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SPATIAL AND TEMPORAL DISTRIBUTION OF PHYTOPLANKTON IN LAKE SKADAR

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Abstract - Phytoplankton seasonal succession and spatial heterogeneity were studied in Lake Skadar from February to December 2004. A total of 167 taxa from 6 algal divisions were observed, with Bacillariophyta being best represented (52.8%). The general pattern of phytoplankton seasonal succession in Lake Skadar was: Bacillariophyta in the spring, Chlorophyta in early summer, Cyanobacteria and Chlorophyta in late summer and Bacillariophyta and Chlorophyta in autumn and winter. Distinct spatial heterogeneity was observed. The central, open part of the lake (pelagic zone) was characterized by dominant euplanktonic species, mostly diatoms, whereas the western and northwestern parts (more isolated and shallower) had higher abundance of greens and blue-greens and a higher percentage of resuspended benthic-epiphytic forms in the phytoplankton community. Comparison with former phytoplankton data showed distinct differences in terms of the qualitative and quantitative composition of the phytoplankton community of Lake Skadar, which indicates lake deterioration.

Key words: Phytoplankton, algae, Lake Skadar, Montenegro

INTRODUCTION

Among the most relevant aspects of phytoplankton studies are those related to community abundance and diversity, and spatial and temporal distribution, as well as those referring to the ecological factors directly related to the determination of primary productivity levels of such communities (Padisak, 2004).

In temperate regions, seasonal successions of organisms belonging to different phytoplankton taxa are often observed. The annual phytoplankton development of lakes is driven mainly by a seasonal change of indirect allogenic and direct autogenic forces, often following a predictable organism succession as described, for example, in the PEG model (Sommer et al., 1986).

The mechanisms explaining the species dominance patterns in lakes during the vegetation period vary greatly and sometimes even show discrepancies. This is especially the case in shallow lakes, which are more responsive to changes in weather conditions. These lakes are typically polymictic, as strong winds can mix the whole water column and prevent the water body from stable seasonal stratification (Wiedner et al., 2002). In very shallow lakes, benthic vegetation (submerged plants) can develop all over the lake and interact with phytoplankton by shading, reducing nutrients and resuspension, and enhancing grazing (Scheffer, 1998). Additionally, a fundamental property of plankton populations is their spatial heterogeneity, especially in shallow lakes with high surface area. Phytoplankton patchiness can result from spatial variations of biological processes such as growth, grazing, regulated buoyancy and vertical migration (Reynolds, 2006) or from advective transports (Wiedner et al., 2002; Stocker and Imberger, 2003; Hillmer and Imberger, 2007; Blukacz et al., 2009), and it is disrupted by irregular or continuous mixing. There is general agreement that the predominant drivers of spatial heterogeneity in phytoplankton distributions are physical (e.g., wind-driven currents) (Martin, 2003; Monino-Fernando et al., 2006).

The present study reports the results of a one-year investigation of the phytoplankton community of Lake Skadar. This paper is the result of the first comprehensive phytoplankton investigation conducted in Lake Skadar after a gap of almost 30 years. The aim of this study was to determine current spatial and temporal variations in phytoplankton composition and abundance in Lake Skadar and to compare present results with those of 30 years ago.

