Institute of Natural Resources and the Environmant (IRENA), Managua, Nicaragua

Nutrient Availability and the Stability of Phytoplankton Biomass and Production in Lake Xolotlán (Lake Managua, Nicaragua)

R. Erikson, M. Pum, K. Vammen, A. Cruz, M. Ruiz & H. Zamora

With 8 Figures and 2 Tables

Abstract

We studied nutrient concentrations, phytoplankton biomass and primary production during an entire annual cycle in tropical Lake Xolotlán. The lake is polymictic and nutrients and phytoplankton were homogeneously distributed throughout the water column. High concentrations of total phosphorus (≈ 0.15 mg l^{-1}) and total nitrogen (≈ 2 mg l^{-1}) were always present. The inorganic forms of phosphorus and nitrogen usually occurred in low concentrations. Phytoplankton biomass was high (≈ 40 mg l^{-1}) and relatively stable. Biomass variations were related to seasonal events of the dry and rainy periods and to the bathymetric characteristics of the lake, which resulted in an almost constant biomass concentration per area unit. Primary production was consistently high (≈ 5 g C m^{-2} d^{-1}) and controlled by the underwater light penetration.

Introduction

Fundamental knowledge of tropical lakes is limited and there are few well documented aquatic ecosystem studies on the tropics. For example, the IBP-program included 110 lakes and reservoirs, of which only 9 were tropical (LeCren & Lowe-McConell 1980). In an analysis of factors governing world-wide lake productivity, only one tropical lake (Lake George, Uganda) had sufficient data on nutrient loading to warrant its inclusion in the analysis (Schindler 1978). Most tropical limnology studies were performed during the sixties and seventies, mainly on African lakes, and a few functional analyses contrasting temperate and tropical lakes were carried out at that time (Talling 1965; Brylinsky & Mann 1973; Melack 1979; Brylinsky 1980; Lemoalle 1981; Lemoalle et al. 1981). However, the number of tropical lakes included in more recent latitude-based comparison (Kalff 1991; Polling-

her & Berman 1991) has not increased significantly. The scarcity of original information on tropical aquatic ecosystems is all the more inadequate when considering that the conclusions of the studies which have been peformed diverge. There is a great need for more ecosystem data from lakes in the tropics (Lewis 1978). Limnological investigations in Lake Xolotlán (Lake Managua), Nicaragua were begun in 1985. Scientific results from these studies have been presented at various symposia over the years. In this paper, we account for the first records on nutrients, phytoplankton biomass and production, and their interrelations in Lake Xolotlán during July 1985 to July 1986. Our purpose is to describe the base of the food chain and to examine the growth regulating factors.

Lake description

Lake Xolotlán is the second largest lake in Nicaragua (and Central America) and like most lakes in the region, it owes its origin to tectonic events. The lake is situated between 12°00′ N and 86°00′ – 87°45′ W. It is part of the Nicaragua depression, a huge 30 – 40 km wide graben formed at the end of the Tertiary period some 25 million years ago. The area is still dotted with both active and dormant volcanos, as well as hot springs and fumaroles. As a result of tectonic activity in 1844, the southern outlet into much larger Lake Nicaragua was blocked, making Lake Xolotlán an endorheic basin.

The surface area of approximately 1000 km² is divided into a larger, deeper central basin and a smaller, shallow southern basin. At a normal elevation of 38 m above sea level, the mean and maximum depths are approximately
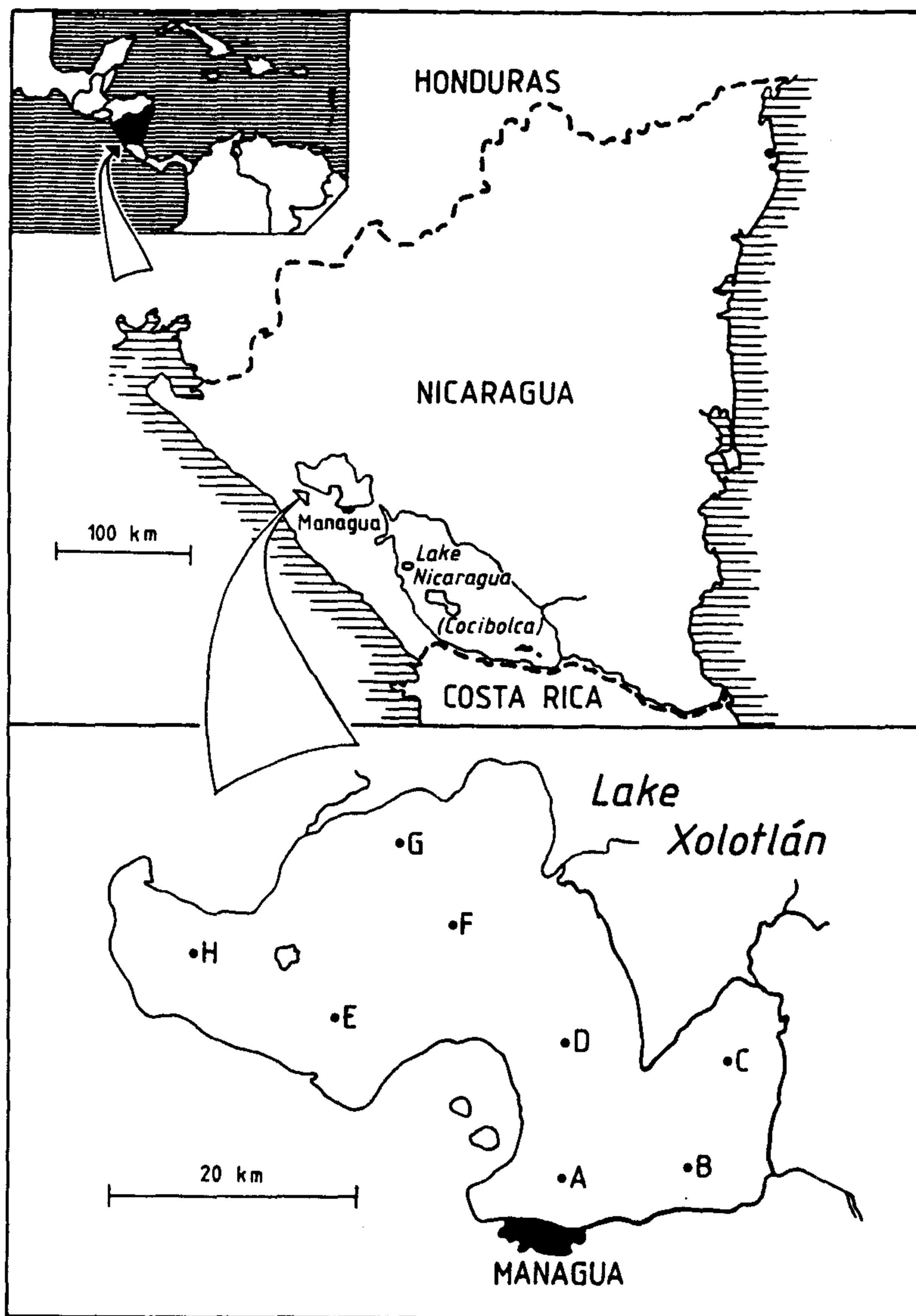
Fig. 1. Lake Xolotlán and the sampling sites (A — H; identical with 1 — 8 in Fig. 6).

