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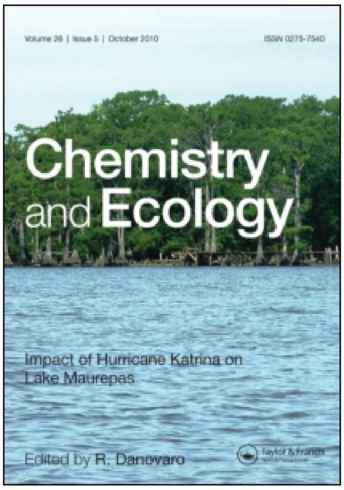

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Nutrient loading and spatial-temporal dynamics of phytoplankton guilds in a Southern Italian Coastal Lagoon (Lake Alimini Grande, Otranto, Italy)

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NUTRIENT LOADING AND SPATIAL–TEMPORAL DYNAMICS OF PHYTOPLANKTON GUILDS IN A SOUTHERN ITALIAN COASTAL LAGOON (LAKE ALIMINI GRANDE, OTRANTO, ITALY)

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The importance of external and internal P-loading to the structural organization and dynamics of phytoplankton guilds in a Southern Italy coastal lagoon (Lake Alimini Grande) was investigated. To this end, phosphorus external loading through localized freshwater inputs was measured, P-release through detritus decomposition on sediments was evaluated, and phytoplankton abundance, biomass and taxonomic composition were quantified at 33 sites and 12 sampling times from September 1998 to September 1999. P-loading in the area was greater in the winter (26.5 μM P m^{-2} d^{-1}) than in the summer (18.4 μM P m^{-2} d^{-1}). In the winter, external inputs were 61.7% of the total, while in summer, internal inputs accounted for 99.8% of the total. Phytoplankton biomass was related to P inputs. In particular, the spatial distribution of phytoplankton biomass was related to external inputs in winter–spring, and to internal inputs in summer–autumn. A total of 228 phytoplankton taxa were identified of which 13 taxa accounted for more than 80% of phytoplankton abundance. The spatial and temporal dynamics of 13 taxa were related to P-availability and habitat heterogeneity.

Keywords: P-loading; Phytoplankton biomass; Taxonomic composition; Temporal dynamics; Niche space

1 INTRODUCTION

Nutrient availability, particularly P-load, is recognized as the main limiting factor for phytoplankton growth in shallow coastal lagoons in the Mediterranean area (Lewis, 1978; Parson *et al.*, 1984; Vadrucci *et al.*, 1995; Escaravage *et al.*, 1996; Lampert and Sommer, 1997; Kormas *et al.*, 2001; Perez-Ruzafa *et al.*, 2002).

In coastal lagoons, phosphorus dynamics are affected by the supply of phosphorus from external and internal sources and by biotic and abiotic processes of P-uptake and release in the water column and sediments.

Sources of external phosphorus loading include: continental freshwater inflows deriving from rivers or drainage canals, groundwater, sewage (Nixon *et al.*, 1996; Swaney, 1998; Viaroli *et al.*, 2001) and atmospheric inputs (including wet and dry deposition; Harper, 1992). Moreover, terrestrial ecosystems can provide additional inputs directly related to structural characteristics and land use in the catchment area (Sorokin *et al.*, 1996). Marine

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ecosystems are more likely to receive phosphorus from lagoon ecosystems than provide it, although Kitheka and Mwashote (2001) report evidence to the contrary.

As far as internal inputs are concerned, phosphorus is typically released from the sediment to the overlying water column through organic-matter decomposition and geochemical processes. Oxygen saturation of the water mass and surface sediments (Gomez *et al.*, 1998), sediment organic content (Valiela, 1995; Gomez *et al.*, 1998), water temperature, hydrodynamism, depth of the mixing layer (Valiela, 1995; Lampert and Sommer, 1997) and the rate of decomposition processes on the sediments (Carpenter and Adams, 1979) are known to be amongst the major factors affecting internal phosphorus input. However, P-internal loading has almost always been estimated in delimited areas of lakes or lagoons by measuring instantaneous rates of P-release in controlled conditions inside benthic chambers (landers; Mac Manus *et al.*, 1997; Frascari *et al.* 2002) while few attempts have been made to assess P-loading from internal inputs taking into account the role of sediment detritus dynamics in a coastal lagoon or lake considered as a whole (Granéli, 1999).

The influence of internal and external P-loading on phytoplankton dynamics and taxonomic composition has been widely documented in many marine (Howarth, 1988) and freshwater ecosystems (Reynolds, 1999), even though the supply of algae from both external systems and sediments may also influence phytoplankton dynamics independently of the nutrient input (Reynolds, 1984; Carrick *et al.*, 1993).

Relationships between external inputs and phytoplankton dynamics have been observed in coastal lagoons (Cabrini *et al.*, 1995; Velikova *et al.*, 1999), coastal marine areas (Mingazzini *et al.*, 1992) and freshwater lakes (Harper, 1992). Relationships between benthic fluxes and phytoplankton dynamics have also been observed in freshwater lakes (Carrick *et al.*, 1993; Nalewajko and Murphy, 1998) and in coastal marine lagoons (Frascari *et al.*, 2002). Nevertheless, few studies have compared the relative importance of internal and external loadings (Harper, 1992), and very little is known about the relative importance of internal and external inputs to phytoplankton dynamics in Mediterranean coastal lagoons.

This paper focuses on the relationship between P-loading and the spatial–temporal dynamics of phytoplankton guilds in a Mediterranean coastal lagoon. In particular, the aims of this investigation were:

(1) to analyse the patterns of temporal and spatial variation of phosphorus inputs coming from freshwater continental inflows;
(2) to analyse the patterns of temporal and spatial variation of internal inputs of phosphorus (released from organic-matter decomposition on the sediments);
(3) to evaluate the contribution of external and internal P-sources to the total phosphorus loading and its influence on patterns of temporal and spatial distribution of phytoplankton abundance and taxonomic composition.

This study was carried out in a coastal lagoon in southern Italy (Lake Alimini Grande, Otranto, Italy), where previous studies had demonstrated the limiting role of phosphorus on phytoplankton dynamics (Basset *et al.*, 2001; Vadrucci *et al.*, 2001). In particular, this investigation was based on data regarding salinity, nutrient concentrations, phytoplankton biomass, taxonomic composition, P-loading from freshwater discharge, organic matter in the sediments and the rate of reed decomposition processes (Basset, 2000). These data belong to a larger data set of structural and functional features of the water column and sediments collected as part of the ‘Master Plan Project on Lake Alimini Grande’ (Basset, 2000).

2 MATERIALS AND METHODS

2.1 Study Area

Lake Alimini Grande is a salt-marsh ecosystem on the Adriatic coast of Southern Italy (40.19–40.22 °N, 18.44–18.46 °E; Fig. 1) connected to the sea by a channel (length: 100 m, width: 15 m). It is also connected to a freshwater lake, Alimini Piccolo, through a natural channel 1.5 km long, called the *Strittu*. Lake Alimini Grande has a surface area of 1.37 km^2, a sinuosity index of 2.29, an average depth of 1.5 m and a volume of 2.1×10^6 m^3. It has an irregular shape (roughly 2.86 km by 1.54 km) and is affected by the dominant winds of the area along its major axis. The lake receives freshwater inputs from Lake Alimini Piccolo in the south, from the *Zuddeo* Channel in the north-west and from the *Traugnano* Swamp in the north (Fig. 1).