MATERIALS AND METHODS

Lake Skadar is located on the border between Montenegro and Albania at latitude 40° 10' N, longitude 19° 15' E. The lake, which is located in karst terrain on the outer part of the southeastern Dinaric Alps, is the largest of the Balkan lakes and has a surface area that fluctuates seasonally from approximately 370 to 600 km^2. The lake's water level also varies seasonally from 4.7 m (summer) to 9.8 m (winter) above sea level. The mean depth of the lake is 5 m and the total volume is 1890x10^6 m^3. The direct drainage basin of Lake Skadar is 5490 km^2, of which 4460 km^2 are in Montenegro and 1030 km^2 are in Albania. The largest inflow is the Morača River (Montenegro), which provides more than 62% of the lake water. Lake Skadar's outlet river is the Bojana River, which converges with the River Drin just a few hundred meters downstream of the outlet. The Drin has a total drainage area of about 14,000 km^2, which is almost three times larger than the catchment of Lake Skadar. It is therefore not surprising that during high water discharges the Drin system impedes the outflow from the lake. Lake Skadar is a subtropical water body lying in an area that has an extremely high evaporation rate. The large amount of precipitation, limited mostly to winter months, coupled with high summer temperatures contributes to chemical weathering and the development of the karst landscape in the area. Mountains rise steeply from the southwestern shores of the lake, while its northern and northeastern shores are flat, thus providing an extensive semi-littoral zone with dense macrophyte cover. Frequent winds and shallow depths do not permit the formation of permanent thermal stratification. The lake is regarded as mesotrophic with a tendency to become eutrophic in the summer months. Lake Skadar has pronounced water-level fluctuations (high levels during winter and low during summer), which has resulted in a large wetland area sustaining rare and endangered bird species. The Montenegrin part of the lake and its surrounding area were declared a national park in 1983. In 1996, Lake Skadar was included in the Ramsar list of wetlands of international importance by the Ramsar Convention on Wetlands.

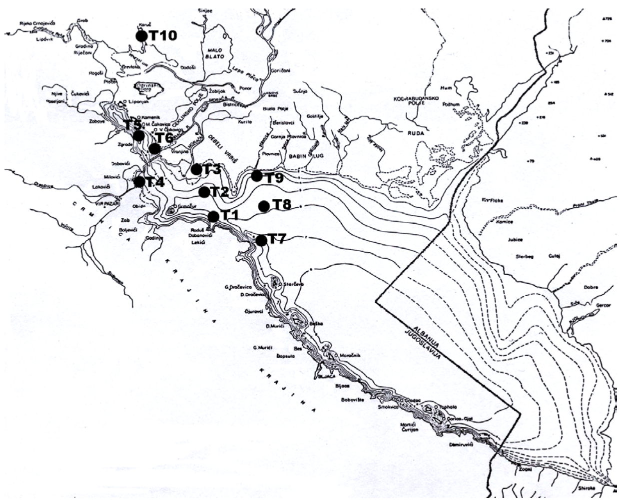

Fig. 1. Map of Skadar Lake with marked sampling stations (T$_1$ – sublacustrine spring Radus, T$_2$ - middle of the first transect, T$_3$ - left mouth of Moraca river, T$_4$ - Virpazar, T$_5$ - Vucko blato, T$_6$ - right mouth of Moraca river, T$_7$ - Petrova ponta, T$_8$ - middle of the second transect, T$_9$ – mouth of Plavnica, T$_{10}$ – sublacustrine spring Karuc)

Ten stations on the Montenegrin part of Lake Skadar (covering the central, open part of the lake and the western and northwestern part, Fig. 1) were sampled monthly from February to December 2004. Six out of ten investigated stations were the same ones sampled in the last phytoplankton investigation (ap-

Tab. 1. Measured physical and chemical parameters in Skadar Lake – monthly average values and range (February-December 2004)

