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Limnological survey of Lake Amvrakia, western Greece

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Abstract

Limnological characteristics of lake Amvrakia, a deep warm monomictic and sulphate lake in western Greece, are presented. A set of physical and chemical variables were monitored for one year cycle (October 1988–September 1989). Phytoplankton community structure and biomass are given for the entire depth of the water column. The trophic status of the lake is compared to that of other temperate and tropical lakes.

Introduction

The province of Aetoloakarnania in western Greece is characterized by a variety of hydrobiotopes, including five natural lakes (Trichonis, Amvrakia, Lyssimachia, Ozeros and Voulkaria), three artificial lakes (Kremasta, Kastraki, Stratos), two rivers (Acheloos, Evinos) and the extensive coastal lagoon system of Messolongi-Aetoliko. Limnological characteristics of some of these sites have already been presented (Overbeck *et al.*, 1982; Overbeck & Anagnostidis, 1982; Tafas, 1991; Danielidis, 1991; Tafas & Economou-Amilli, 1991), and data on their algal flora are available (Economou-Amilli, 1979, 1982; Kristiansen, 1980, 1983; Anagnostidis *et al.*, 1985; Economou-Amilli & Spartinou, 1989a, b, 1991; Anagnostidis *et al.*, 1988a, b; Falniowski *et al.*, 1988; Danielidis, 1991; Tafas, 1991).

Amvrakia represents the only sulphate lake of Aetoloakarnania. Reference of taxonomically and phytogeographically interesting algae (Kristiansen, 1980; Anagnostidis *et al.*, 1985; Economou-Amilli & Spartinou, 1989b, 1991) initiated a recent study on its algal community structure and seasonal succession (Spartinou, 1992, diss.) with emphasis on the chlorophyte taxonomy. The present paper examines the insufficiently known physical and chemical status of this unusual lake through annual monitoring (October 1988–September 1989), and documents several aspects of its planktic microflora.

Description of the study site

Lake Amvrakia (Fig. 1) is a triangularly shaped deep lake (estimated max. depth 35 m), situated along a 40 km depression at the northwest of lake Ozeros and west of the mountain Thyamos or Petalas (long. 21 °N 09′, lat. 38 °E 45′). The figure for a maximum surface area of 13.6 km^2 (1987, Greek National Statistic Services) has been significantly reduced due to a prolonged drought and the recent draining of the northern shallow part of the basin. The drainage basin, estimated at about 112 km^2, is rather small – a feature shared with the other nearby lakes. Amvrakia is a lake of tectonic origin, karstic, of semipolje type formed from deposits of Mesozoic limestone (Verginis & Leontaris, 1978; Overbeck *et al.*, 1982). The water level undergoes yearly fluctuations attributed to the hydraulic communication with karst aquifers, evaporation during summer, and intensive use of water for agricultural purposes. A high concentration of sulphuric anions distinguishes lake Amvrakia from the adjacent lakes. It is subject to moderate pollution by runoff of tobacco fields located in the eastern and southern regions of the drainage basin; the east coast, in particular, is intensively cultivated up to only few meters away from the water edge, and serves as pasture land for sheep.

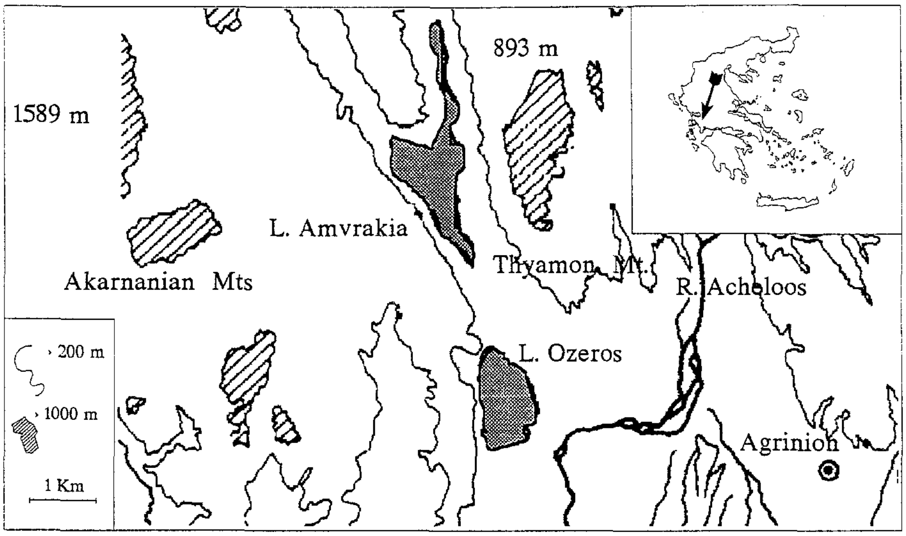


Fig. 1. Map of the lake Amvrakia area.

Materials and methods

Net plankton (mesh 45–55 μm) and also water samples were monthly collected (the latter with a 2 liter Ruttner sampler) at the deepest part of the lake from October 1988 to September 1989. Samples were taken from at least 10 different depths ranging from 0 to 30 m, depending on the lake thermal status (more sampling depths during stratification). Dissolved oxygen and temperature readings were obtained by a YSI 51B oxygen meter. Light attenuation was measured by a LI-185B quantum radiometer, conductivity by a YSI 33 SCT-meter, and pH and alkalinity with a WTW pH 39-meter. Chlorophyll-*a* was estimated after filtration *in situ* through glass-fiber filters (mesh 0.45 μm) and extraction with methanol in the dark, after Holm-Hansen & Reimann (1978). Water samples for nutrient analysis were preserved independently and analyzed according to A.P.H.A. (1980). Inorganic phosphorus was estimated photometrically after filtration through nitrate cellulose filters (mesh 0.45 μm). Ammonia (NH_3-N) measurements were made potentiometrically (ammonia electrode, Orion 95-12) (Midgley & Torrance, 1978). Quantitative analysis of phytoplankton was carried out using a Zeiss inverted microscope (Utermöhl, 1958; Lund *et al.*, 1958); biomass determination was based on the calculation of species volume using appropriate geometric formulae and assuming a specific gravity of one (Willen, 1976; Heusden, 1972; Rott, 1981).