is increasing annually by approximately 22 mg l^{-1} due to high evaporation and lack of outflow, and originates predominantly from the weathering of surrounding soils (ERIKSON, unpubl. data). The ionic composition of the lake water is accounted for in more detail by LACAYO (1991). Large quantities of domestic sewage and industrial waste water enter the lake via the southern basin. The population within the catchment area is approximately 1 million, most of them in and near the city of Managua. Managua is also the site for the industrial activities, mainly food processing, that affect the lake.

Methods

Water samples were collected with a Van Dorn sampler from eight sampling sites on Lake Xolotlán (Fig. 1) monthly from July 1985 to June 1986 (excluding January) at 6 — 7 depths and immediately above the sediment. Samples were kept on ice during transportation to the laboratory. Dissolved nutrients were determined from filtrate which had been passed through Whatman GF/C filters. Molybdate reactive phosphorus (MRP) was analyzed using the ascorbic acid modification of the molybdenum blue method (MURPHY & RILEY 1962). Nitrite was determined by the colorimetric method of diazotation (APHA 1985) and nitrate by the salicylate method (APHA 1985). Ammonia was determined by the indophenol-blue method (APHA 1985). Analysis of the inorganic nitrogen fractions from July and August 1985 failed, so no data are available from that period. Total phosphorus and nitrogen were determined in unfiltered water. Samples were digested using the sulfuric acid and peroxide method and then analyzed for phosphorus using the above ascorbic acid method to obtain total P. Total N was determined as Kjehldahl-nitrogen.

Phytoplankton samples were taken with the nutrient samples at each meter of the water column. In the laboratory, two volume-weighted, integrated water samples, one from the photic and another from the aphotic zone, were preserved with Lugols-acetic-acid solution and formaline. Following sub-sample sedimentation, algae counts were made using an inverted microscope (LUND 1958). Cell counts were converted to wet-weight biomass by calculating cell volume, assuming a density of unity. The amount of algal carbon was estimated to be 20% of algal wet-weight biomass (LEMOALLE et al. 1981).

Primary production was measured in situ every second or third month at the same eight sampling sites, using the light and dark bottle technique and Winkler oxygen analysis (STRICKLAND & PARSONS 1968; VOLLENWEIDER 1989). Three sets (initial, clear, dark) of paired bottles were filled with water from specific depths

8 and 20 m, respectively. The mean depth in the central basin is about twice that in the southern basin (≈ 10 m and 5 m). However, depending on evaporation and precipitation, which may vary greatly from year to year, the surface elevation fluctuates both seasonally and annually (1 — 5 m; IRENA 1982), producing great variations in lake volume. The rainy period comprises the months May to November (most rains occur towards the end of the season), and the dry period is from December to April.

The average annual water inflow is $2.2 \cdot 10^9$ m^3 and derives equally from direct rainfall on the lake surface and runoff from the catchment area. Water balance is maintained by evaporation and occasional overflows to the south during extremely high water level conditions (IRENA 1982). pH is about 9.2. Annual mean conductivity is approximately 1800 µS cm^{-1} and varies with the lake volume. Salinity, dominated by carbonates (≈ 800 mg l^{-1}),

(0.1, 0.1, 0.4, 0.6, 1.0, 1.5, 2.0 m) of the photic zone. Initial bottles were fixed immediately. Clear and dark bottles were incubated at the depths of collection for one to two hours around 10 a.m. and fixed when taken on board. Bottles at maximum depths were incubated the longest. Gross production was calculated for each depth as the difference in oxygen content between clear (exposed) and dark (unexposed) bottles. Community respiration was calculated in the same way as the difference between initial and dark bottles. Depth integrated production and community respiration were determined by planimetry of the oxygen evolution and oxygen consumption depth curves, respectively. Incident irradiance was measured by a pyranometer situated in nearby Managua. Mean hourly incident irradiance during incubations was about the same as the mean hourly incident irradiance during the days. Therefore, we used a factor of 9 for the conversion of hourly to daily production in the lake (TALLING 1965; LEMOALLE et al. 1981). The depth of the productive zone (Z_p: prod. = 0) was used as an approximation of relative vertical light penetration.

The following physical data were obtained from institutes in Managua: incident irradiance (UCA), wind speed (Airport), precipitation and water level (INITER).

Significant differences between groups of data were tested via one-way ANOVA (model 1) and SNK (Student Neuman K-test). A level of significance of $p > 0.05$ was selected.