The temperature ranges from 8.9 to 28.2 °C, salinity ranges from 19.1 to 34.6 PSU, and dissolved oxygen ranges from 4.9 to 11.2 ml l^{-1}. The average TDN and TDP concentrations in the water column are 105.14 ± 52.91 and 1.66 ± 1.40 μM, respectively. Freshwater inputs vary seasonally because of the Apulian climate, which is very hot and dry during summer. Generally, freshwater inflow is higher in autumn–winter (7.01×10^3 m^3 d^{-1}) than in summer (3.71×10^3 m^3 d^{-1}; Vadrucci *et al.*, 2001). Lake sediments have a high organic matter content (on average 13%). The rate of plant detritus decomposition processes is intermediate (on average, $k = 0.0083$ d^{-1}), although values are higher in summer than in other seasons (Basset, 2000).

2.2 Sampling Sites and Periods

Samples for determining salinity, phytoplankton biomass, taxonomic composition, organic-matter content in the sediment and the rate of reed decomposition processes were collected in a grid of 33 sampling stations from September 1998 to September 1999. Sampling was carried out on a monthly basis for salinity, phosphorus concentration (as total dissolved phosphorus (TDP) and as dissolved inorganic phosphorus (DIP)), phytoplankton biomass and taxonomic composition, and seasonally for organic matter content in the sediments and the rate of decomposition processes. In order to quantify P-external loading (as TDP),

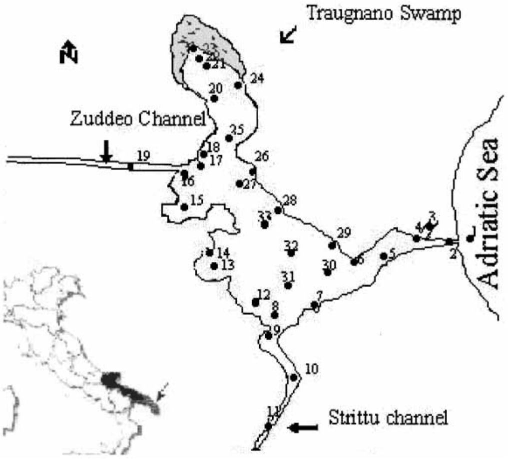

FIGURE 1 Map of Lake Alimini Grande showing the position of sampling stations and the localization of the mouth and of the main freshwater inputs.

freshwater discharge was measured, and freshwater samples were collected each month in *Strittu*, *Zuddeo* and a channel linking the lake to *Traugnano* swamp. Furthermore, to obtain a more accurate assessment of P-loading in the lake, sampling was carried out at daily intervals for a week after each rainy day.

2.3 Field and Laboratory Measurements

Water salinity was measured in the field with a conductivity hand-held meter (WTW mod. LF-340; accuracy, 1 PSU) and in the laboratory with a laboratory salinometer (Guildline Autosal mod. 8400B, accuracy, 0.002 PSU) on water samples collected with a 5-1 Niskin bottle, using standard sea water (NIO) with a salinity close to the salinity of the lake (30 PSU) as the standard solution for calibration.

The analysis of TDP and DIP of water samples collected in the lake and in freshwater channels was carried out on 50 ml of filtered water using GF/F Whatman filters (porosity ≈0.5 μm), according to the standard spectrophotometric method (Murphy and Riley, 1962). For TDP determination, oxidation of the organic fraction was performed with a solution of persulfate (Basset, 2000). P-external loading was calculated for each channel as the product of the P concentrations in the freshwater and the freshwater discharge. The overall P-external loading was determined as the sum of the P-loading from the three channels.

Organic matter in the superficial layer of sediments was quantified using the gravimetric method. Samples of the upper sediment layer were collected at each site. The percentage of organic matter (percentage ash-free dry mass) was determined after burning in a muffle furnace at 500°C for 6 h to prevent the loss of carbonate (Rosa *et al.*, 1994).

The rate of decomposition processes was analysed using the leaf-pack technique, that is, by measuring the mass loss of dead leaves of *Phragmites australis* (Cav) Trin. ex Steud from litterbags in accordance with the procedure reported in Basset (2000).

The leaf-pack technique provides an estimate only of the rate of decomposition process of plant detritus and not of the rate of decomposition processes of all the organic matter in the sediments. However, additional laboratory experiments (Sangiorgio, pers. commun.), carried out on sediments collected in just two of the 33 stations (30 and 22; Fig. 1) in Lake Alimini Grande and incubated at different temperatures and under different oxygenation and nutrient conditions (included in a range of values observed in the lake), revealed similar trends for sediment organic matter and plant detritus decomposition processes, though the former had rates about one order of magnitude lower than the latter. Here, we use the rate of decomposition process of plant detritus determined at 33 sampling stations in the lake because the laboratory measurements of decomposition processes in the sediments do not provide information about the spatial variation of sediment decomposition. However, in order to take into account the difference between the decomposition of sediment detritus (as measured in the laboratory) and that of plant detritus (as measured using the leaf-packs), the data concerning the decomposition rates of plant detritus have been corrected with a correction factor (C). In this paper, C was taken to be constant at 0.1, in accordance with the comparison between laboratory and field data.

Phytoplankton biomass was estimated as chlorophyll *a* (chl*a*) using a spectrofluorimetric method with the following procedure. Lake water (500 ml) was filtered immediately after collection, using glass microfibre filters (Whatman GF/F) which were frozen at −20 °C until analysis. Chl*a* was extracted in 90% acetone for 24 h at 4 °C in the dark, and measured with a Shimatzu-1051 spectrofluorimeter before and after acidification with 0.5 N hydrochloric acid. Excitation and emission wavelengths (429 and 669 nm) were selected after standardization with a solution of chl*a* extracted from *Anacistys nidulans* (Sigma 6).

To estimate phytoplankton numerical abundance and taxonomic composition, 500-ml samples of lake water were immediately fixed after collection with Lugol's solution (15 ml per litre of sample).

Phytoplankton counts were performed using a Nikon inverted microscope (×400), after sedimentation in 5-, 10- and 25-ml counting chambers, in accordance with the Uthermöhl method and the statistical approach for counting proposed by Lund *et al.* (1958). The nomenclature of the phytoplankton was updated according to Streble and Krauter (1984) and Tomas (1997).

2.4 Estimation of Contribution from External P-Loading

The contribution of external P-loading was quantified each month at 33 sampling sites (Fig. 1) as a function of the external P-loading resulting from freshwater discharge and the freshwater content at each sampling site for each sampling time; the latter was estimated as the ratio between the salinity of the sampling site and the average salinity of the sea in the nearshore marine area (Vadrucci *et al.*, 2001).