Results

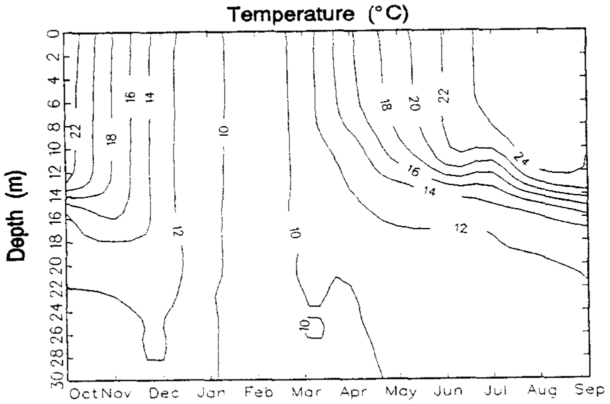
Physical variables

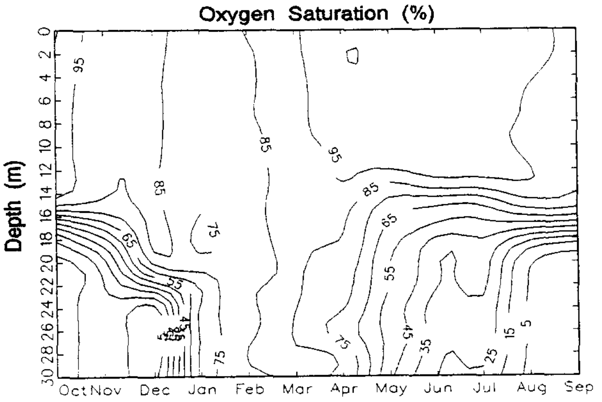
Stratification (Fig. 2) started deteriorating in late October, the thermocline being at that time between 15 and 20 m depth (*c.* 5 m wide). Turnover started in early December and lasted until the end of March, with lowest temperature in February (homothermy from surface to bottom, 9.5 °C and 9.2 °C respectively). Stratification resumed in early April, with a shallow thermocline between 8 and 12 m, followed by a stable thermocline of 6–7 m depth (between 10–*c.* 17 m) in early July (surface and bottom temperatures 25 °C and 10.5 °C, respectively). During August and September, the thermocline persisted between 10 and 20 m; thereafter, it sank to even deeper strata until turnover.

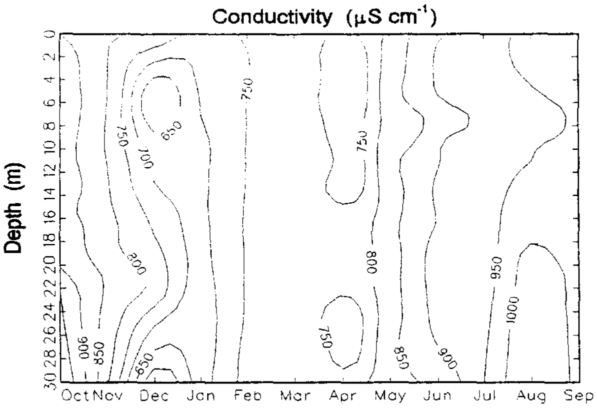
Light energy penetrating into the lake water was significant throughout the year; expressed as a percentage of surface light intensity at noon time, the 1% value was found between 12 and 20 m (mean depth 16.5 m). The white light extinction coefficient (*n*) in the euphotic zone ranged between 0.23 and 0.38 ln m^{-1}.

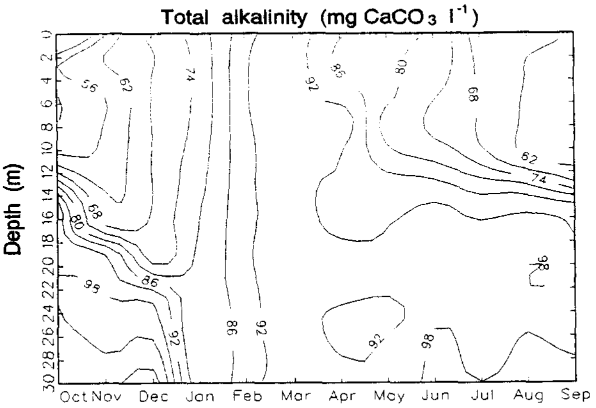
Chemical variables

Oxygen saturation values of 70 to 104% were recorded in the entire water column during turnover and in early stratification (Fig. 3). In mid May, saturation values declined to about 50% in the hypolimnion, and this lack of oxygen intensified during June and July.









Figs 2–5. Vertical profile of temperature (Fig. 2), oxygen saturation (Fig. 3), conductivity levels (Fig. 4) and total alkalinity (Fig. 5) in lake Amvrakia (October 1988–September 1989).

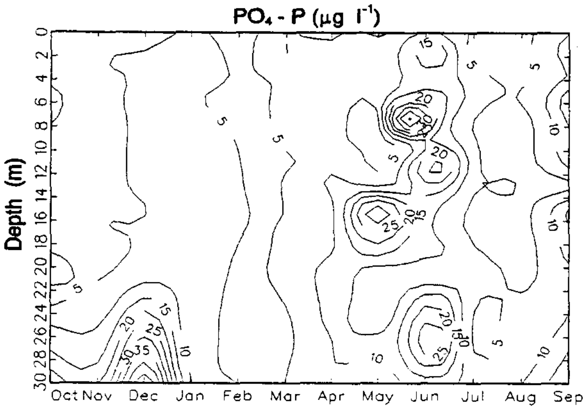
Complete anoxia occured in hypolimnion and up to the lower metalimnion by late August, whereas milder anoxia conditions were observed lateron (September and October).