Results

1. Physical factors

Incident irradiance varied between 5000 and 7000 W m^{-2} with the highest value during the dry season (Fig. 2A). Average monthly wind speeds varied between 1.5 and 3.5 m s^{-1} (Fig. 2B), according to data from the nearby airport, but the lake surface experienced much more wind ($\approx 5-10$ m s^{-1}). The NE trade winds are predominant winds blowing steadily during the entire year, stronger during the dry season and weaker toward the end of the wet season. Wind-induced turbulence and convective overturn due to nocturnal cooling prevented water column stratification, making oxygen and temperature gradients rare (PLX 1987). The annual mean water temperature was 29 °C. Diurnal variations larger than those occurring annually were likely. When the regimes of wind and rain during the study year were compared to corresponding long term averages, it was notable that there was more rain during October and that the dry season (more wind, less rain) was prolonged into June (Fig. 2C). The rainfall measured in May resulted from one single rain storm. Water level variation due to precipitation and evaporation throughout the study year was about 1 m (Fig. 2D), corresponding to a 10% change in volume.
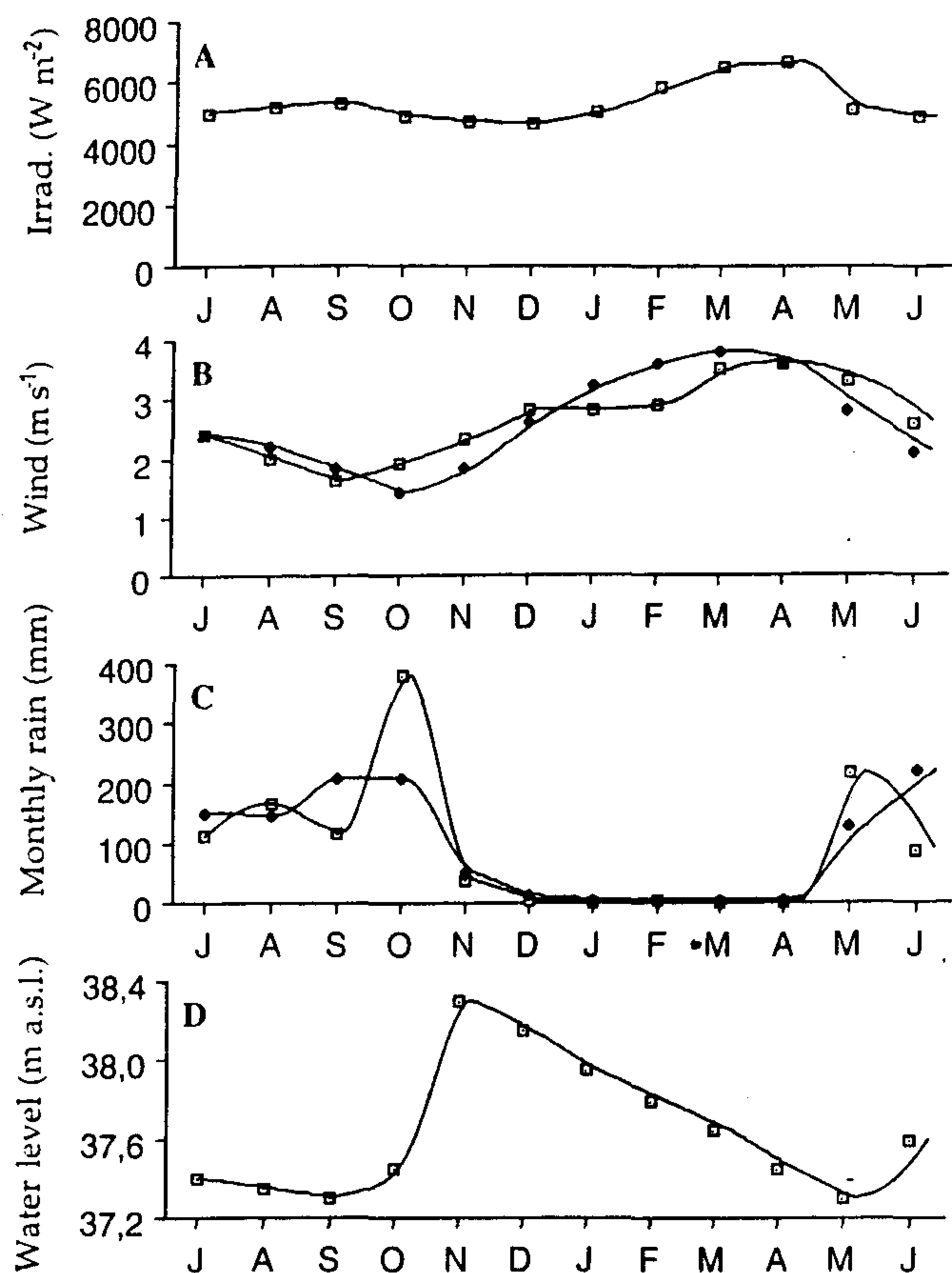

Fig. 2. Monthly averages for 1985/86: (A) incident irradiance, (B) wind speed, (C) rain, (D) water level. Average values for wind speed and rain (dark dots) for 1957–1989 are also shown.
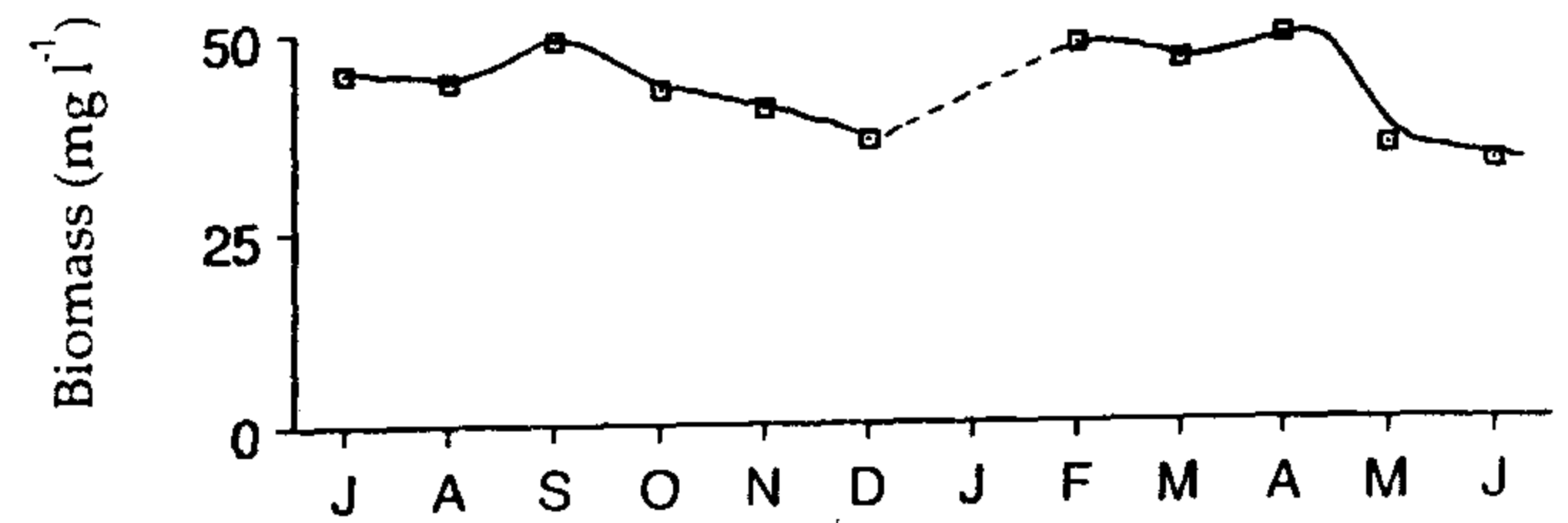
2. Nutrients

There was no statistically significant difference in nutrient levels between the designated depths at any of the sampling sites. Therefore, an average of all depths was calculated for each sampling site and month. The annual ranges and averages of nutrients (in total and for both basins) are given in Table 1. High concentrations of total phosphorus and nitrogen were present, with total P levels placing Lake Xolotlán in the hypertrophic classification. The inorganic forms usually occurred in very low concentrations. Total P levels were significantly higher in the southern basin compared to the central. MRP and total N were also found in higher concentrations in southern basin, whereas the inorganic nitrogen fraction was higher in the central basin.