	T (°C)	Secchi (m)	ph	Oxygen (mg/l)	TP (μg/l)	TN (μg/l)	Conduct. (μS/cm)
II	8.1 (4.2-8.6)	2.5 (1.9-3)	7.9 (7.2-8)	9.6 (9-11)	6.5 (6-7.2)	150 (150-170)	258 (179-333)
III	13.8 (11.6-15.3)	2.7 (2-3.5)	8.3 (7.9-8.6)	11.7 (10.4-13)	6.2 (6-7)	160 (150-210)	248 (238-285)
IV	15.5 (14-16.5)	2.3 (2-3.1)	8.2 (7.8-8.2)	11 (10-12)	10 (6-20)	170 (150-200)	250 (206-310)
V	24 (22-25.6)	2.4 (1-2.8)	8.2 (7.6-8.4)	9.3 (7.3-10)	12.5 (8-30)	330 (260-380)	249 (210-365)
VI	28.7 (24.9-29.9)	1.7 (1-2.2)	8.1 (7.7-8.4)	9.3 (7.6-11.9)	26.1 (10-50)	660 (360-990)	260 (199-378)
VII	28.5 (25.2-30.1)	1.3 (0.8-2)	8.2 (7.8-8.4)	8.8 (5.8-11)	25.2 (12-41)	620 (250-970)	251 (199-404)
VIII	28.6 (25.4-31.2)	1.2 (0.6-1.9)	8.3 (7.6-8.9)	8.7 (5.7-11.7)	19.4 (10-35)	480 (170-810)	238 (191-415)
IX	20.4 (17.8-21.9)	2 (1.2-2.6)	8.1 (7.8-8.3)	8.2 (7-9.1)	14.2 (8-24)	360 (160-700)	257 (207-371)
X	13.5 (12-14.8)	2.3 (1.3-2.6)	8 (7.6-8.4)	9.8 (8.5-11.4)	10.2 (8-18)	180 (160-330)	263 (197-310)
XI	11.2 (9.9-12.3)	2.5 (1.8-3)	8 (7.7-8.3)	10.3 (8.6-11.5)	6.2 (6-8)	280 (200-400)	288 (254-366)
XII	6.5 (4.4-8.8)	2.8 (2-3.5)	8.4 (8-8.7)	11.1 (10-11.6)	6.1 (6-7)	160 (150-180)	298 (255-303)

proximately 30 years ago; Petković, 1981), chosen in order to compare present and former results. Samples were collected from 0.2, 1, 2 and 3 m depths. Water temperature, pH, dissolved oxygen concentrations and conductivity were measured *in situ* with a Multi 340i water quality monitoring system. Water transparencies were measured with a Secchi disk. Water samples were collected using a Ruttner hydrobiological bottle and transported to the laboratory for the counting of phytoplankton and measurement of total phosphorus (molybdate blue procedure) and total nitrogen (indophenol blue absorption spectrometry). Phytoplankton abundance was determined using the sedimentation method (Utermöhl, 1958) and expressed as cells/l. Samples for determining the qualitative composition of algae were collected with a 28 μm-mesh, with a Wisconsin plankton net drawn from the bottom to the top of the water column and fixed with formalin. Data comparison and the influence of environmental factors on the phytoplankton were evaluated by stepwise multiple regression using software STATSOFT 7 (2004).

RESULTS

Physical and chemical variables

Physico-chemical variables changed with the season; monthly minimum, maximum and mean values of measured environmental factors are given in Table 1.

The water temperature of Lake Skadar ranged from 4.2°C in February to 31.2°C in August. The very small vertical differences in temperature (ranging from 0 to 1.5°C) can be explained by the lake's shallowness and consequent absence of thermal stratification (frequent and complete mixing events). Horizontal differences were observed only at the mouths of the rivers Morača (T_3 and T_6) and Plavnica (T_9), due to the cold-water inflow from these rivers.

Secchi depth ranged from 0.8 to 3.5 m, with higher values observed in winter (2.7 m) than in summer (1.7 m). At localities Karuc (T_{10}) and pelagic station T_8 the transparency was greater in comparison with the other investigated localities (summer average: 2.5 and 2.2 m, respectively). The lowest transparency during summer characterized the locality Vučko blato (T_5): 1.5 m. Previous investigations of Lake Skadar (Petrović, 1981) documented a higher average transparency during the summer months (2.5 m).

Dissolved oxygen concentrations ranged from 5.7 to 13 mg/l with an average of 11 mg/l in winter and 8.8 mg/l in summer. The lowest oxygen concentrations characterized localities T_9 (Plavnica) and T_4 (Virpazar) during the entire investigated period.

The mean seasonal surface pH value ranged from 7.2 in winter to 8.9 in summer. Localities T_9, T_{10} and T_4 had lower pH values in comparison with other parts of the lake (pH < 8 during entire investigated period).

Mean surface conductivity values ranged seasonally from 260 µS/cm in summer to 330 µS/cm in winter. Localities T_4 (Virpazar), T_6 (right mouth of the Moraca) and T_9 (mouth of the Plavnica) had the highest conductivity values, which is probably the consequence of riverine influence and waste waters from surrounding villages.