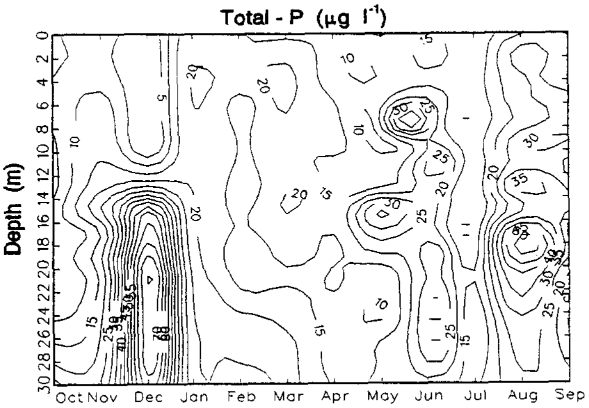
Conductivity ranged from 550 to 1060 μS cm^{-1} (Fig. 4) with higher values occuring in the warmer period of the year (June–early October). Total alkalinity and pH were markedly different and seasonally differentiated between the trophogenic and tropholytic zones during stratification. Total alkalinity – predominately bicarbonates at pH 7.8–8.3 – was reduced in epilimnion to 1/2–2/3 of the corresponding turnover value, whereas increased concentrations occurred in hypolimnion especially by the end of stratification (Fig. 5). Concurrently, similar vertical distribution was observed in total CO_2, free CO_2 and bicarbonates, the carbonates attaining an extremely minor contribution. The pH values of 7.2–7.8 recorded during turnover, were increased in the trophogenic zone and rapidly decreased with depth at the boundary of metalimnion to hypolimnion to a minimum of 7.2–7.3.

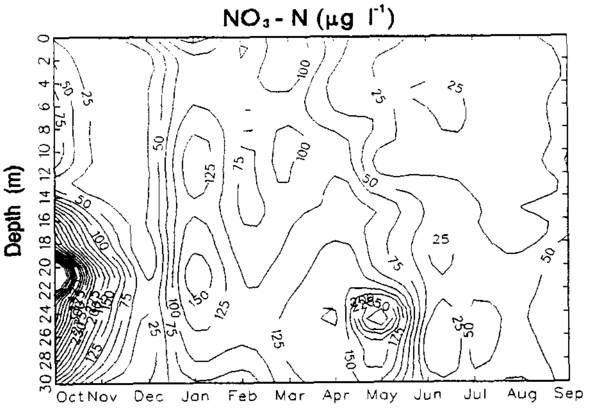
Inorganic phosphorus (PO_4-P) showed a rather uniform vertical distribution during turnover (Fig. 6) with low values in the range of 5–10 μg l^{-1}. Complete phosphorus depletion was never observed, although extremely low levels (<5 μg l^{-1}) were often recorded especially during stratification. Increased phosphorus concentrations (15–30 μg l^{-1}) occured in May and June with considerable depth variations (local maxima up to 65 μg l^{-1}). Distinct accumulation of PO_4-P in hypolimnion (25–50 μg l^{-1}) was found only at the end of stratification.

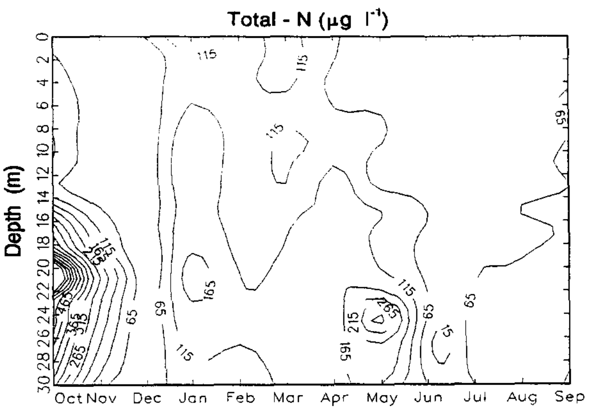
Total phosphorus content was in the range of 10–23 μg l^{-1} during turnover to a depth of *c.* 28 m (Fig. 7); in deeper strata (28–35 m) twofold values were recorded during February and March. High phosphorus concentrations were measured in metalimnion during August (*c.* 60 μg l^{-1}), whereas a strong accumulation (up to *c.* 75 μg l^{-1}) was observed in metalimnion and hypolimnion at the end of stratification. Epilimnetic total phosphorus concentrations were very low (<10 μg l^{-1}) throughout the stratification.

Nitrate nitrogen (NO_3-N) concentrations were in the range of 65–185 μg l^{-1} during turnover (Fig. 8),









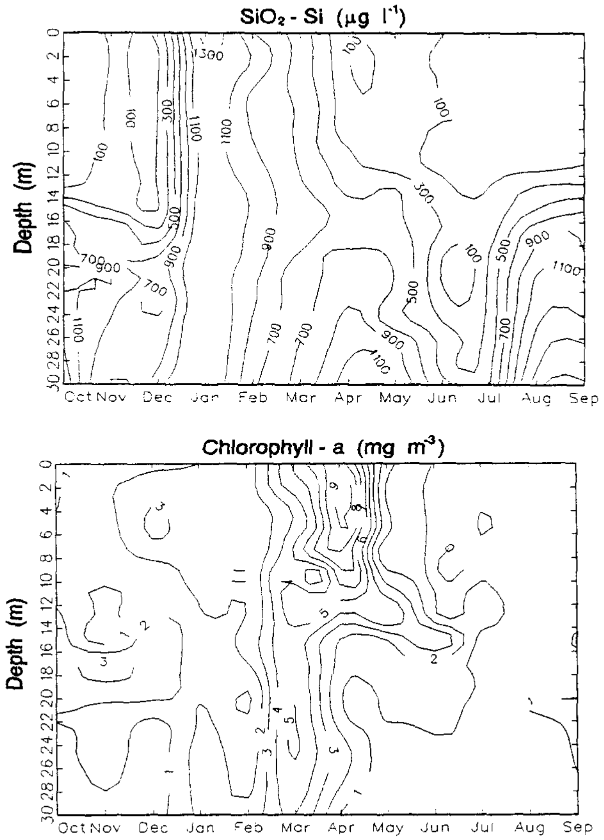
Figs 6–9. Vertical profile of inorganic phosphorus (Fig. 6), total phosphorus (Fig. 7), nitrate nitrogen (Fig. 8) and total nitrogen concentrations (Fig. 9) in lake Amvrakia (October 1988–September 1989).