The monthly mean concentrations of all forms of nitrogen and phosphorus, except nitrite, exhibited definite annual cycles, with significant seasonal differences (Fig. 3). Total N and P showed a gradual decrease during the rainy season, followed by an increase during the dry season. The ratio by weight between total N and total P was on average 13.5; in the southern basin during the dry period the ratio was close to 10. There was a significant correlation between
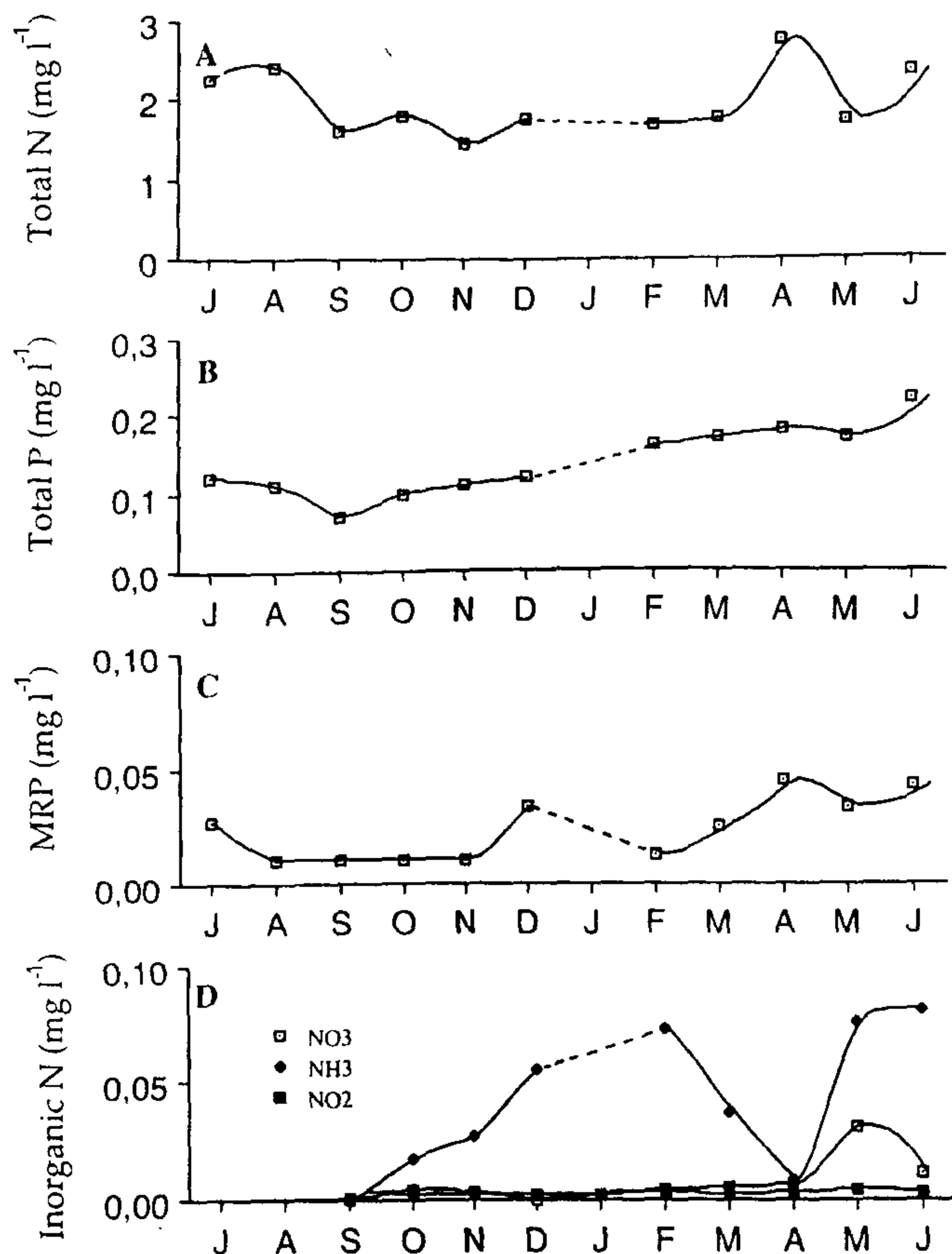
Fig. 3. Monthly concentration averages of (A) total nitrogen, (B) total phosphorus, (C) phosphate and (D) inorganic nitrogen fractions for 1985/86.

Fig. 4. Monthly phytoplankton biomass (fresh-weight) averages for 1985/86.

3. Phytoplankton

The annual mean phytoplankton biomass, expressed as wet-weight and derived from 154 counts, was $42.7 \, \text{g m}^{-3}$. The biomass level was relatively stable over the annual cycle (CV = 14%). Maximum biomass occurred in the periods July to September and February to April, and the minima in October to December and May to June (Fig. 4). Thus, biomass decreased during the rainy period and increased during the dry period. These variations, although not very pronounced, varied simultaneously with seasonal characteristics, such as, changes in water volume and wind-induced turbulence (Fig. 2) and with the variation of total N and P (Fig. 3). On the other hand, minimum biomass levels coincided with maximum concentrations of nitrate, ammonia and MRP (Fig. 3).

The horizontal distribution of biomass per volume (Table 1) was characterized by the very significant difference between two comparatively homogeneous areas: the shallow southern basin had a higher biomass than the deeper central basin. Biomass was spatially correlated with both total phosphorus and total nitrogen (r = 0.87 and 0.74, respectively). On the other hand, the phytoplankton biomass was inversely correlated with the inorganic nitrogen concentration (r = −0.84). Biomass was also spatially correlated with Secchi disc depth (r = −0.94).

Biomass per unit area was more or less equal in the two basins (Table 1: $Z_m \approx 5$ m and 10 m, respectively. Thus, the annual mean was approximately $340 \, \text{gm}^{-2}$ (average $Z_m \approx 8$ m).

total P and Secchi disc depth (r = −0.77). MRP exhibited an increase during the dry period. Inorganic nitrogen fractions varied in a less predictable manner. Ammonium nearly always constituted more than 70% of the inorganic nitrogen. Nitrate levels were extremely low and only of significance in May and June 1986 when a maximum of $30 \, \mu\text{g l}^{-1}$ was reached. Nitrite concentrations were constant at very low levels.

Table 1. Annual ranges and averages of nutrient concentration and phytoplankton biomass.

Nutrients (mg l⁻¹)	Annual range (sampling site averages)	Annual averages		
		Total	Southern basin	Central basin
MRP	<0.010−0.050	0.023	0.025	0.019
Tot-P	0.071−0.216	0.139	0.159	0.119
Ammonia-N	<0.005−0.076	0.043	0.039	0.046
Nitrate-N	<0.005−0.030	0.007	0.004	0.010
Nitrite-N	0.002−0.004	0.003	0.002	0.003
Tot-N	1.319−2.904	1.986	2.043	1.893
Phytoplankton biomass (mg l⁻¹)	27−69	47	60	32

Fig. 5. Relative species composition for 1985/86.