Finally, the relative contribution of external P-loading was estimated as μM P m^{-2} d^{-1} in all 33 sampling sites for each month according to the following formula:

$$\text{External P-loading} = [(\text{input of } P_{\text{tot}} \times 1/\text{Lake Area})] \times [1 - (S_{\text{sta}}/S_{\text{sea}})],$$

where: input of P_{Tot} = input of total phosphorus deriving from freshwater input (μM d^{-1}); S_{sta} = salinity of the sampling station; S_{sea} = salinity of the seawater in the nearshore marine area

2.5 Estimation of Contribution from Internal P-Loading

The release of phosphorus from sediments (internal input) was estimated from:

- the data reported in the literature on phosphorus content in plant organic matter (Ricklefs, 1997), which were compared with the analysis of total P content in the lake sediments (Basset, 2000);
- the data on the organic matter content of the top sediment layer (with a thickness of 5 cm);
- the data concerning decomposition rates of organic matter in Lake Alimini Grande.

Finally, the contribution of internal P-loading was estimated as μM P m^{-2} d^{-1}, in all 33 sites for each season, according to the following formula:

$$\text{Internal P-loading} = (W_5 \times P_{\text{OMS}}/P_{\text{sed}} \times TP_{\text{OMS}}) \times [(100 - e^{-kct} \times 100)]/365,$$

where: W_5 = weight of the top 5 cm of sediment (mg m^{-2}); $P_{\text{OMS}}/P_{\text{sed}}$ = contribution of organic matter in the sediment; TP_{OMS} = total phosphorus in the organic matter (μmol mg^{-1}, $100 - (e^{-kt} \times 100))/365$ = daily percentage loss in weight of organic biomass in the sediment; k = decomposition coefficient of plant detritus (d^{-1}); C = correction factor.

2.6 Data Treatment

Total P-loading was calculated as the sum of external and internal inputs, assuming a constant internal input for each season. The inputs were thus analysed on a monthly timescale. A two-way ANOVA was used to estimate the statistical power of variation of internal and external P-loading among sampling times and stations and phosphorus concentration in the lake.

The taxa identified at species or genus level were pooled into four groups: dominant, frequent, abundant and rare. The dominant taxa group included the most frequent species that together comprised 75% of total phytoplankton cell density in each station and that were observed in the same station on at least 25% of the sampling dates. The frequent taxa group included taxa that were observed in the same station on at least 25% of the sampling dates. The abundant taxa group included taxa that together comprised 75% of total phytoplankton cell density in each station. The remaining taxa were included in the rare taxa group. Regression analysis was used to evaluate the statistical power of: the relationship between phytoplankton biomass and total P-loading; the monthly and seasonal spatial relationships between biomass and P-loading deriving from external and internal input; and the spatial–temporal distribution of dominant taxa in relation to P-loading and salinity gradients.

3 RESULTS

3.1 Patterns of Temporal and Spatial Variation in Phosphorus Concentration and P-Loading

The phosphorus concentration in the lake averaged $1.66 \pm 1.40\ \mu$M for TDP and $0.06 \pm 0.11\ \mu$M for DIP. TDP concentration varied significantly from month to month but not among sampling stations (two-way ANOVA: among months $F_{11,383} = 47.18$, $P < 0.001$, among sites $F_{31,383} = 0.90$, n.s.). TDP concentrations were higher in autumn–winter than in spring-summer. The maximum value of 7.598 μM was observed in January, while the minimum value, 0.086 μM, was observed in May. DIP concentrations ranged from 0.005 to 0.788 μM and did not show any evident patterns of spatial or temporal variation.

Phosphorus loading to the lake was on average 8.99×10^3 mol P yr^{-1}. P-loading was higher in winter ($26.5 \pm 23.16\ \mu\mathrm{M\ P\ m^{-2}\ d^{-1}}$) than in summer ($18.4 \pm 15.75\ \mu\mathrm{M\ P\ m^{-2}\ d^{-1}}$), with the highest contribution of external loading in winter (61.7% of total input) and the highest contribution of internal loading in summer (99.8% of total input). The lowest phosphorus loading was observed in spring ($11.2 \pm 18.08\ \mu\mathrm{M\ P\ m^{-2}\ d^{-1}}$) when both external (55%) and internal loadings (45%) were low and similar.

Patterns of temporal and spatial variation in P-loading deriving from external and internal inputs are shown in Fig. 2A and B. These patterns of variation were analysed on a monthly scale for external input and on a seasonal scale for internal input. Both internal and external input varied significantly among sampling times and sampling sites (two-way ANOVA for external input: among months $F_{11,330} = 23.49$, $P < 0.001$, among sites $F_{31,330} = 8.12$, $P < 0.001$; two-way ANOVA for internal input; among seasons $F_{3,93} = 28.46$, $P < 0.001$, among sites $F_{31,93} = 3.43$, $P < 0.001$). Phosphorus loading derived from external input showed the highest values in winter and lower values in autumn and in spring, and was negligible in summer (Fig. 2A). In contrast, estimated phosphorus loading from internal input was higher in summer than in the other seasons (Fig. 2B).

3.2 Patterns of Phytoplankton Abundance and Their Relationship to P-Loading

The average phytoplankton biomass was 3.62 ± 3.01 mg(chl*a*) m^{-3} and was highest in autumn–winter and late summer. Average chl*a* concentrations peaked in December (7.30 ± 2.97 mg(chl*a*) m^{-3}) and August (6.87 ± 5.48 mg(chl*a*) m^{-3}) and remained low

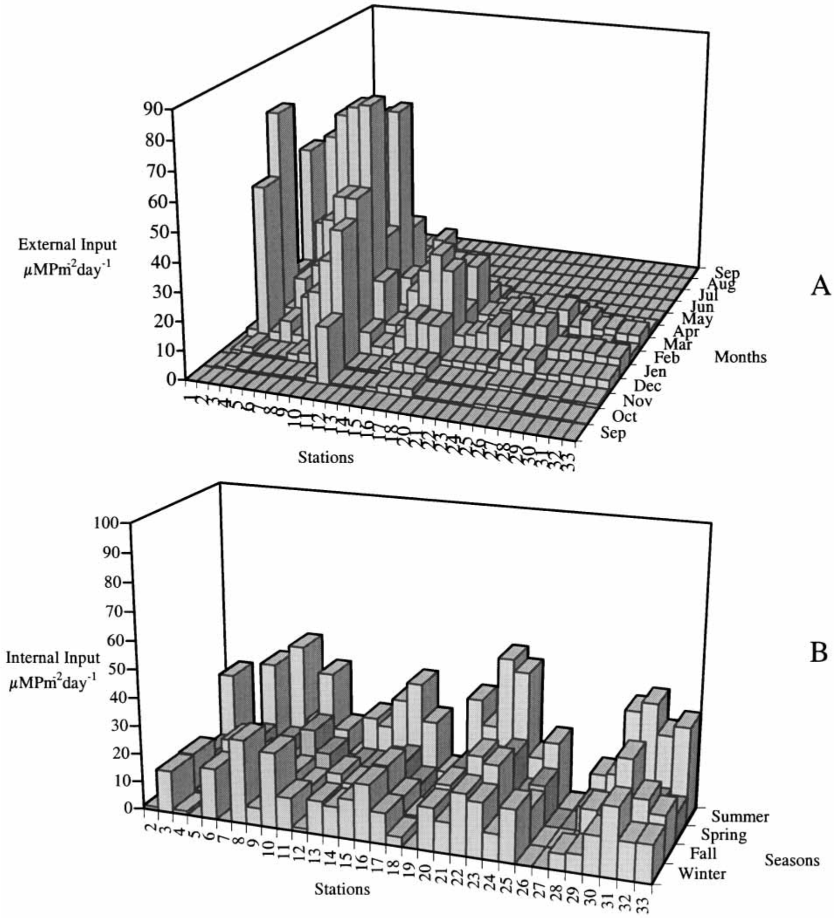

FIGURE 2 Space–time patterns of distribution of P-loading in Lake Alimini Grande derived from external input (A) and from internal input (B).