but from early April till mid May they were declining rapidly in epilimnion (minimum values occasionally below the detection limit in August) and increasing up to 290 $\mu g\ l^{-1}$ in the adequately oxygenated (*c.* 6–7 mg $O_2\ l^{-1}$) hypolimnion. Nitrate nitrogen increased again in the euphotic zone in late September–early October with a maximum value (up to 630 $\mu g\ l^{-1}$) recorded in the metalimnion/hypolimnion interface (*c.* 20 m). During this period a gradual decrease of NO_3-N was notable immediately below the thermocline with a corresponding increase of NO_2-N, NH_3-N and a local maximum of organic nitrogen. These conditions seemed to persist for the next two months, gradually degrading till the end of stratification. Ammonia nitrogen (NH_3-N) content was at the lower detection level (5–7 $\mu g\ l^{-1}$) during turnover, increasing thereafter but remaining at very low levels till the last two months of stratification, when a moderate hypolimnetic accumulation was observed (30–140 $\mu g\ l^{-1}$). Also, nitrite nitrogen (NO_2-N) was never present in measurable quantities with the exception of the deep hypolimnetic layers at the end of stratification. Total nitrogen distribution (Fig. 9) followed that of nitrates. In most occasions the total N/P ratio has been extremely low (in the range of 1–9), with the only exception the month of October (N/P ratio 16–114).

Silica (SiO_2-Si) concentrations were uniformly distributed in the range of 600–1600 $\mu g\ l^{-1}$ during turnover (Fig. 10). Deterioration of this uniformity started in early April, leading to a strong accumulation of silicates (300-1760 $\mu g\ l^{-1}$) in hypolimnion and their concomitant dramatic drop (30–200 $\mu g\ l^{-1}$) in epilimnion throughout the stratification. Homogenous silica distribution in the water column attained by mid December.

Plankton community structure

Chlorophyll-*a* content (Fig. 11) reached the value of 1–3 mg m^{-3} during turnover, tending to increase (4–5 mg m^{-3}) towards the end of this period, and reaching peak values (5–9 mg m^{-3}) in the epilimnion in late March to mid April. These high values remained at deeper layers



Figs 10–11. Vertical profile of silica (Fig. 10) and chlorophyll-*a* concentrations (Fig. 11) in lake Amvrakia (October 1988–September 1989).

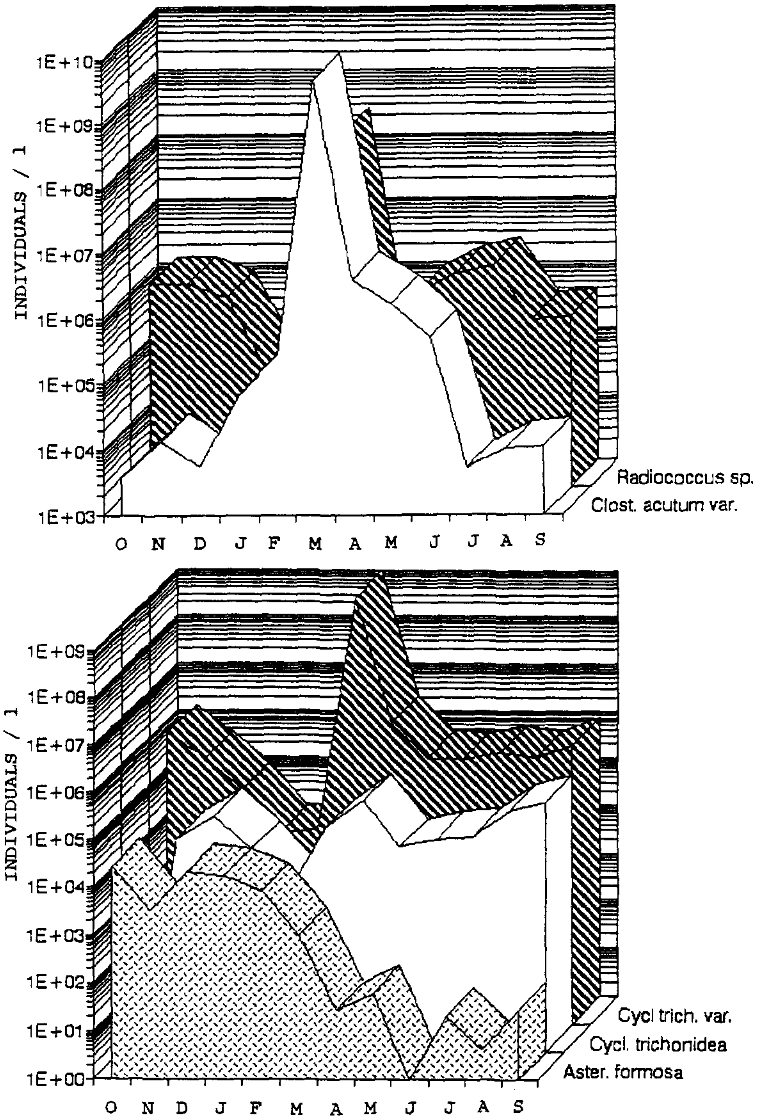
till mid May, indicating a better development of metalimnetic phytoplankton populations. During summer stratification, chlorophyll-*a* content declined considerably throughout the water column with a tendency to increase again in autumn (October to November), especially in the metalimnion.

Microalgae from 7 different algal groups (Cyanophyta, Chlorophyta, Bacillariophyta, Dinophyta, Cryptophyta, Prymnesiophyta, Chrysophyta) were identified in the studied phytoplankton. Chlorophyta and Cyanophyta were prevailing in terms of quantity of taxa; they were also the dominant groups in the euphotic zone in terms of species abundance (*c.* 12–81% and up to 55% respectively, whereas for Dinophyta <1%) (Fig. 14). In terms of biomass however, the leading position was kept by Chlorophyta (13–92%, autumn-spring), whereas the Dinophyta reached almost 50% of the total biomass during summer stratification (Fig. 15).