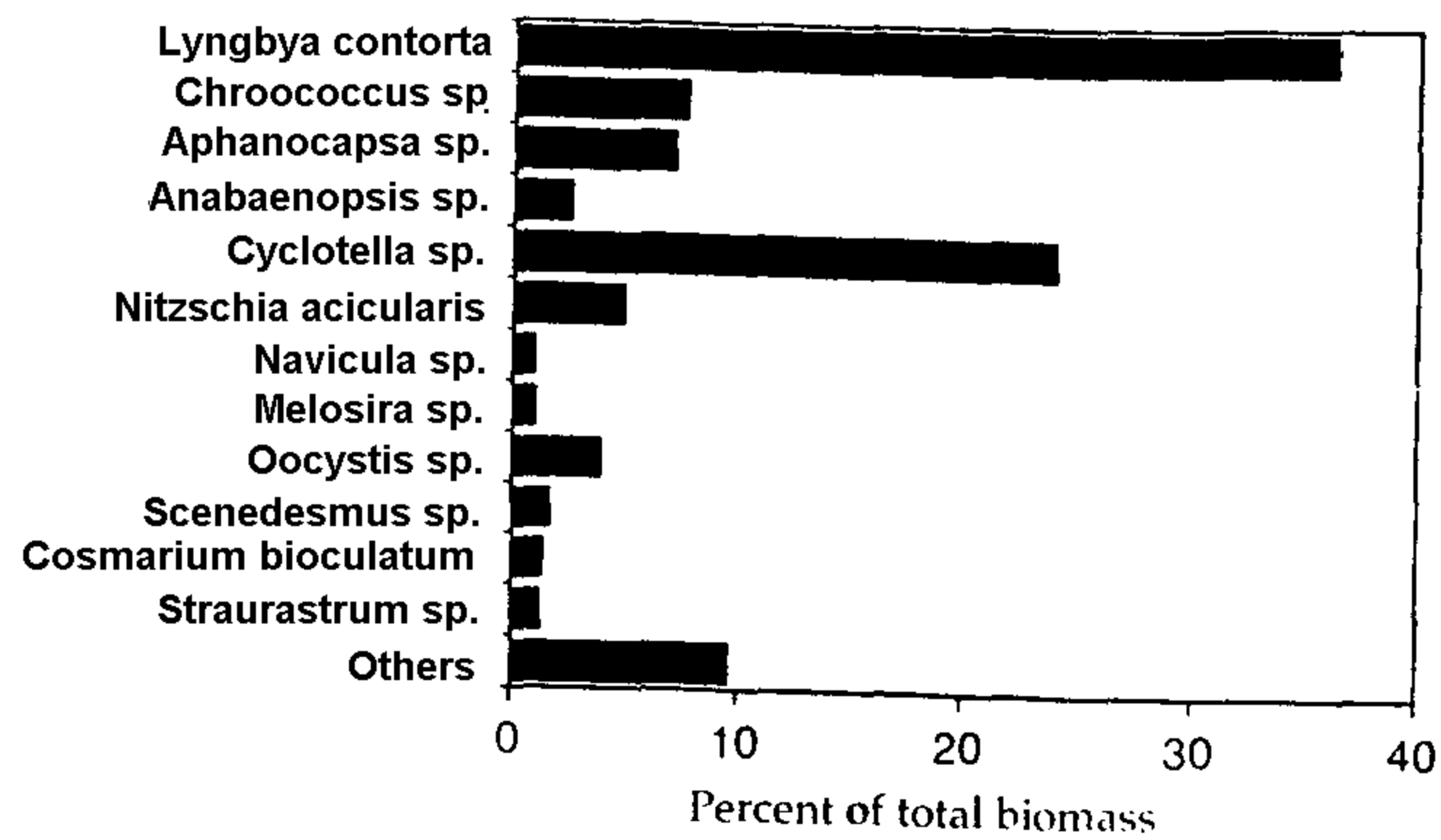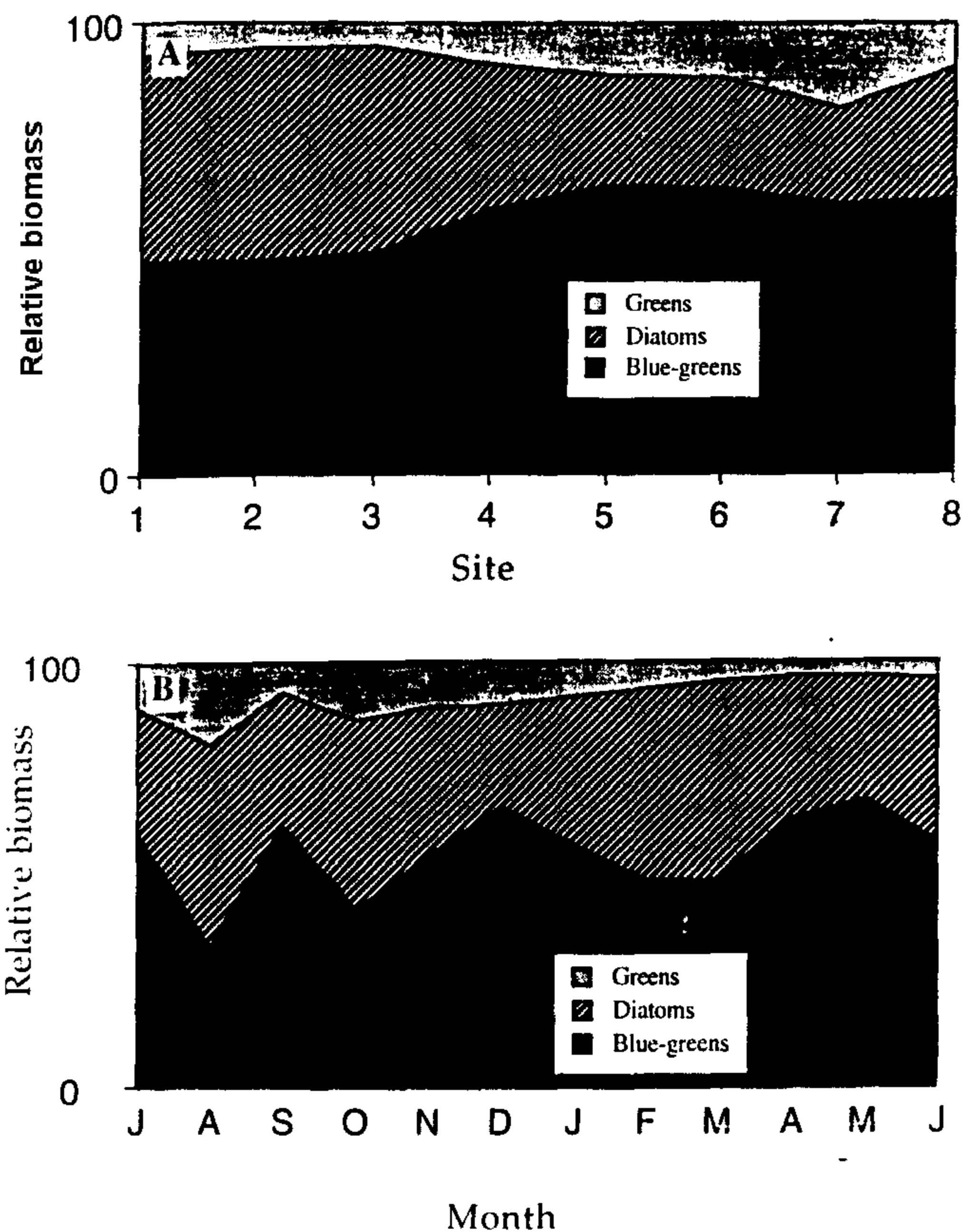**Fig. 6.** Relative biomasses of blue-greens, diatoms and green algae, (A) as average from each sampling site (1–8; see Fig. 1); (B) as average from each month for 1985/86.