in spring. The minimum value, observed in April, was 0.699 ± 0.741 mg(chl*a*) m^{-3} (Fig. 3). Phytoplankton biomass showed a significantly larger temporal variation than spatial ($F_{12,31} = 4.28$, $P < 0.05$). The spatial variability was generally low (C.V. 28.9%), indicating an even distribution of phytoplankton biomass in the lake for each sampling period.

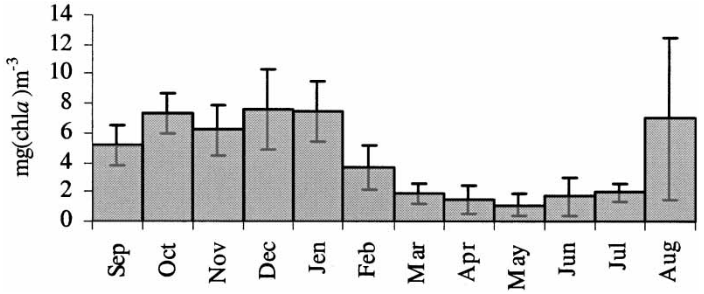

FIGURE 3 Average values of phytoplanktonic biomass during the 12 sampling dates, in the study area. The vertical bars are ±1 S.D.

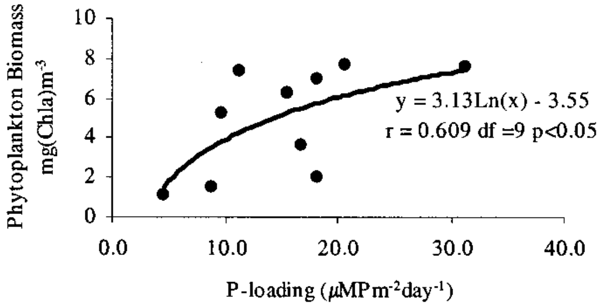

FIGURE 4 Relationship between phytoplanktonic biomass (chl*a*) and total P-loading.

Phytoplankton biomass did not vary with phosphorus concentration (neither TDP nor DIP concentrations appeared to have any relationship to phytoplankton biomass) but was directly related to phosphorus loading (Fig. 4). Moreover, the relationships of phytoplankton biomass spatial distribution to P-external loading on the one hand and to P-internal loading on the other were analysed for each month and for each season, respectively. The spatial distribution of phytoplankton biomass was associated with the distribution of external inputs in winter and spring (four relationships out of six were statistically significant; see Tab. I), and with the distribution of internal inputs in autumn and summer (Tab. II). The relationships were direct in all cases for internal input, whereas for external input, inverse relationships were also observed, though only in the autumn–winter months (Tabs I and II).

TABLE I Monthly average values of P-external loading, relationships with phytoplanktonic biomass (mg(chl*a*)m^{-3}) and regression coefficients (Pearson *r*).

Month	*Year*	*External input ($\mu M\ P\ m^{-2}\ day^{-1}$)*	*Relationship with biomass*	*r*
September	1998	0.0	–	
October	1998	1.6	$\text{chl}a = -0.62\ \ln(P_{\text{tot}}) + 7.28$	0.372^*
November	1998	5.7	$\text{chl}a = -0.45\ \ln(P_{\text{tot}}) + 6.56$	0.230
December	1999	12.1	$\text{chl}a = +0.21\ \ln(P_{\text{tot}}) + 7.22$	0.070
January	1999	22.7	$\text{chl}a = -0.94\ \ln(P_{\text{tot}}) + 7.07$	0.389^*
February	1999	8.1	$\text{chl}a = -0.54\ \ln(P_{\text{tot}}) + 4.53$	0.349^*
March	1999	16.6	$\text{chl}a = +1.63\ e^{0.004(P_{\text{tot}})}$	0.217
April	1999	5.7	$\text{chl}a = +1.07\ e^{0.03(P_{\text{tot}})}$	0.393^*
May	1999	1.5	$\text{chl}a = +0.88\ e^{0.09(P_{\text{tot}})}$	0.397^*
June	1999	0.5	$\text{chl}a = +1.23\ \ln(P_{\text{tot}}) + 1.55$	0.950^*
July	1999	0.1	$\text{chl}a = -0.56\ \ln(P_{\text{tot}}) + 2.05$	0.130^*
August	1999	0.0	–	

$^*P < 0.05$.

TABLE II Seasonal average values of P-internal loading, relationship with phytoplanktonic biomass mg(chl*a*)m^{-3} and regression coefficients (Pearson *r*).

	Year	*Internal input ($\mu MPm^{-2}day^{-1}$)*	*Relationship with biomass*	*r*
Autumn	1998	9.8	$\text{chl}a = +0.091(P_{\text{tot}}) + 4.90$	0.593^*
Winter	1999	8.7	$\text{chl}a = +0.025(P_{\text{tot}}) + 4.98$	0.170
Spring	1999	3.1	$\text{chl}a = +0.0075(P_{\text{tot}}) + 1.40$	0.066
Summer	1999	18.3	$\text{chl}a = +0.42\ln(P_{\text{tot}}) + 2.20$	0.366^*

$^*P < 0.05$.

TABLE III List of phytoplankton taxa identified in lake alimini grande from September 1998 to September 1999.

Centric diatoms
- *Asterolampra marylandica* (Ehr)
- *Bellerochea* sp.
- *Cerataulina pelagica* (Clev) Hend
- *Chaetoceros compressus* (Laud)
- *Chaetoceros constrictus* (Meun)
- *Chaetoceros curvisetus* (Clev)
- *Chaetoceros danicus* (Clev)
- *Chaetoceros decipiens* (Clev)
- *Chaetoceros radicans* (Schütt)
- *Chaetoceros similis* (Clev)
- *Chaetoceros simplex* (Paul)
- *Chaetoceros socialis* (Laud)
- *Chaetoceros* sp.
- *Chaetoceros tenuissimus* (Meun)
- *Chaetoceros teres* (Clev)
- *Chaetoceros wighamii* (Brig)
- *Coscinodiscus excentricus* (Ehr)
- *Coscinodiscus granii* (Ehr)
- *Coscinodiscus radiatus* (Ehr)
- *Coscinodiscus* sp.
- *Cyclotella* sp.
- *Discoaster* sp.
- *Epithemia Sorex* (Kütz)
- *Guinardia delicatula* (Clev)
- *Guinardia striata* (Stolt)
- *Hemiaulus haukii* (Grun) Van Heurck
- *Lauderia annulata* (Clev.)
- *Leptocylindrus danicus* var. *adriaticus* (Clev)
- *Leptocylindrus* sp.
- *Melosira* sp.
- *Paralia sulcata* (Ehr)
- *Proboscia alata* (Bright) Sund
- *Rhizosolenia* sp.
- *Rhizosolenia ostenfeldii* (Sund)
- *Rhizosolenia styliformis* (Bright)
- *Skeletonema costatum* (Grev) Clev
- *Thalassiosira gravida* (Clev)
- *Thalassiosira* spp.