Phytoplankton development showed a peak in both abundance of individuals and biomass towards the end of turnover, i.e in early March; biomass pattern showed a distinctly lower second peak in mid summer (Figs 16–17). The spring phytoplankton bloom was composed mainly of species of Chlorophyta, Bacillariophyta and Cryptophyta [*Closterium acutum* var. *variabile* (Lemmermann) W. Krieger, *Radiococcus* sp., *Cyclotella trichonidea* var. *parva* Economou-Amilli, *Chroomonas acuta* Utermöhl]. The summer biomass peak is ascribed primarily to the abundance of cell-sized Dinophyta [i.e. *Ceratium furcoides* (Levander)Langhans (?), *Ceratium hirundinella* (O. F. Müller)Schrank, *Peridinium inconspicuum* Lemmermann, *Peridinium* sp.]. During the same period, there were observed large populations of both Chlorophyta [*Radiococcus* sp., *Elakatothrix genevensis* (Reverdin) Hindak, *Planktosphaeria gelatinosa* G. M. Smith] and Cyanophyta [*Epigloeosphaera* cf. *glebulenta* (Zalessky) Komarkova-Legnerova, *Radiocystis geminata* Skuja forma, *Cyanodictyon imperfectum* Cronberg et Weibull, *Radiocystis geminata* Skuja, *Cyanodictyon reticulatum* Lemmermann Geitler]. Each of the aforementioned taxa of the spring and summer phytoplankton blooms, as well as several others [i.e. *Planktolyngbya subtilis* W. West Anagnostidis et Komarek, *Snowella atomus* Komarek et Hindak, *Asterionella formosa* Hassal, *Oocystella parva* (W. et G. S. West) Hindak, *Oocystella submarina* var. *variabilis*, Skuja, *Ankistrodesmus bernardii* Komarek, *Dictyosphaerium subsolitarium* Van Goor, *Chrysochromulina parva* Lackey] were represented in the entire water column with a contribution of over 1% of the total species abundance.

The seasonal periodicity of the main algal groups and of the dominant algal species was as follows:

- Chlorophyta – after their vernal peak – showed stable populations being at the lower level of development during stratification. The two dominant species of the vernal peak showed lateron contradictory modes of annual distribution, with *C. acutum* var. *variabile* and *Radiococcus* sp. populations developing better during the periods of turnover and stratification respectively (Fig. 12). The group of Chlorophyta was generally richly represented in species abundance but with very few dominant species.
- Cyanophyta showed optimal development during stratification, decreasing thereafter during turnover. The coccoid genus *Cyanodictyon* dominated the summer phytoplankton populations, with only *C. imperfectum* exhibiting mass development by end of the hot season. The taxonomically inter-



Figs 12–13. Annual variation in the abundance of the chlorophytes *Closterium acutum* var. *variabile* and *Radiococcus* sp. (Fig. 12) and in the abundance of the diatoms *Cyclotella trichonidea*, *C. trichonidea* var. *parva* and *Asterionella formosa* (Fig. 13) in lake Amvrakia (October 1988–September 1989).

esting species *Aphanizomenon flos-aquae* Ralfs ex Bornet et Flahault (?) represented the only nitrogen fixing species, mainly observed during stratification.

- Bacillariophyta (diatoms) showed a vernal maximum development, mainly ascribed to the endemic nannoplanktic *Cyclotella trichonidea* var. *parva*; the coexisting nominate variety (*C. trichonidea* Economou-Amilli) seemed to prefer the turnover period showing considerable smaller populations with three annual maxima (Fig. 13). Another important element of the diatom composition (*Asterionella formosa*) seems to better develop during stratification in lake Amvrakia.

- Dinophyta (dinoflagellates), although never dominant in terms of species abundance, contributed considerably to the lake's phytoplankton biomass showing maximum development at the peak of stratification (with *Ceratium* and *Peridinium* species responsible for the summer peak, and with *Gymnodinium* species forming the weaker winter development).

The zooplankton composition of lake Amvrakia consisted of Cladocera (*Bosmina longirostris, Ceriodaphnia pulchella, Daphnia cucullata, Diaphanosoma* cf. *brachyurum*), Copepoda (*Eudiaptomus drieschii, Macrocyclops albidus, Thermocyclops dybowski*) and Rotatoria (*Asplanchna priodonta, Brachionus sessilis, Collotheca polyphema, Euchlanis* sp., *Filinia longiseta, Gastropus stylifer, Hexarthra mira, Polyarthra vulgaris, Ptygura seminatans, Trichocerca similis*). Two of the Rotatoria (i.e. *Collotheca polyphema* and *Ptygura seminatans*) were very rare. Besides, a small planktonic bivalve, presumably a *Corbicula*-species, was found in large numbers.

Discussion

With regard to the thermal pattern, Amvrakia is classified as a warm monomictic lake with stratification lasting from early April till late November. The generally short turnover can be considerably delayed by the mild winters prevalent in this region during the last decade. Stratification is evidently quite stable resulting from a deep-lying thermocline with a relatively steep and constant thermal gradient (1.3–1.6 °C m^{-1} in June to September 1989; 1.6 °C m^{-1} in September 1981; Overbeck *et al.*, 1982). The thermocline extends from 10–20 m during its maximum development (July to September), whereas the euphotic zone ranges from 12 to 20 m depth all year round.