Over one hundred phytoplankton species were identified: 52 green algae, 29 blue-green algae, 25 diatoms, 3 Euglenophyceae, 2 Cryptophyceae and 1 Dinophyceae. Two taxa, *Lyngbya contorta* and *Cyclotella meneghiniana*, comprised approximately 60% of the total autotrophic biomass and were consistently the most abundant species in the total biomass (Fig. 5). The phytoplankton community was dominated by Cyanophyta throughout the entire year, constituting nearly 50% and 60% of the community biomass in the southern and central basins, respectively (Fig. 6A). Diatom biomass equalled that of the blue-greens in the southern basin, but made up only 30% of the total biomass in the central basin. Green algae biomass was 6% and 10% in the southern and central basins, respectively. Diatoms were relatively more abundant during the dry season and the blue-greens during the rainy season in both basins (Fig. 6B).

4. Primary production

The average annual hourly rate of gross photosynthetic activity (ΣA) was 1860 mg O_2 $m^{-2} h^{-1}$ (CV = 15%; n = 29). There was no significant difference in the hourly rate, neither spatially (Table 2) nor temporally (Fig. 7A). Daily production was 16.7 g O_2 $m^{-2} d^{-1}$. Using the carbon/oxygen stoechiometric relationship (12/32) and a photosynthetic quotient of 1.2, organic production was estimated at 5 g C $m^{-2} d^{-1}$ for the entire lake, throughout

the year. Based on an algal carbon content of 78 g C m^{-2} (20% of the wet-weight), the renewal rate of the algal community was 0.07 d^{-1} (doubling time $\approx$ 14 days).

Photosynthetic activity at optimum depth (A_{max}) ranged from 1400 to 3300 mg O_2 $m^{-3} h^{-1}$, increasing significantly during the dry period (Fig. 7B) and coinciding with a significant decrease in productive zone depth (Z_p: Fig. 7B). Typical production profiles for the dry and rainy periods are presented in Fig. 8. Spatial and temporal A_{max} variations generally paralleled variations in phytoplankton biomass (Table 2; Figs. 4, 7, 8). ΣA and A_{max} variations did not correlate with variations in irradiance or temperature.

Table 2. Annual ranges and averages of integral gross production, production at optimum depth, integral photic zone respiration, and phytoplankton biomass concentrations. Biomass concentrations in the table are averages from data which correspond to production data.

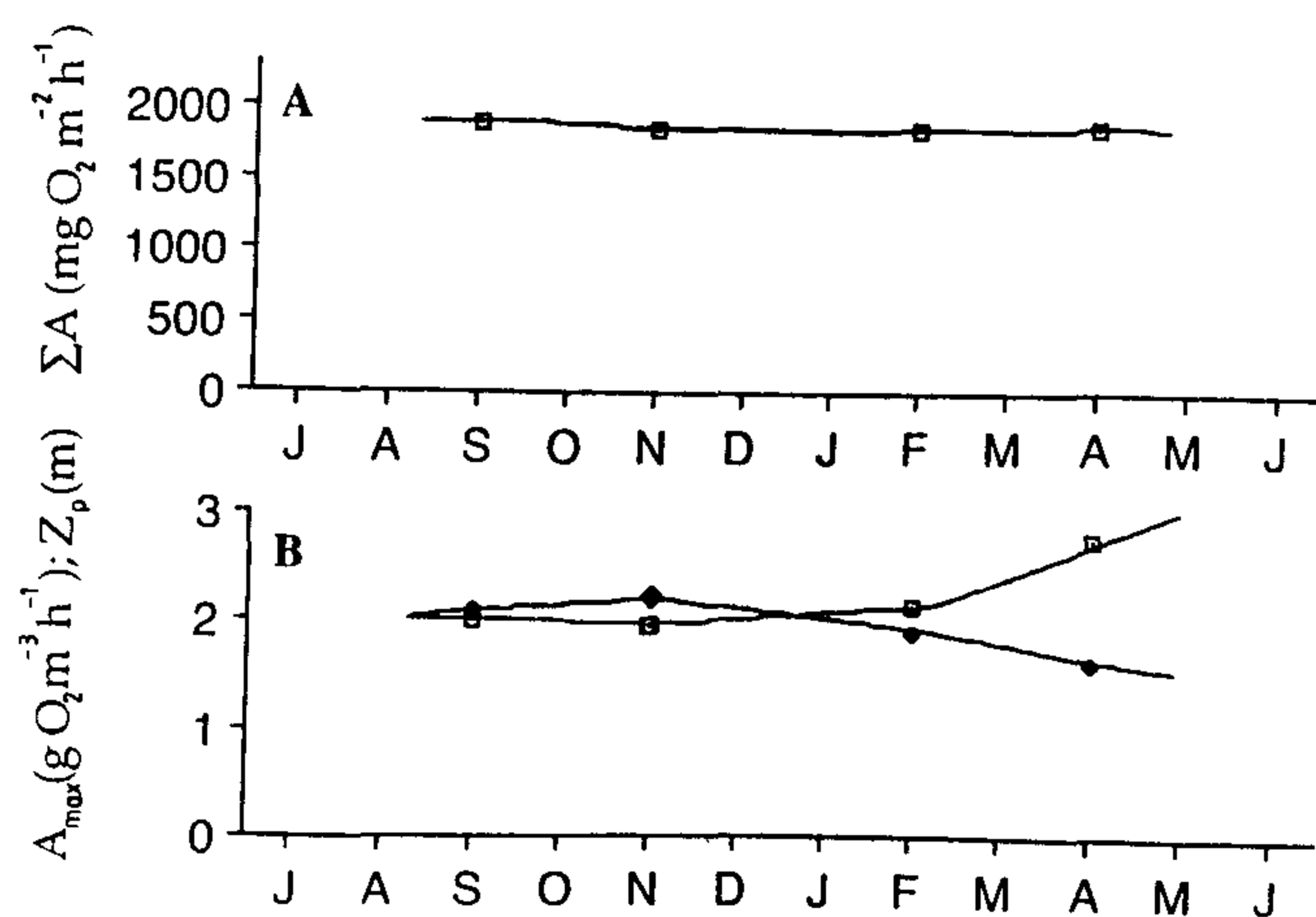|	Annual range (sampling site averages)	Annual averages		
		Total	Southern basin	Central basin
ΣA (mg O_2 $m^{-2} h^{-1}$)	1530–2080	1860	1785	1992
A_{max} (mg O_2 $m^{-3} h^{-1}$)	1970–2750	2330	2390	2290
ΣR (mg O_2 $m^{-2} h^{-1}$)	175– 455	345	365	325
Phytoplankton biomass (mg l^{-1})	26– 72	43	54	33

