring to early summer. Similarly as flagellate cryptophytes, *Chlamydomonas* spp. developed during periods of water stability and were inversely related to underwater light intensity (Table 2).

The general seasonal pattern for the abundance of the phytoplankton species of the Albufera of Valencia can be summarized as follows (Fig. 3): vernal phytoplankton was dominated by *Planktothrix agardhii* (Romo & Miracle, 1993) but in early spring, during the period of high water renewal and nutrient loading (especially phosphate), the centric diatom *Cyclotella meneghiniana* also represented important percentages (46–15% of the total phytoplankton abundance). At the onset of water stabilisation after the closing of the sluices, the periodicity of subdominant species shifted to *Scenedesmus* and *Chlamydomonas* spp. Their populations were lower than those of *Cyclotella meneghiniana*, represented each up 11% of the total abundance. In summer and early autumn, phytoplankton was dominated by the slender filamentous cyanophyte *Geitlerinema* sp. At this time, the prolonged water retention and nutrient depletion, led to a greater presence of blue-green algae and in some periods of changes in the water level also of *Nitzschia* species. These latter also developed in September–October, during the drainage of ricefields. Water stability of mid-summer selected in favour of coccal blue-green algal species, and in periods of steep nitrogen depletion of N_2-fixing species, such as *Anabaenopsis elenkinii*. In 1987, when phosphate levels were severely reduced in late summer but nitrate concentrations were high, *Planktolyngbya* taxa became dominant in the lake (80–90% of total abundance). Finally, in late autumn periodicity progressed towards the dominance of *Pseudanabaena galeata*, and in winter also of *Planktothrix agardhii*. The subdominant species at these seasons were *Monoraphidium contortum*, *Nitzschia gracilis*, *Cryptomonas erosa* and *Rhodomonas lacustris* var. *nannoplanctica*. The populations of each of these species represented up 10% of the total algal density. Their density was mainly related to temperature and irradiance.

Discussion

Similarly as has been reported in other hypertrophic and eutrophic lakes (Sommer, 1989; Horne & Commins, 1989), horizontal differences in the populations dynamics of the phytoplankton species of the Albufera of Valencia were less pronounced than annual and seasonal changes.

The factors regulating the recession pattern of *Anabaenopsis elenkinii*, *Scenedesmus acuminatus*, *Scenedesmus quadricauda* and *Cyclotella meneghiniana*, and the increase of *Planktolyngbya* species, *Cylindrospermopsis raciborskii*, *Microcystis incerta*, *Nitzschia palea* var. *tenuirostris* and *Rhodomonas lacustris* var. *nannoplanctica* from 1980 to 1988, could be related to the progressive rise of nitrogen and phosphorus loading in the lake and the hydrological events occurred in 1987 and 1988. The higher presence of *Planktolyngbya subtilis*, *Pl. contorta* and *Cylindrospermopsis raciborskii* in the lake during the latter years coincided with a rise of the N:P ratio followed by quiescence of the water, which agrees with the conditions described for the development of these species (Harris, 1986; Tóth & Padisák, 1986). Similarly to that reported by Gross & Pfiester (1988), *Planktolyngbya subtilis* and *Pl. contorta* co-occurring in the Albufera under alike environmental conditions. Despite the fact that *Cylindrospermopsis raciborskii* is generally considered a tropical species (Horecká & Komárek, 1979), it has been cited as a planktonic algae in the summer and autumn phytoplankton of some lakes and reservoirs of Czechoslovakia and Greece (Hindák, 1988; Hindák & Moustaka, 1988), together with an algal assemblage composed of similar filamentous species to those of the Albufera. Moreover, Tóth & Padisák (1986) also observed in a shallow eutrophic lake, the development of *Cylindrospermopsis raciborskii* after the increase of *Planktolyngbya subtilis*.

The seasonal variation found between *Anabaenopsis elenkinii* and the *Microcystis* species confirms Reynolds's (1984) observations that the N_2-fixing species, such as *A. elenkinii*, prevailed under higher water stability but lower phosphate concentrations than *Microcystis* species. This pattern could be also related to the opposite annual trends observed between *A. elenkinii* and *Microcystis incerta*. The development of colonial coccal blue-green algae at the sampling point 2 and during periods of low water renewal, agree with the buoyancy advantage of these taxa against sedimentation (Reynolds, 1984) and the influence on their populations of losses during periods of water renovation (Paerl *et al.*, 1983).