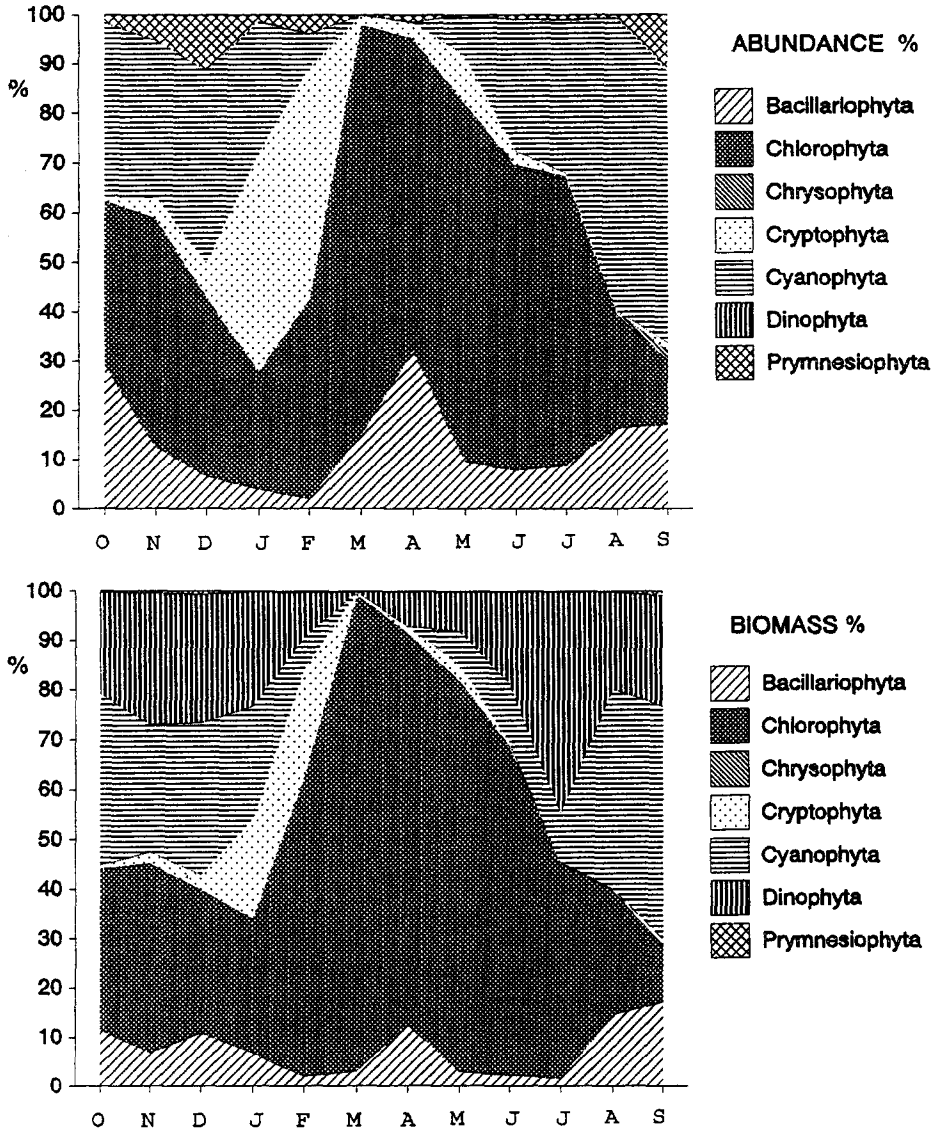
During turnover no oxygen depletion was observed, whereas at the end of the prolonged summer stratification, a sharp decline of oxygen was detected starting at the thermocline and extending to the anoxic hypolimnion. Anoxia was always accompanied by the presence of hydrogen sulphide (H_2S) – due to decomposition activities but also to the nature of the rocks surrounding the karstic lake basin – which although not measured analytically, should have been in considerable amounts judging by its characteristic smell in the hypolimnetic samples (Overbeck *et al.*, 1982).

The greater turbidity compared to previous measurements (0.23–0.38 ln units m^{-1} *vs* October 1979: 0.15 ln units m^{-1}, Overbeck *et al.*, 1982) might be related to increased suspended particles rather than to higher algal growth. Increased surface water turbidity in lake Amvrakia has been resulted from artificial drainage of the northeastern part into the main water body (Fig. 1), i.e. at a direction coinciding with the known (NE-SW) movements of the lake water (Verginis & Leontaris, 1978). Local maxima of (*n*) at specific depths, observed during the period of March to September, seem to correlate with increased chlorophyll-*a* content of the lake water.

High conductivity values resulted from the increased concentrations of calcium and sulphate ions (summer values at 1 m depth: $Ca^{2+} = 140$ mg l^{-1}, $SO_4^{2-} = 578$ mg l^{-1}; Overbeck *et al.*, 1982), apparently due to the presence of gypsum and breccia in the black limestones of the surrounding karstic environment (Verginis & Leontaris, 1978). This type of very hard water lakes have been shown to undergo intense decalcification in epilimnion during stratification related to the $CaCO_3$ precipitation in the pelagic and littoral zones. As described for other hard water lakes (e.g. lake Lawrence, Otsuki & Wetzel, 1974) the epilimnetic decalcification is biogenically induced due to the increased vernal and summer rate of photosynthesis in the euphotic zone. Moreover, the rising water temperature itself accelerates both the metabolic rates and the $CaCO_3$ precipitation in epilimnion (Wetzel, 1983). The expected conductivity decrease in epilimnion was hard to perceive in the case of Amvrakia. On the contrary, higher values were recorded as a result of the increased concentration in dissolved substances due both to the intense evaporation and to the land wash by irrigation drainage waters rich in residual fertilisers (Overbeck *et al.*, 1982).

The aforementioned decalcification – as verified through total alkalinity measurements – is accompanied by a fall of inorganic carbon values in the epilimnion and a rise in the hypolimnion. Furthermore, this type of hard water lakes actually lose available amounts of CO_2 to the atmosphere. The approximate partial pressure of CO_2 in the pelagic zone of lake Amvrakia – as calculated by the temperature, pH and ΣCO_2 concentrations (Park *et al.*, 1970; Otsuki & Wetzel, 1974) – is constantly 2–3 times higher than that of the overlying atmosphere even during spring and summer stratification, i.e at a time of maximum photosynthetic utilization of CO_2 in the trophogenic zone and enhanced $CaCO_3$ precipitation. Under the reducing conditions prevailing in the anoxic hypolimnion during stratification, a considerable contribution of HCO_3^- as well as a relative conductivity increase are expected due to dissolution of $CaCO_3$ (Golderman, 1975; Wetzel, 1983).