Pennate diatoms
- *Achnantes brevipes* (Agar)
- *Achnantes inflata* (Kutz)
- *Achnantes* sp.
- *Amphiprora alata* (Kutz)
- *Amphora caffeaeformis* (Kutz)
- *Amphora ostearia* (Clev)
- *Amphora ovalis* (Kutz)
- *Amphora marina* (H.V.H.)
- *Amphora* sp.
- *Bacillaria paradoxa* (Grun) Clev
- *Cocconeis pellucida* (Hant)
- *Cocconeis placentula* (Ehr) Clev
- *Cocconeis scutellum* (Ehr)
- *Cocconeis scutellum* f. parva (Ehr)
- *Cocconeis* sp.
- *Cylindrotheca closterium* (Ehr)
- *Cylindrotheca fusiformis* (Rei & Lew)
- *Cymbella* sp.
- *Denotula* sp.
- *Diploneis crabro* (Ehr)
- *Diploneis* sp.
- *Eunotia* sp.
- *Fragilaria crotonensis* (Kitt)
- *Fragilaria virescens* (Ralf)
- *Fragilaria* sp.
- *Fragilariopsis kergulensis* (O'Mea) Hust
- *Gomphonema* sp.
- *Licmophora flabellata* (Carm) Ag
- *Licmophora gracilis* (Ehr) Grun
- *Licmophora* sp.
- *Navicula Beyrichiana* (A, S)
- *Navicula cryptocephala* (Kutz)
- *Navicula cuspidata* (Kutz)
- *Navicula bicapitata* (Lager)
- *Navicula major* (Kutz)
- *Navicula northumbrica* (Donk)
- *Navicula pelagica* (Sys)
- *Navicula granii* (Jorg)
- *Navicula* spp.
- *Navicula transitans* (Grun)
- *Nitzschia angustata* (W.Sm) Grun
- *Nitzschia cuspidata* (Kutz)
- *Nitzschia insignis* (Greg)
- *Nitzschia lanceolata* (Grun)
- *Nitzschia linearis* (Agar)
- *Nitzschia longissima* (Breb) Ralfs
- *Nitzschia sigma* (Wm Sm)
- *Nitzschia* sp.
- *Nitzschia spatulata* (Breb)
- *Nitzschia thermalis* (Kutz) Grun
- *Phaeodactylum tricornutum* (Boh)
- *Pinnularia lata* (Breb) Wm Sm
- *Pinnularia* sp.
- *Pleurosigma angulatum* (Wn Sm)
- *Pleurosigma balticum* (Wn Sm)
- *Pleurosigma* sp.
- *Pseudonitzschia granii* (Halse)
- *Pseudonitzschia prolungatoides* (Halse)
- *Pseudonitzschia seriata* (Halse)
- *Pseudonitzschia* sp.
- *Stauroneis* sp.
- *Synedra* sp.
- *Synedra ulna* (Ehr)
- *Thalassionema nitzschioides* (Grun)
- *Thalassionema* sp.
- *Thalassiothrix curvata* (Cast)
- *Thalassiothrix fauenfeldii* (Grun)
- *Thalassiothrix* sp.
- *Toxarium* sp.
- *Toxarium undulatum* (Bail)
- *Triceratium* sp.

Dinoflagellates thecate
- *Alexandrium* sp.
- *Alexandrium tamarense* (Leb) Bal
- *Ceratium furca* (Ehr)
- *Dinophysis sacculus* (Stein)
- *Dinophysis* sp.
- *Exuviaella marina* (Cien)
- *Gonyaulax spinifera* (Clap & Lach)
- *Gonyaulax* sp.
- *Katodinium rotundatum* (Loh)
- *Oxyrrihs marina* (Duj)
- *Oxytoxum viride* (Sch)
- *Phalaocoma* sp.
- *Porella globulus* (Sch)
- *Porella* sp.
- *Prorocentrum arcuatum* (Iss)
- *Prorocentrum marinum* (Cien) Loe
- *Prorocentrum micans* (Ehr)
- *Prorocentrum minimum* (Pavil) Sch
- *Prorocentrum rotundatum* (Sch)
- *Prorocentrum* sp.
- *Protogonyaulax* sp.
- *Protoperidinium breve* (Paul) Bal
- *Protoperidinium cornutum* (Sch)
- *Protoperidinium divergens* (Ehr) Bal
- *Protoperidinium* sp.
- *Scrippsiella* sp.
- *Scrippsiella trochoidea* (Stein) Loe
- *Dinoflagellates thecate* $>20\,\mu$m
- *Dinoflagellates thecate* $<20\,\mu$m

Dinoflagellates athecate
- *Amphidinium acutissimum* (Sch)
- *Amphidinium curvatum* (Sch)
- *Amphidinium longum* (Lohm)
- *Amphidinium* sp.
- *Gymnodinium* sp.
- *Gymnodinium articum* (Wulff)
- *Gymnodinium biconicum* (Sch)
- *Gymnodinium catenatum* (Grah)
- *Gymnodinium elongatum* (Hope) Sch
- *Gymnodinium lacustre* (Sch)
- *Gymnodinium lohmanni* (Paul)
- *Gymnodinium mirabile* (Pen)
- *Gymnodinium paulseni* (Sch)
- *Gymnodinium punctatum* (Pou)
- *Gymnodinium splendens* (Lebour)
- *Gyrodinium fusiforme* (Kof)
- *Gyrodinium spirale* (Bergh) Kof
- *Gyrodinium* sp.
- *Goniodoma* sp.
- *Oxiphisis oxytoxoides* (Kof)

(*continued*)

TABLE III Continued.

Cyanophyceae
Anabaena sp.
Aphanizonium sp.
Chroococcus dispersus (Keissl)
Chroococcus sp.
Oscillatoria sp.
Snowella septentrionalis (Kom & Hin)
Snowella sp.
Spirulina sp.
Microcystis sp.
Microcystis viridis (A.Br.) Lem.
Nostoc sp.
Woronichinia elorantae (Kom & Kom Leg)
Woronichinia sp.
Filamentous cyanobacteria n.i.
Coccoid cyanobacteria n.i.

Euglenophyceae
Euglena gracilis (Ehr)
Euglena viridis (Ehr)
Euglena sp.
Eutreptia sp.