The annual trend to decrease of *Senedesmus* from 1983 onwards seems unexplained by the arguments of a reduction in the underwater light climate (Loogman *et al.*, 1980; Van Liere & Mur, 1980) and CO_2 availability (Shapiro, 1989), since no differences between irradiance and pH values were found between the two periods. The similar periodicity of *Sc. acuminatus* and *Sc. quadricauda* agrees with the homogeneous physiological features described in this genus (Kessler, 1982). It seems unlikely that nutrients have limited the growth of these chlorophytes, due to they are able to consume organic substances (Soeder & Hegewald, 1988). The optimun growth temperature of *Sc. quadricauda* below 30 °C (Moss, 1973), and the high sedimentation rates of these taxa (Reynolds, 1984) could be against the presence of them in summer, during prolonged water stability and high temperatures. A changing environment seems also to favour their development (Padisák & Tóth, 1991).

It is interesting to note that the composition of diatoms in the Albufera was different to that usually described in other shallow hypertrophic lakes of Europe (Gibson *et al.*, 1971; Moed & Hoogveld, 1982; Klapwijk, 1987). In these lakes, centric diatoms, such as *Melosira* or *Stephanodiscus* are the most representative taxa, whereas the *Nitzschia* species are scarcely present. The diatom flora of the surrounding ecosystems could account for this discrepancy, since most of the identified Diatom species in the Albufera have also been reported, sometimes with high density, at the surrounding ricefields and drainage ditches (Soria *et al.*, 1991). The seasonal pattern of *Cyclotella meneghiniana* and the *Nitzschia* taxa in the lake seems mainly influenced by silicate and phosphate levels and turbulence. *Cyclotella meneghiniana* appeared under much higher phosphate but lower silica levels than *Nitzschia* species, which agree with the studies on competition between these taxa (Tilman, 1982; Grover, 1989). However, the causes of the annual decreasing trend of *Cyclotella meneghiniana* remains unknown and perhaps is related to the increasing dominance of blue-green algae in the lake (allelopathy: Irwin, 1978; competition: Tilman *et al.*, 1986). For the three *Nitzschia palea* forms the hypothesis of Smith & Kalff (1986) was confirmed, the average Si:P ratio being inversely proportional to their cell size.

The inverse relationship found in the lake between *Cryptomonas erosa* and irradiance is in accordance with the experimental observations of Morgan & Kalff (1979). The nutrient conditions observed for this species and *Rhodomonas lacustris* var. *nannoplanctica* were different to that described in other lakes (Sommer, 1982; May, 1987; Rojo, 1990), adding more controversy to the understanding of the abiotic requirements of these algae (Lund, 1962).

For the winter species, *Monoraphidium contortum* and *Nitzschia gracilis*, the main factors regulating their density were temperature and irradiance, which agree with the variables claimed to be the most important for their growth (Partzsch, 1987; Alvarez-Cobelas, 1991).

Although zooplankton grazing on the populations of *Monoraphidium contortum*, *Scenedesmus acuminatus*, *Scenedesmus quadricauda*, *Cryptomonas erosa* and *Rhodomonas lacustris* var. *nannoplanktica* was not regarded in this study, the zooplankton composition of the lake (Alfonso & Miracle, 1988; Oltra & Miracle, 1991) could have also influenced these species dynamics (Lund, 1962; May, 1987; Sommer, 1989).

Despite the fact that the phytoplankton assemblage of the Albufera of Valencia is characteristic of a very shallow hypertrophic lake (*sensu* Reynolds, 1984), the general seasonal variation observed for the abundant non-dominant species remains similar to that described in other temperate lakes (Hutchinson, 1967; Sommer *et al.*, 1986).

Acknowledgements

The authors wish to thank to Ros Jagoe for kindly correcting the English manuscript; Caridad Herraiz for typing the references; J. M. Soria for providing unpublished limnological data; Dr E. Barba and Dr J. Padisák for their valuable comments on the manuscript and the City Council of Valencia for the sampling facilities. This research was performed under a grant held by Susana Romo from the Spanish Ministry of Education and Science.

References

Alboal. M., 1988. Aportación al conocimiento de las algas epicontinentales del sudeste de España. III: Cianofíceas

(Cyanophyceae Schaffner 1909). Anal. Jard. Bot. Madrid 45: 3–46.

Alfonso, M. T. & M. R. Miracle, 1990. Distribución espacial de las comunidades zooplanctónicas de la Albufera de Valencia. Scientia gerundensis, 16: 11–25.

Alvarez-Cobelas, M. & C. Rojo, 1990. Population dynamics of *Nitzschia gracilis* (Bacillariaceae) in a hypertrophic lake. Br. phycol. J. 25: 263–273.

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

Berger, C. & H. E. Sweers, 1988. The IJsselmeer and its phytoplankton with special attention to the suitability of the lake as a habitat for *Oscillatoria agardhii* Gom. J. Plankton Res. 10: 579–599.