Increase of total alkalinity, already observed in metalimnion but more apparent in hypolimnion, could be attributed to the respiratory generation of CO_2 in the moderately oxygenated thermocline, to the degradation of organic matter and to other processes such as

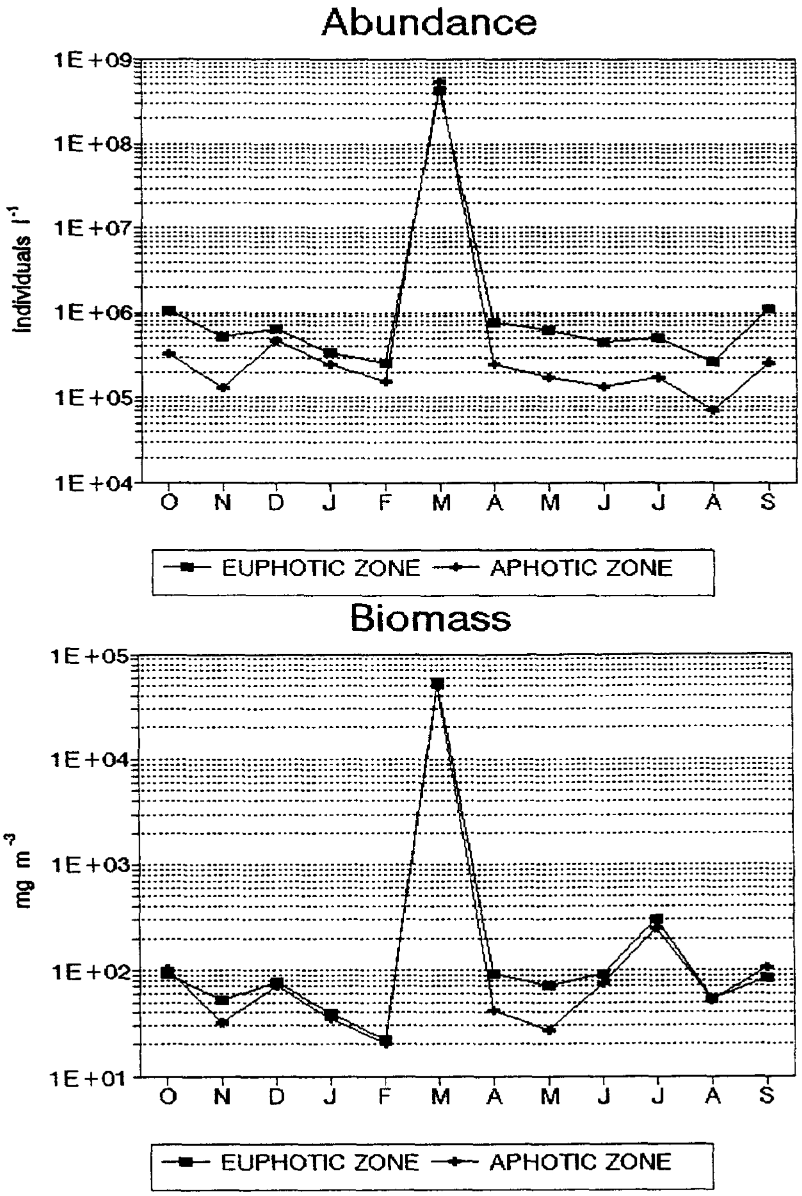


Figs 14–15. Annual variation of phytoplankton in the euphotic zone (abundance of algal groups: Fig. 14; biomass of algal groups: Fig. 15) of lake Amvrakia (October 1988–September 1989).

nitrification of ammonia and sulphide oxidation (Otsuki & Wetzel, 1974).

The relatively low nutrient levels are subjected to seasonal fluctuations affected by the lake thermal cycle and the structural shifts in the phytoplankton species composition. With regard to absolute total nitrogen and phosphorus values, Amvrakia is classified as oligotrophic to mesotrophic lake (Vollenweider, 1968; USEPA, 1974). The low (<10) epilimnetic total N:P ratio is suggesting a nitrogen limitation in the lake for most of the year cycle (Sakamoto, 1966; Chiadani & Vighi, 1974). The exceptional higher epilimnetic ratios of N:P (15–45) at certain periods (October, November to December) are the only indications of phosphorus limitation. Higher values of phosphorus in hypolimnion by the end of stratification may result from accumulation of phosphorus ions by sinking or sediment release (Hutchinson, 1957; Wetzel, 1983).

Nitrates (NO_3-N) represent the only nitrogen compound found in considerable concentrations all over the year cycle. Although low N:P ratios in the range of 5:1 are known to favour the development of nitrogen fixing cyanophytes (Schindler, 1977), the presence



Figs 16–17. Annual variation of phytoplankton in the entire water column (total abundance: Fig. 16; total biomass: Fig. 17) of lake Amvrakia (October 1988–September 1989).

of nitrates – which inhibit heterocyst formation (Fay *et al.*, 1968) and decrease nitrogenase activity (Bone, 1971) – may explain the limited growth of nitrogen fixing cyanophytes. Only one nitrogen fixing species is present [i.e. *Aphanizomenon flos-aquae* (?)] mainly during stratification, despite the great participation of other (coccoid) cyanophytes (mostly *Cyanodictyon imperfectum*).

Accumulation of nitrates in the boundary of metalimnion to hypolimnion is probably the result of intense bacterial nitrification in the upper, moderately oxygenated, metalimnetic layers and of diffusion of NO_3-N to the hypolimnion (Hutchinson, 1957); whereas the recorded values of the other nitrogen compounds (gradual decrease of NO_3-N with a corresponding increase of NO_2-N, NH_3-N and with a local maximum of organic nitrogen) might be attributed to the heterotrophic denitrification in the upper layers of the anoxic hypolimnion (Hutchinson, 1957; Stadelmann, 1971; Chan & Campbell, 1978). Besides, participation of denitrifying sulphur bacteria can not be excluded in the hypolimnion (Kuznetsov, 1970). Bacterial activity and detailed study of the nitrogen cycling are interesting topics for further analysis in lake Amvrakia.