Fig. 7. Monthly sampling site averages of (A) integrated gross production and (B) production at optimum depth (□) and depth of the productive zone (♦). Data from June are excluded because measurements were only taken in the southern basin.
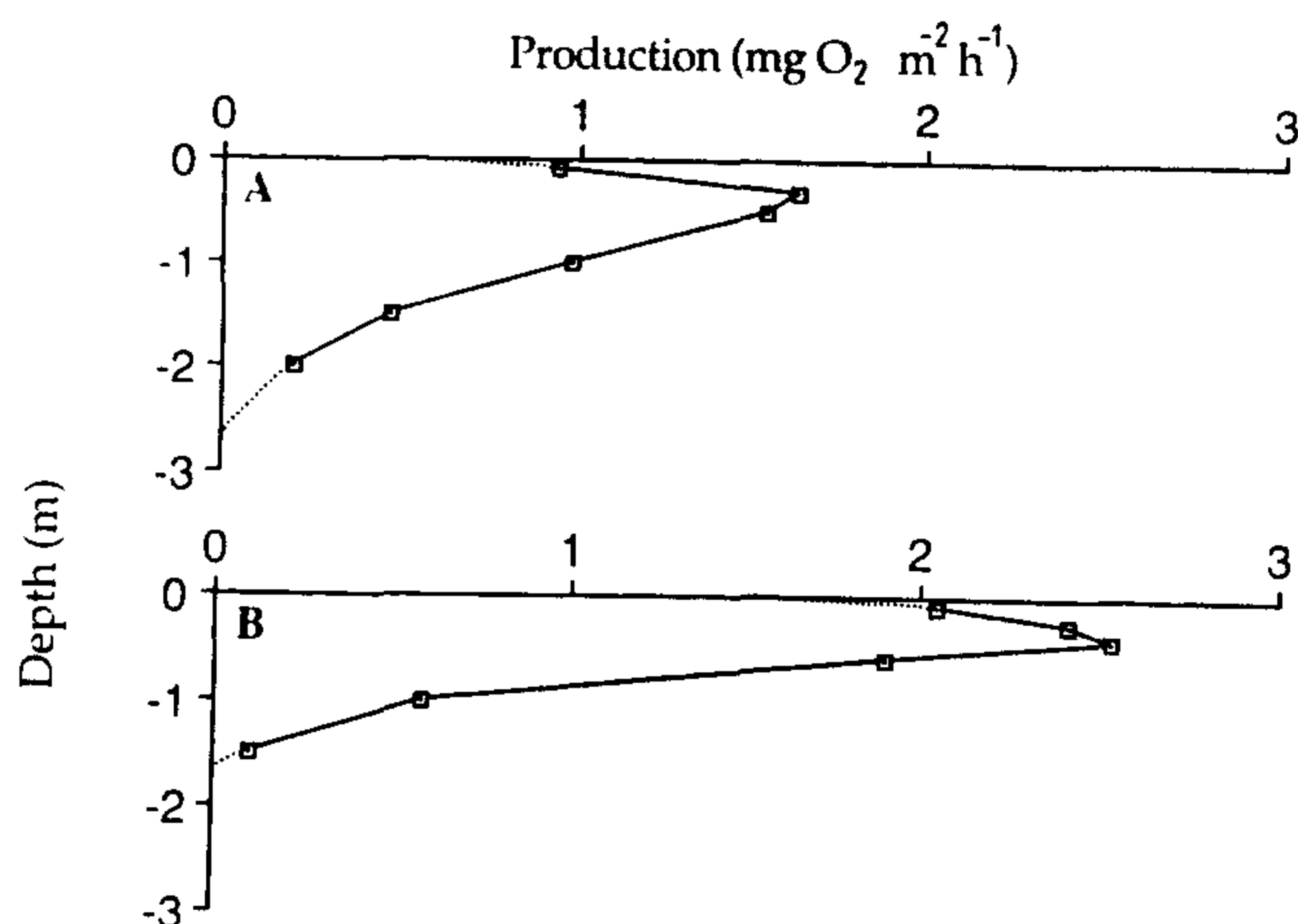

Fig. 8. Primary production depth profiles for the center of the lake (site F) during (A) the rainy season (Oct. 8, 1985) and (B) the dry season (April 15, 1986). Oct. 8, 1985: $\Sigma A = 1930$ mg O_2 $m^{-2} h^{-1}$, biomass $= 29$ mg l^{-1} and Secchi disc depth $= 0.65$ m; April 15, 1986; $\Sigma A = 1970$ mg $O_2 m^{-2} h^{-1}$, biomass $= 39$ mg l^{-1} and Secchi disc depth $= 0.35$ m.

Net production $(\Sigma A - \Sigma R)$ within the photic zone during the day was $\approx 80\%$ of gross production (Table 2). However, considering light penetration and the hours of sunshine available, only $\approx 10\%$ of the lake and biomass were within the photic zone during a diurnal cycle. Day time respiration within the photic zone averaged 345 mg O_2 $m^{-3} h^{-1}$ (Table 2). The lowest oxygen consumption occurred in the deepest part of the photic zone, averaging 160 mg O_2 $m^{-3} h^{-1}$. Still, with this value representing true dark-community respiration, heterotrophic activity throughout the entire water column $(Z_m = 8$ m) over 24 hours would be $160 \cdot 8 \cdot 24 = 37.7$ g O_2 $m^{-2} d^{-2}$, or twice that of primary production.