Chlorophyceae
Closterium lanula
Crucigenia sp.
Crucigenia tetrapedia (Kirch)
Gonium pectorale (Stein)
Lepocinelis ovum (Perty)
Monoraphidium circinnale (Nyg)
Oocystis lacustre (Boh)
Oocystis sp.
Pediastrium biradiatum (Smith)
Pediastrium boryanum (Smith)
Pediastrium simplex (Smith)
Pediastrium sp.
Scenedesmus abundans (Smith)
Scenedesmus obliquus (Smith)
Scenedesmus quadricauda (Smith)
Scenedesmus sp.
Sticochoccus sp.
Tetraedon trigonium (Tiff) Britt
Tetraedon sp.
Tetraselmis gracilis (Kylin)

Coccolithophorids
Acanthoica aculeata (Sch)
Acanthoica monospina (Sch)
Acanthoica qrattrospina (Lohm)
Calciopappus caudatus (Gaar & Ram)
Calyptrosphaera oblonga (Lohm)
Calyptrosphaera pirus (Kamp)
Emiliana huxleyi (Lohm)
Syracosphaera pulchra (Lohm)
Syracosphaera sp.
Helladosphaera sp.
Halopappus sp.

Dictyochophyceae
Dictyocha fibula (Ehr)
Dictyocha speculum (Ehr)

Chrysophyceae
Calycomonas poscheri (Vann Goor)
Calycomonas sp.
Chrysochromulina sp.
Dinobryon belgica (Meu)
Dinobryon divergens (Imhof)
Dinobryon sp.
Ebria tripartita (Sch) Lemm
Marmiella sp.
Meringosphaera mediterranea (Lohm)
Meringosphaera tenerrima (Sch)
Meringosphaera sp.
Padlova parva (Skuja)
Parapedinella sp.
Phaeocystis pouchetii (Har) Lag

Cryptophyceae

Other flagellates

3.3 Taxonomic Structure of the Phytoplankton Guilds and Its Relationship with P-Loading and Environmental Heterogeneity

In the study period, 228 phytoplankton taxa were identified. A total of 111 taxa were diatoms, 49 taxa were dinoflagellates, 20 taxa were chlorophyceae, 15 taxa were cyanophyceae, and the other 33 taxa were coccolitophorids, phytoflagellates, cryptophyceae, dictyochophyceae, euglenophyceae and chrysophyceae (See Tab. III). Only 13 of the 228 taxa identified were included in the dominant taxa group (see Section 2.6). These accounted for more than 80% of total phytoplankton abundance in terms of cell density (Tab. IV). The

TABLE IV List of dominant taxa and relative contribution (%) of each taxon to total cell density.

List of dominant taxa	*Relative importance (%)*
Achnantes sp.	0.1
Chaetoceros socialis	7.1
Chaetoceros wighamii	11.3
Chaetoceros sp.	1.3
Cyclotella sp.	1.0
Navicula sp.	0.1
Thalassiosira sp.	34.2
Dinoflagellates thecate $> 20\ \mu m$	0.6
Prorocentrum minimum	1.0
Undetermined coccoid cyanophyceae	13.2
Snowella sp.	3.9
Criptophyceae	1.8
Undetermined phytoflagellates 1	6.0

spatial–temporal dynamics of the phytoplankton taxonomic structure were analysed on the basis of spatial–temporal variations in the dominant taxa. In terms of numerical abundance, diatoms were dominant in all seasonal periods, with centric diatoms (54.9% of cell density) prevailing over pennate diatoms (0.2%). Among the centric diatoms, one unidentified species of *Thalassiosira* (mean apical axes = 12 μm; Fig. 5A) was the most abundant. Its abundance was positively correlated with chl*a* concentration ($y = 507, 509x - 96{,}281$; $r = 0.673$; d.f. = 10; $P < 0.02$) and cell density ($y = 0.41x - 83{,}066$; $r = 729$; d.f. = 11; $P < 0.01$). Other taxa from the dominant group prevailed at certain times or in certain areas of the lake, associating with, or replacing, *Thalassiosira* sp.

Some species of *Chaetoceros* (*C. socialis*, Fig. 5B), the dinoflagellate *Prorocentrum minimum* (Fig. 5C) and another five taxa from the dominant group rose to prevalence temporarily and at different times. Some phytobentonic taxa (Fig. 5E) and taxa with a higher freshwater affinity (Fig. 5D) prevailed in the areas of the lake that were mostly affected by freshwater input.

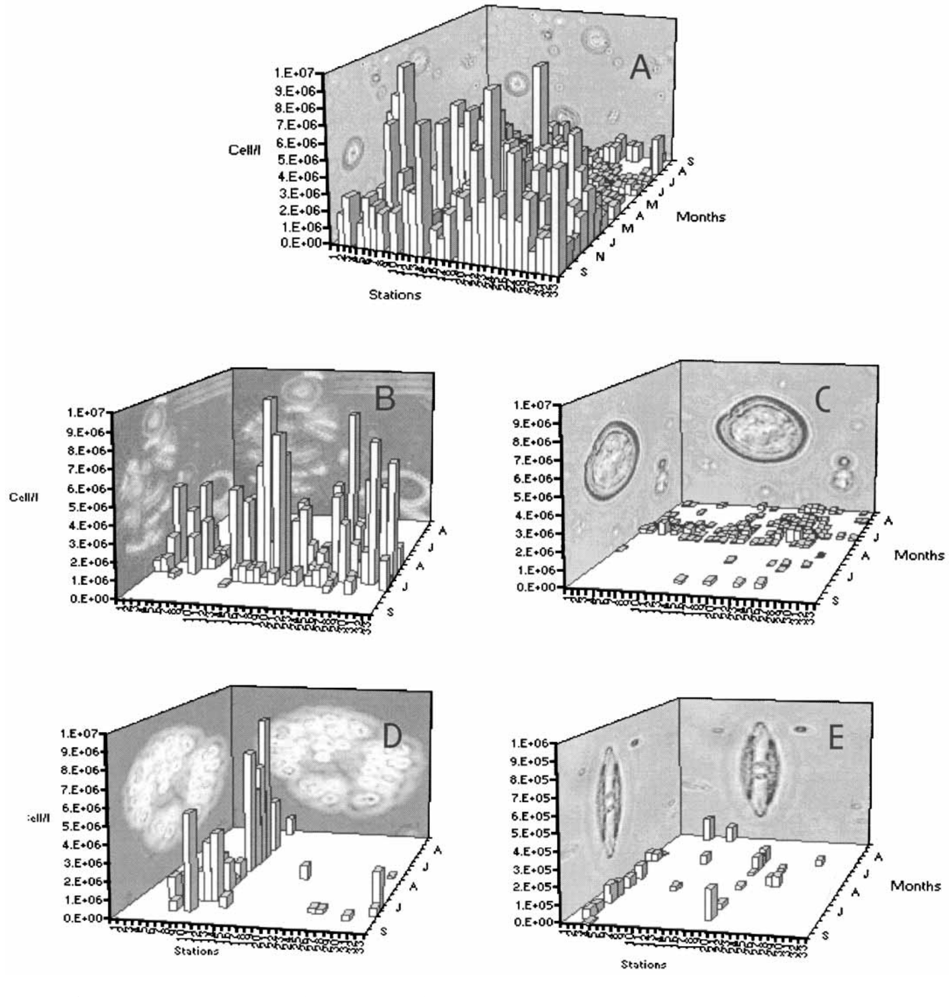

FIGURE 5 Space-time patterns of variation of some dominant taxa that replaced or were associated to *Thalassiosira* sp. with different importance on temporal or spatial scale: *Thalassiosira sp (A)*; *Chaetoceros socialis (B)*; *Prorocentrum minimum (C)*; *Snowella* sp.*(D)*; *Navicula* sp.*(E)*.