The mean total phosphorus (TP) concentrations of surface samples ranged from 6.1 to 50 µg/l. Seasonal concentrations ranged from an average of 6.2 µg/l in winter to 23 µg/l in summer, and are not only a consequence of inputs coming from inflows: low winter concentrations of total phosphorus in comparison with the summer months are usual for Lake Skadar and are due to a higher number of falls and water discharges from the Morača River (a high water level during winter creates a dilution effect). Higher TP concentrations during the summer are also derived from factors such as the release of TP from the lakebed sediments, resuspension of sediments due to wave action or input from near-shore areas. Higher summer TP concentrations were recorded at the following stations: Virpazar (T_4: 30 µg/l), mouth of the Morača (T_6: 23 µg/l), mouth of the Plavnica (T_9: 22 µg/l) and Vučko blato (T_5: 21 µg/l). On the other hand, stations T_2 and T_8 (pelagic stations) had lower TP concentrations (summer average: 13 µg/l) and the lowest TP concentration characterized station T_{10}, near the sublacustrine spring Karuč (TP <10 µg/l during the entire investigated year). Former investigations (Petrović, 1981) recorded similar TP values in Lake Skadar (4–40 µg/l), also with the highest concentration at the mouth of the Morača River.

Mean total nitrogen (TN) concentrations of samples ranged from 150 to 990 µg/l, with seasonal concentrations ranging from an average of 160 µg/l in winter to 590 µg/l in summer. The locality Virpazar (T_4) had the highest TN concentration (summer average: 560 µg/l), followed by localities T_1 (500 µg/l), T_5 (460 µg/l) and T_9 (400 µg/l). Similar to TP, the lowest TN concentration characterized locality Karuč (summer average 0.15 µg/l) and pelagic stations T_8 and T_2 (summer average: 0.25 and 0.30 µg/l, respectively). Former investigations (Petrović, 1981) recorded lower TN values in Lake Skadar (year average 200 µg/l), which is half of the present TN concentration (400 µg/l).

Generally, lakes are phosphorus-limited in the case of TN/TP>15, nitrogen limited in the case of TN/TP<7; f the TN/TP ratio is between 7 and 15, any of them – phosphorus, nitrogen or both – could be limiting factors (OECD, 1982). The TN/TP ratio in Lake Skadar was 22–26 during the dry period, but considering a whole year of investigation (all seasons) it was 33, which indicates that phosphorus is a limiting nutrient in Lake Skadar. Considering previous investigations in Lake Skadar, the TN/TP ratio was much lower (6). Continuous utilization of fertilizers in the agricultural area of Lake Skadar basin during the last 30 years is probably the main reason for this shift in TN/TP ratio.

Phytoplankton

The phytoplankton species composition of Lake Skadar revealed the presence of 167 taxa, with Bacillariophyta being best represented (87 species, 52.8%), followed by Chlorophyta (49 species, 29.7%). Cyanobacteria were moderately represented (20 species, 12.1%). Less well represented were Dinophyta (2.4%),