Berger, C., 1984. Consistent blooming of *Oscillatoria agardhii* Gom. in shallow hypertrophic lakes. Verh. int. Ver. Limnol. 22: 910–916.

Fott, J., 1975. Seasonal succession of phytoplankton in the fish pond Smyslow near Blatná, Czechoslovakia. Arch. Hydrobiol. Suppl. 46: 249–279.

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

Gibson, C. E., R. B. Wood, E. L. Dickson & D. H. Jewson, 1971. The succession of phytoplankton in L. Neagh, 1968–1970. Mitt. int. Ver. Limnol. 19: 146–160.

Gross, J. L. & L. A. Pfiester, 1988. Blue-green algae of lake Thunderbird. Proc. Okla. Acad. Sci. 68: 39–44.

Grover, J. P., 1989. Effects of Si:P supply ratio, supply variability, and selective grazing in the plankton: An experiment with a natural algal and protistan assemblage. Limnol. Oceanogr. 34: 349–367.

Harris, G. P., 1986. Phytoplankton ecology. Cambridge University Press. Cambridge, 384 pp.

Hindák, F. & M. T. Moustaka, 1988. Planktic cyanophytes of lake Volvi, Greece. Arch. Hydrobiol. Suppl. 80 (50–53): 497–528.

Hindák, F., 1988. Planktic species of two related genera *Cylindrospermopsis* and *Anabaenopsis* from Western Slovakia. Arch. Hydrobiol. Suppl. 80 (50–53): 283–302.

Horecká, M. & J. Komárek, 1979. Taxonomic position of three planktonic blue-green algae from the genera *Aphanizomenon* and *Cylindrospermopsis*. Preslia, Praha 51: 289–312.

Horne, A. J. & M. L. Commins, 1989. Phytoplanktonic monotony: I. Low spatial heterogeneity for nitrogen fixation, algae, nutrients, and temperature, but not for zooplankton, in Lake Rotongaio, New Zealand. Arch. Hydrobiol. Beih. Ergebn. Limnol. 32: 83–97.

Hutchinson, G. E., 1967. A Treatise on Limnology, 2. J. Wiley & Sons, New York.

Irwin, K., 1978. Blue-green algae inhibition of Diatom growth: Transition from mesotrophic to eutrophic community structure. Science 199: 971–973.

Javornicky, P., 1976. Minute species of the genus *Rhodomonas* Karsten (Cryptophyceae). Arch. Protistenk. 118: 98–106.

Kessler, E., 1982. Chemotaxonomy in the Chlorococcales. Progress Phycol. 1: 111–135.

Kiss, K. T. & J. Padisák, 1990. Species succession of Thalassiosiraceae: Quantitative studies in a large shallow lake (Lake Balaton, Hungary). In H. Simola (ed.), Proceedings of the 10th International Symposium on Living and Fossil Diatoms, Koeltz Scientific Books, Koening: 481–490

Klapwijk, S. P., 1988. Eutrophication of surface waters in the dutch polder landscape. PhD Thesis. Universidad of Delft, The Netherlands, 227 pp.

Komárek, J., 1975. Blaualgen aus dem Naturschutzgebiet Rezabinec bei Razice. Nova Hedw. 26: 601–643.

Koppe, F., 1924. Die Schlammflora der ostholsteinischen Seen und des Bodensees. Arch. Hydrobiol. 14: 619–672.

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

Loogman, J. G., A. F. Post & L. R. Mur, 1980. The influence of periodicity in light conditions, as determined by the trophic state of the water, on the growth of the green alga *Scenedesmus protuberans* and the cyanobacterium *Oscillatoria agardhii.* In J. Barica & L. R. Mur (eds), Hypertrophic Ecosystems. Developments in Hydrobiology 2. Dr W. Junk Publishers, The Hague: 79–82.

Lund, J. W. G., 1962. A rarely recorded but very common British alga, *Rhodomonas minuta* SKUJA. Br. Phycol. Bull. 2: 133–139.

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

May, L., 1987. Culturing freshwater, planktonic Rotifers on *Rhodomonas minuta* var. *nannoplanktica* SKUJA and *Stichococcus bacillaris* NÄGELI. J. Plankton Res. 9: 1217–1223.

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

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

Morgan, K. & J. Kalff, 1979. Effect of light and temperature interactions on growth of *Cryptomonas erosa* (Cryptophyceae). J. Phycol. 15: 127–134.

Moss, B., 1973. The influence of environmental factors on the distribution of freshwater algae: an experimental study. III. Effects of temperature, vitamin requirements and inorganic nitrogen compounds on growth. J. Ecol. 61: 179–192.