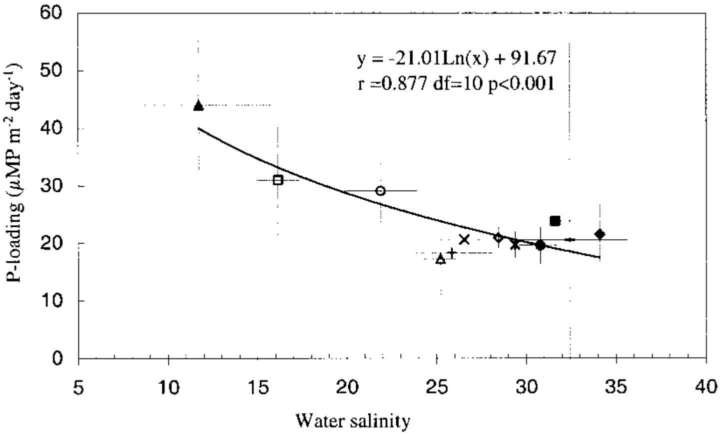

FIGURE 6 Spatial distribution of the dominant taxa along salinity and phosphorus-loading gradients: ▲, *Snowella* sp.; □, *Navicula* sp.; ○, Cryptophyceae; +, undetermined coccoid cyanophyceae; ×, *Chaetoceros whigamii*; ◇ , *Thalassiosira* sp.; ∗, Phytoflagellates 1; −, *Cyclotella* sp.; ■, *Dinoflagellates thecate* >20 μm; △, *Chaetoceros socialis* sp.; ◆ *Chaetoceros* sp.; ●, *Prorocentrum minimum.*

Finally, the 13 dominant taxa were distributed in relation to their numerical abundance within a two-dimensional niche space, with P-loading and water salinity as niche dimensions (Fig. 6). Each species was described by its average requirements on the two dimensions with a 95% confidence interval. Requirements for each species were calculated as mean P-loading and water salinity values at all sites where they were present. Species observed in winter and in areas closer to freshwater input (e.g. *Chaetoceros whigamii*, *Chaetoceros socialis*, *Snowella* sp. and pennate diatoms) were associated with low salinity and high phosphorus loading niche conditions, whereas species observed in summer (e.g. *P. minimum*) and year-round (e.g. *Thalassiosira* sp. and *Phytoflagellates*) were associated with a higher salinity and lower phosphorus loading.

4 DISCUSSION

The results of this study indicated first that P-loading to Lake Alimini Grande is generally low in comparison with phosphorus inputs measured in other coastal ecosystems; and second that the relative importance of internal and external inputs displayed a seasonal pattern of variation.

The first point is supported by the comparison of both external and internal input with data from the literature. On the basis of a comparative analysis of P-external loading carried out on a series of 20 shallow coastal ecosystems including coastal lagoons, fjords, estuaries and bays (data published on http://data.ecology.su.se/MNODE.html, in Nilsson and Jasson, 2002 and in Vollenweider, 1992, and recalculated by the authors of this work), Lake Alimini Grande was among those ecosystems receiving the lowest phosphorus supply from external input. Indeed, P-external loading values ranged from 11.2 μmol P m^{-2} d^{-1} (observed in the Gulf of Riga) to 656 μmol P m^{-2} d^{-1} (observed for a eutrophic coastal area in the northern Adriatic sea), while P-loading in Lake Alimini Grande averaged 12.1 μmol P m^{-2} d^{-1}, putting it in the lower band of the range of values observed. This was probably due to two factors: (1) we evaluated P-loading only from localized inputs and did not estimate non-source input, which may have been significant; (2) freshwater discharge into lake Alimini Grande was limited in comparison with other brackish environments (Sacca di Goro $1.9 \times 10^6\,\mathrm{m^3\,d^{-1}}$,Viaroli *et al.*, 2001; Corunian lagoon $26 \times 10^6\,\mathrm{m^3\,d^{-1}}$; Swaney, 1998; Valli di Comacchio $50 \times 10^3\,\mathrm{m^3\,d^{-1}}$; Giordani and Viaroli, 2001), and displayed a strong seasonal variation: freshwater discharge from channels was high in winter but low and often absent in summer. Furthermore, the lower freshwater discharge to the lake in summer was also strongly affected by water drainage for irrigation. The low phosphorus supply from external inputs may also result from the limited extension of the catchment area, which, at 103 $\mathrm{Km^2}$, is lower than other coastal lagoons (Swaney, 1998; Viaroli *et al.*, 2001). Moreover, its abundant vegetation (Basset, 2000) may limit phosphorus losses from soil.

Levels of phosphorus concentration from internal loading were relatively low in comparison with other freshwater or brackish lakes: the P-internal loading values observed in summer in Lake Alimini Grande (average 18.4 $\mu\mathrm{mol\,P\,m^{-2}\,d^{-1}}$) were one to two orders of magnitude lower than benthic fluxes reported for more eutrophic ecosystems (1560 $\mu\mathrm{mol\,P\,m^{-2}\,d^{-1}}$; Harper, 1992, 447 $\mu\mathrm{mol\,P\,m^{-2}\,d^{-1}}$; Søndergaard *et al.*, 1999, data recalculated), but were higher than those observed in coastal lagoons with oligotrophic conditions (0.04 $\mu\mathrm{mol\,P\,m^{-2}\,d^{-1}}$; Wu *et al.*, 2001) and in coastal marine areas (5–10 $\mu\mathrm{mol\,P\,m^{-2}\,d^{-1}}$; Barbanti *et al.*, 1992).

To quantify external and internal inputs, we made a number of assumptions. For the external inputs, we assumed that non-source inputs, including the atmosphere, groundwater and superficial runoff, were negligible. This is probably true for atmospheric and groundwater inputs (Swaney, 1998; Basset *et al.*, 2001), but superficial runoff could be significant. For the internal input, we assumed that organic-matter decomposition in the lake sediments is the most important source of phosphorus supply, that reed detritus decomposition was a good predictor of sediment detritus decomposition and that the active volume of lake sediments was limited to a thickness of 5 cm. Reeds are by far the dominant vegetation along the shores of lake Alimini Grande, and they can thus be considered the main component of the lake sediments (Rossi and Costantini, 2000). Therefore, leaf decomposition is likely to be a good descriptor of sediment decomposition, although reed decomposition rates can be one to two orders of magnitude higher than the rate of decomposition of lake sediments (Howes *et al.*, 1984, 1985). In this investigation, on the basis of the results obtained in a laboratory experiment (see Section 2), we used a correction factor of 0.1 to correct reed decay rates. This correction factor was calculated as the ratio between the rate of organic matter decay processes in the sediments under the experimental conditions and the rate of reed leaf decay processes in the study area. However, this value varied from 0.1 to 0.8. The value of 0.1 was obtained by calculating the ratio between the rate of decomposition processes of sediments at a higher temperature (24 °C) under the experimental conditions and the rate of reed decomposition processes in summer, while the value of 0.8 was obtained by calculating the ratio between the rate of decomposition processes of the sediments at a lower temperature (8 °C) under the experimental conditions and the rate of reed decomposition processes in winter. In this investigation, the value selected for the constant C (0.1) could affect the winter phosphorus budget, but this bias can be considered negligible, since the winter budget is affected above all by external input.