Discussion

Most phytoplankton species are cosmopolitan, and species composition and abundance in tropical lakes do not, in principal, differ from those of temperate lakes (POLLINGHER 1990). Concerning photosynthetic activity, opinions differ on whether or not latitude trends exist (BRYLINSKY & MANN 1973; MELACK 1979; BRYLINSKY 1980; POLLINGHER & BERMAN 1991; KALFF 1991). However, due to higher photosynthetic capacity (production per time and biomass) in warm waters (HARRIS 1978), tropical lakes at low altitudes should be relatively more productive. In Lake Xolotlán, phytoplankton biomass was high in comparison to other tropical lakes, and primary production was in the upper range of what had been previously recorded (MELACK 1979; LEMOALLE et al. 1981). The water temperature was very high, but other factors in Lake Xolotlán also support enhanced photosynthetic production and a high phytoplankton biomass. Due to its shallow character, constant winds and nocturnal cooling, Lake Xolotlán is polymictic and shows no signs of vertical gradients in any of the chemical or biological parameters of this study. Circulation of the entire water column prevents algae from sinking and ensures that they are exposed to light in the photic zone from time to time. It will also reduce the effects of photoinhibition as they are rapidly circled back to the dark portion of the water column (MARRA 1978). Therefore, the proportion of photic zone to mixing depth should also be of importance for primary production (TALLING 1971), but without direct measurements of the photic zone depth we can not precisely determine that ratio for Lake Xolotlán. High nutrient concentrations in runoff and sewage waters, as well as the endhoreic character of the lake, are factors promoting nutrient accumulation and eutrophication, which additionally should support enhanced photosynthetic production and high phytoplankton biomass.

Total phosphorus and total nitrogen are often the most important indicators of the actual nutrient status of waters because inorganic nutrients can be constantly incorporated into the biomass (VINER 1973; GOLTERMAN 1973). Our data suggest that this is also the case in Lake Xolotlán. Total phosphorus and total nitrogen levels were high and coupled to phytoplankton biomass. Concentrations of inorganic nutrients were very low. Of these, the dominance of ammonium is characteristic of high organic contamination and is also indicative of a system with rapid internal regeneration of nitrogen. Extremely low levels of nitrate are a consequence of this and have often been observed in other productive tropical lakes (TALLING 1965). Low inorganic nutrient levels and their inverse relationship to phytoplankton biomass (Figs. 3, 4) also indicate rapid uptake and constant recycling of nutrients within the large algal community. Only when biomass decreased was there a shift toward nutrients in their inorganic forms. It is thus

notable that in the southern basin, where total P and algal biomass were significantly higher and where nutrient input occurred, there were lower average concentrations of inorganic nitrogen than in the central basin (Table 1). However, high temperatures speed up metabolic rates and internal recycling of nutrients. This, combined with strong mixing processes, sustained the constant availability of nutrients, as is demonstrated by consistently high production at the optimal depth (A_{max}) and the absence of any sudden break down in the algal community. In addition to high incident irradiance and temperature, constant availability of nutrients favours the development of a stable and conservative phytoplankton community and consistent photosynthetic activity. Studies of zooplankton biomass and fish diet (Mangas & Garcia 1991; Vela 1991) imply that the grazing pressure on phytoplankton was relatively low. These features of the phytoplankton of Lake Xolotlán were demonstrated by a small coefficient of variation ($<15\%$) and slow growth rate ($\approx 0.07\,d^{-1}$), a pattern previosly described by Melack (1979) as characteristic of certain shallow tropical lakes.

However, seasonal variations influenced the phytoplankton biomass in Lake Xolotlán to some extent. As in many other tropical lakes, wind velocities increased during the dry season, causing even stronger turbulence during that period. The increases in algal biomass (Fig. 4) during the dry season, could thus be attributed to lower sinking rates due to turbulence. There may also have been a concentration effect with concern to evaporation and decrease in the water volume of the endorheic basin. Furthermore, because it is advantageous for algae to be near the watersurface, there was a combined positive effect on them by both stronger turbulence and a shallower water column.

The same discussion may also be applied to the seasonality of algal species composition. As high diatom abundance is related to water column circulation and low sinking rates (Talling 1966; Lewis 1978; Margalef 1983), conditions for diatom growth would be more favourable in the dry season; diatoms did contribute most to the algal biomass peak in February and March (Fig. 6). During the rainy season, conditions would be more favourable for the blue-green algae, due to their special buoyancy regulation, giving them a competitive advantage over other phytoplankton fractions when the water column is deeper and circulation weaker; blue-green algae were more abundant from May to December (Fig. 6). Furthermore, diatoms were always more abundant in the shallow, well mixed southern basin, whilst blue-greens dominated in the central basin(Fig. 6). Accordingly, seasonal variations in circulation and depth of water column seemed to have had an influence on phytoplankton species composition.

Due to the slight seasonal variation in the equatorial incident irradiance, the role of light on photosynthesis can be generalized and expressed as a constant factor. The mathematical expression (Talling 1957) for gross photosynthetic productivity is thus simplified under tropical conditions to $\Sigma A = A_{max}/K \cdot \text{const.}$ (Talling 1965), and has also been verified in other tropical lakes (Ganf & Viner 1973; Lemoalle 1981; Robarts 1979). K is the vertical extinction coefficient, for which we have no data, but it should be inversely proportional to Z_p. Because both A_{max} and K are functions of algal density in the photic zone, both decrease in Lake Xolotlán during the rainy season and increase during the dry season (Fig. 7), thus keeping the A_{max}/K ratio stable and the integral productivity constant throughout all seasons. Therefore, underwater light penetration seemed to be an important factor in establishing the maximum limit and stabilizing primary production in Lake Xolotlán.

We estimated community respiration to be twice that of primary production, which would indicate that Lake Xolotlán is a heterotrophic system depending on allochthonous carbon. Thus, beside algal respiration, community respiration must include a large proportion of bacterial respiration. Much allochthonous organic matter enters the lake, but probably not enough ($>5\,g\,C\,m^{-2}\,d^{-1}$) to support such a high degree of heterotrophism. Therefore, community respiration was probably overestimated in this study. A reason for that might be that our measurements are limited in time and space and cannot be used to estimate the total community respiration. In Lake George, Uganda, diurnal measurements showed that respiration rates were enhanced during daytime in the photic zone and the diurnal average rate of dark respiration of the water column was much lower (Ganf 1974).

In conclusion, algal growth in Lake Xolotlán was not limited by nutrients. Instead, primary production was very high and regulated only by under water light. Phytoplankton biomass was, however, also high and the renewal rate and temporal variability of the algal community were kept low.

Acknowledgements

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Present address of the author: R. ERIKSON. Institute of Limnology. Uppsala University. Norbyvägen 20. S-75236 Uppsala.