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

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

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

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

Padisák, J. & L. G. Tóth, 1991. Some aspects of ecology of subdominant green algae in a large, nutrient limited shallow lake (Balaton, Hungary). Arch. Protistenk. 139: 225–242.

Paerl, H. W., J. Tucker & P. T. Bland, 1983. Carotenoid enhancement and its role in maintaining blue-green algal (*Microcystis aeruginosa*) surface blooms. Limnol. Oceanogr. 28: 847–857.

Partzsch, M., 1987. Growth and development of *Scenedesmus acutus* Chodat, *Kirchneriella lunaris* (Kirchn.) Moeb. and *Monoraphidium contortum* (Thur.) Kom.-Leng. in dependence on light and temperature. Arch. Hydrobiol. Algological Studies 46: 89–98.

Quesada, A., 1990. Estudio de las poblaciones naturales de Cianobacterias presentes en los arrozales valencianos. PhD Thesis. University Autonoma of Madrid, Spain, 344 pp.

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

Rojo, C., 1990. Estructura de la comunidad fitoplanctonica de la laguna hipertrofica '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, 303 pp.

Romo, S. & R. M. Miracle, 1993. Long–term periodicity of *Planktothrix agardhii*, *Pseudanabaena galeata* and *Geitlerinema* sp. in a shallow hypertrophic lagoon, the Albufera of Valencia, Spain. Arch. Hydrobiol., 126: 469–486.

Romo, S., M. Hernández-Mariné & M. R. Miracle, 1993. *Geitlerinema amphibium* (Ag. ex Gom.) Anagn. (Cyanophyceae): morphology, ultrastructure and ecology. Arch. Hydrobiol. Algological Studies, 69.

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

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

Shapiro, J., 1989. Currents beliefs regarding dominance by blue-greens: The case for the importance of CO_2 and pH. Verh. int. Ver. Limnol. 1: 38–54.

Shoeman, F. R. & R. E. M. Archibald, 1980. The diatom flora of Southern Africa. Núm. 6. National Institute for Water Research. CSIR Special Report Wat 50. Pretoria.

Smith, R. E. & J. Kalff, 1983. Competition for phosphorus among co-occurring freshwater phytoplankton. Limnol. Oceanogr. 28: 448–464.

Soeder, C. J. & E. Hegewald, 1988. *Scenedesmus*. In M. A. Borowitzka & L. J. Borowitzka (eds), Microalgal Biotechnology, Cambridge University Press: 59–84.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry. 2nd edn. Freeman, New York, 832 pp.

Sommer, U., 1982. Vertical niche separation between two closely related planktonic flagellate species (*Rhodomonas lens* and *Rhodomonas minuta* v. *nannoplanctica*). J. Plankton Res. 4: 137–142.

Sommer, U., 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnol. Oceanogr. 34: 1162–1173.

Sommer, U., Z. M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in freshwaters. Arch. Hydrobiol. 106: 433–471.

Soria, J. M., Colom, W., S. Romo & M. Ros, 1991. Aportación al estudio del fitoplancton del Parque Natural de la Albufera de Valencia: Diatomeas. Vl Congreso Español de Limnología, Abstract book: 67 pp.

Soria, J. M., M. R. Miracle & E. Vicente, 1987. Aporte de nutrientes y eutrofización de la Albufera de Valencia. Limnetica 3: 227–242.

Tilman, D., 1982. Resource competition and community structure. Princeton Univ. Press. Princeton, 296 pp.

Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham & F. Johnson, 1986. Green, blue-green and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. 106: 473–485.

Tóth, L. G. & J. Padisák, 1986. Meteorological factors affecting the bloom of *Anabaenopsis raciborskii* Wolosz. (Cyanophyta: Hormogonales) in the shallow lake Balaton, Hungary. J. Plankton Res. 8: 353–363.

Trimbee, A. M. & G. P. Harris, 1983. Use of timeseries analysis to demostrate advection rates of different variables in a small lake. J. Plankton Res. 5: 819–833.

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

Van Liere, L. & L. R. Mur, 1980. Occurrence of *Oscillatoria agardhii* and some related species, a survey. In: J. Barica & L. R. Mur (eds), Hypertrophic Ecosystems. Developments in Hydrobiology 2. Dr W. Junk Publishers, The Hague: 67–77.

Zevenboom, W. & L. R. Mur, 1980. N_2-fixing cyanobacteria: Why they do not become dominant in Dutch hypertrophic ecosystems? In J. Barica & L. R. Mur (eds), Hypertrophic Ecosystems, Developments in Hydrobiology 2. Dr W. Junk Publishers, The Hague: 123–130.