The selected sediment depth (5 cm) was supported by the analysis of a core of lake sediment that showed a superficial well-mixed layer with well-oxygenated sediments (Cenci *et al.*, 2002), and losses of phosphorus due to geochemical processes can therefore be considered negligible. In any case, it is important to emphasize that our assumptions only affect absolute P-loading values and have no relevance to the patterns of temporal and spatial variability that are the focus of this paper. Furthermore, this investigation does not concern itself with the fate of the phosphorus released from the organic matter but seeks only to assess the potential budget deriving from organic-matter decomposition and how this may affect phytoplankton biomass.

It was also observed that the relative importance of internal and external inputs in Lake Alimini Grande displayed a seasonal pattern of variation. The highest external inputs were observed in winter and spring (67% of total phosphorus inputs), while internal inputs dominated in summer (99.8% of total phosphorus input). These different contributions can be explained by the temporal patterns of variation in freshwater inflow and decomposition processes.

The temporal and spatial distribution of phytoplankton abundance and taxonomic composition is affected by the seasonally variable dynamics of internal and external phosphorus input. This is confirmed by the existence of a significant direct relationship between the temporal variation of phytoplankton biomass and overall P-loading, and by the absence of any relationship between phytoplankton biomass and phosphorus concentration in the water. Phosphorus concentration in the lake was very low, especially its inorganic fraction, with values comparable to those observed in the adjacent coastal marine area ($<0.1\ \mu$M), and often below the detectable limit of the analytical method utilized (*c.* 0.005 μM with a 10 cm optical length). Further, the high N/P ratio (average $N_{\mathrm{TOT}}/P_{\mathrm{TOT}} = 64.78 \pm 21.04$; Basset *et al.*, 2001) and the levels of phytoplankton biomass typical of mesotrophic ecosystems (Marchetti, 1994) suggest a high rate of P-uptake and thus the existence of P-limitation in the lake. A direct relationship between P-input and phytoplankton biomass is expected (De Angelis, 1992) under these conditions and has generally been observed in other brackish environments of the Mediterranean area where phosphorus is the limiting nutrient (Vadrucci *et al.*, 1995; Escaravage *et al.*, 1996; Gomez *et al.*, 1998; Kormas *et al.*, 2001). In Lake Alimini Grande, the high rate of P-removal from the waters is supported by the results obtained in an experiment carried out in enclosures (Basset *et al.*, 2001) and is predicted by the mathematical model based on the LOICZ approach, according to which Lake Alimini Grande is a sink for nutrients, especially DIP (Vadrucci *et al.*, 2001).

The dependence of the two sources of phosphorus supply on the dynamics of phytoplankton biomass can be further emphasized by considering separately the relationships of external and internal P-loading to the spatial distribution of phytoplankton biomass. The external P-loading/biomass relationship was more significant in winter, when freshwater discharge was higher. The negative external P-loading/biomass relationship observed in some months (such as in November and January) can be explained as a wash-out phenomenon (i.e. a dilution effect *sensu* Zakardijan *et al.*, 2000) occurring when the rate of freshwater inflow is higher than the rate of algal growth, causing in turn a spatial separation between the localized point of resource input and the effect on the phytoplankton biomass. In contrast, the internal P-loading/biomass relationship was more significant in the summer and the early autumn. The relationship was always direct, supporting a closer link between P-release from sediments and the response of phytoplankton biomass (Velikova *et al.*, 1999).

Finally, the influence of phosphorus loading dynamics on phytoplankton guilds in lake Alimini Grande was also reflected in the taxonomic structure. As observed for other brackish environments at temperate latitudes (Giacobbe *et al.*, 1996; Watson *et al.*, 1997; Mallin *et al.*, 2000), diatoms are present in Alimini Grande throughout the year (averaging 54.9% in term of cell density). The predominance of a few centric diatoms seems to be due to their high growth rate in specific environmental conditions characterized by frequent allocthonous inputs (Lewis, 1978; Willen, 1991; Tryfon and Moustaka-Gouni, 1997; Mallin *et al.*, 2000). Moreover, Tilman *et al.* (1982) demonstrated that diatoms are good competitors for phosphorus but poor competitors for nitrogen. The strong phosphorus limitation and the direct dependence on phosphorus inputs in lake Alimini Grande are in agreement with these observations (Tilman *et al.*, 1982).

The spatial–temporal succession of the dominant taxa can also be explained with reference to a two-dimensional niche space with P-loading and water salinity (here used as a measure of environmental heterogeneity) as niche dimensions.

The phosphorus availability and salinity gradients can be considered the most important in defining the niche space of the major groups of phytoplankton guilds in Lake Alimini Grande, since other factors such as availability of light and other nutrients did not play a significant role in controlling phytoplankton dynamics (Basset *et al.*, 2001). In addition, the two variables can be considered independent from each other, because in summer at least, phosphorus availability was influenced almost exclusively by the contribution of internal loading and consequently was completely independent of salinity variation.

In relation to the position of species in the niche space, freshwater and winter species were associated with high phosphorus availability and low salinity, whereas typical summer species (such as dinoflagellates) were more abundant in high-salinity and lower-phosphorus conditions. Nevertheless, if one takes into account the temporal and spatial heterogeneity of the environment (salinity gradients), the positions of taxa in the niche space were more closely linked to temporal than spatial variation. Indeed, 10 of the 13 dominant taxa had a relatively homogeneous distribution in the lake. Only Cyanophyceae (i.e. *Snowella sp.*) and pennate diatoms showed patterns of spatial variation, being more abundant in the Strittu area and in the freshwater channels. In other words, only freshwater inputs determined local spatial heterogeneity of the phytoplankton guilds, and only at specific times. The results of this study seem to indicate that temporal fluctuations of phosphorus availability and salinity were perceived as being heterogeneous by the phytoplankton, whose dynamics were more closely related to seasonal variation than to the spatial distribution of the two environmental gradients. The position of the *Thalassiosira* sp in the niche space is in agreement with its wide spatial–temporal distribution, the co-ordinates of its position being the average salinity and the average P-loading in the lake.

In conclusion, the results of this investigation point to the strong dependence of phytoplankton dynamics on phosphorus inputs and especially on P-internal inputs in summer. This has important implications for ecosystem management, since this is the period when dystrophic crises in the lakes are more frequently observed.

Nutrient inputs are clearly a driving ecological force for phytoplankton dynamics in Lake Alimini Grande. Further research is needed in this field in order to preserve coastal ecosystems from the dystrophic crises which have characterized several warm periods over the last decade (Basset, 2000).

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