According to the general pattern of phytoplankton composition and particularly the restricted presence of Chrysophyta, Amvrakia is reminiscent of medium sized lakes in the low altitude of the tropical zone (Pollingher & Berman, 1991) which might indicate tendencies of eutrophication (Cronberg, 1982). This type of composition pattern – with the groups of Chlorophyta, Cyanophyta and Bacillariophyta being abundant in terms of number of taxa and density of individuals – resembles more that of eutrophic tropical and subtropical lakes than that of eutrophic lakes of the temperate zone (Lewis & Riehl, 1982). Abundance of Chlorophyta is another element of resemblance with tropical lakes (Lewis, 1978); besides species of the genera *Pediastrum* and *Scenedesmus*, which are known to have intense growth in eutrophic lakes of the temperate zone (Round, 1981), exibit rather sporadic appearance in the phytoplankton composition of lake Amvrakia. On the contrary, Dinophyta constituting an important element of the lake's phytoplankton biomass, and being present sometimes in mass development in the neighbouring lake Trichonis (Tafas, 1991) and in lake Kinneret (Pollingher, 1978), were observed in the tropical zone in restricted numbers (Serruya & Pollingher, 1983). Maximum development of Dinophyta at the peak of stratification – which is the most common environment for their development (Sommer *et al.*, 1986) – might be attributed to their capability to remain in the euphotic zone (Rodhe, 1948), to grazing deficiency due to their large size (Pollingher, 1978), and to the capacity of 'luxury consumption' and subsequent storage of phosphorus at a time of phosphorus depletion in stratified lakes (Pollingher, 1987a; Serruya & Berman, 1975).

Vernal diatom peak characterizes the phytoplankton composition of most european lakes, and seems to follow the consumption of the available SiO_2 pool during the period of May to June (see also Fogg, 1965; Round, 1981; Reynolds, 1984). This is especially exemplified in the endemic small sized variety *C. trichonidea* var. *parva* (Economou-Amilli, 1979) which seems to be favoured by the raising vernal temperature and increased depth of the euphotic zone, being competitive towards other species of phytoplankton at depths of reduced nutrients; the coexisting larger nominate variety of the species (*C. trichonidea*) seems to prefer the turnover period where the heavily silicified frustules may be better suspended in the euphotic zone. Better development of *Asterionella formosa* during turnover, in contrast to what is known from other European lakes where spring and summer blooms are reported (Lin, 1972; Reynolds, 1973; Round, 1981; Rott, 1985; Dokulil, 1987), is rather justified since reduced development for this species has been reported at phosphate concentrations over 10 $\mu g\ l^{-1}$ (Rodhe, 1948); thus, vernal decrease of its population in lake Amvrakia correlates with the corresponding increase of phosphate concentrations (max. 10–30 $\mu g\ l^{-1}$ in May to June). Free CO_2 concentration seems to be another factor controlling *A. formosa* populations (Jaworski *et al.*, 1981) and the reduced CO_2 concentrations in March can be considered cause of the small population development since there existed significant amounts of SiO_2 (*c.* 700 mg l^{-1}) and the phosphates were less than 10 mg l^{-1}.

Cyanophyte increase during stratification represents a pattern known from other lakes around the world (Fogg, 1966; Lin, 1972; Pollingher, 1987b). Especially interesting is the recently acknowledged contribution to phytoplankton populations of the coccoid cyanophyte species of *Cyanodictyon* (Economou-Amilli & Spartinou, 1991). Maximal development of the nitrogen fixing *Aphanizomenon flos-aquae* (?) by end of summer coincides with minimal inorganic nitrogen concentrations, being in agreement with other findings for the type species (Horne *et al.*, 1972); the extremely low phosphate concentrations (*c.* 5 $\mu g\ l^{-1}$) of that period favour the species development under mesotrophic conditions (Uehlinger, 1983).

Biomass pattern (with a higher peak by the end of turnover and a lower peak in the middle of summer) can be considered intermediary between the monoacmic and the clearly diacmic mode of biomass development, which characterize the oligotrophic and mesotrophic lakes of Central Europe respectively (Rott, 1984). According to the generalized phytoplankton sequences (Reynolds, 1984; Rott, 1984), dominance of Bacillariophyta and Cryptophyta during the vernal phytoplankton peak and of Dinophyta, Chlorophyta and Cyanophyta during the summer peak, are typical of mesotrophic lakes of the temperate zone; whereas increase in Chrysophyta and decrease in coccoid Chlorophyta and Cyanophyta are observed in eutropic lakes after restoration (Cronberg, 1982). Hence, Amvrakia might be classified as an oligotrophic to mesotrophic lake. Moreover, the same lake characterization is attained through the chlorophyll-*a* values, always recorded below 10 $\mu g\ l^{-1}$ (NAS, NAE 1972; Chapra & Tarapchak, 1976). It is noted that phytoplankton structure in lake Ambrakia deviates from that reported for other Greek lakes, e.g. the eutrophic lakes Volvi and Vegoritis with triacmic mode of biomass development (Moustaka-Gouni, 1988; Moustaka-Gouni & Tsekos, 1989; Moustaka-Gouni & Nikolaidis, 1990) or the oligotrophic lake Trichonis with monoacmic mode of biomass development (Tafas, 1991).

Phytoplankton total abundance and total biomass were uniform from surface to maximum depth during overturn, showing similar patterns in the euphotic and aphotic zones during stratification, but with lower values in the aphotic zone. The existing light regime of lake Amvrakia allows for sufficient photosynthetic activity even in the deep water layers (euphotic zone till 20 m). Other factors accounting for sustained viability of phytoplankton in the aphotic zone of ultraoligotrophic lakes include: low sinking velocities of small phytoplankton species and slow decomposition rates in the aphotic zone (Tilzer *et al.*, 1977), decreased grazing pressure and increased nutrient availability in the hypolimnion (Wasmund, 1989) or heterotrophic mode of nutrition (Vincent, 1980).

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