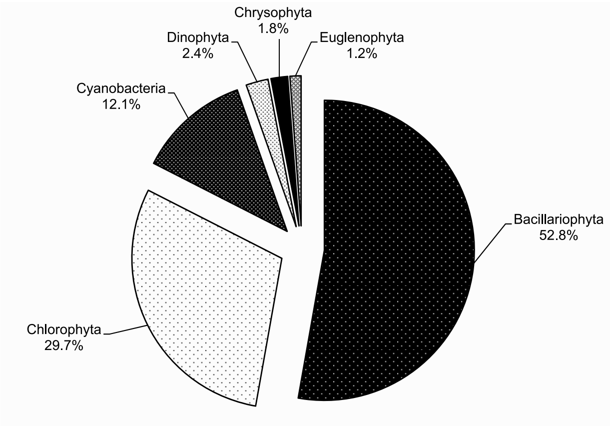

Fig. 2. Percentage of algal divisions in phytoplankton community of Skadar Lake

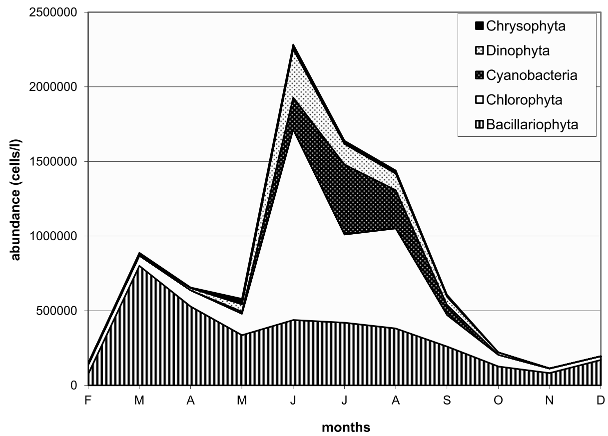

Fig. 3. Seasonal succession of main phytoplankton groups in Skadar Lake during investigated period (monthly averages)

Chrysophyta (1.8%) and Euglenophyta (1.2%), as shown in Fig. 2. Earlier investigations of phytoplankton in Lake Skadar (Petković, 1981) reported a higher percentage of greens in the phytoplankton community (>50%) because of the distinctly higher number of taxa from the order Desmidiales (29%).

The phytoplankton community of Lake Skadar may be discussed generally in terms of pelagic populations (centric diatoms and greens, mostly Chlorococcales) and benthic-epiphytic populations (which contain a lot of taxa that are resuspended from benthic and epiphytic communities, mostly pennate diatoms), represented in the general structure of the phytoplankton community with a ratio of 1:1.8.

The highest floristic diversity was recorded in August at locality T_4 (46 taxa). In general, higher diversity was characteristic for littoral localities (T_3, T_4, T_5, T_9), probably because of the lower water depth and closeness to macrophytic vegetation (benthic and epiphytic forms – *Navicula*, *Cymbella*, *Gomphonema*, etc. – resuspended from the lakebed and macrophytes). On the contrary, lower diversity was recorded at the pelagic localities (T_1, T_2, T_7, T_8) where euplanktonic species dominated in the phytoplankton community (*Scenedesmus*, *Pediastrum*, *Oocystis*, *Microcystis*, *Merismopedia*, *Cyclotella*, etc.). The lowest diversity characterized the right mouth of the Morača River (T_3 – stronger water turbulence) and the sublacustric spring, Karuč (T_{10} – station with the lowest nutrient concentration).

The total phytoplankton abundance in Lake Skadar ranged from 100 cells/l (winter) to $5x10^6$ cells/l (summer). In general, two peaks of abundance were recorded: the first (lower) peak in March (average 8.7×10^5 cells/l), due to high density of diatoms, and the second (higher) peak in June (average 2.4×10^6 cells/l) as a consequence of the explosion of greens (Fig. 3). The phytoplankton was distributed uniformly throughout the water column and seasonality did not apparently exert an effect on vertical phytoplankton zonation, which was absent during the entire investigated period due to lake shallowness and frequent winds.

Using stepwise multiple regression, a correlation was made between phytoplankton abundance and the investigated physico-chemical parameters (water temperature, transparency, oxygen concentration, conductivity, pH, TN and TP), and 62% of phytoplankton abundance variation could be explained by the investigated parameters (R^2=0.62; $p<0.00005$). The phytoplankton community in Lake Skadar showed a marked variation in seasonal-abundance, its peaks associated with the highest nutrient concentrations and water temperature values, which were in turn influenced by the alternation of a dry season (low water level) and a rainy season (high water level).

Water temperature has a direct effect through metabolism and reproduction intensity, and an indirect effect through nutrients (decomposition rate of debris by bacteria and intensity of internal loading) and the grazing of zooplankton. Other similar studies have detected strong relationships between temperature and phytoplankton composition (del Giorgio et al., 1991; Komarkova et al., 2003; Grover and Chrzanowski, 2005). In shallow lakes, the effect of warm weather is especially strong when it synchronizes with low water level, and the deterioration of water quality usually takes place in the warm period (Pettersson et al., 2003; Sondergaard et al., 2003). Nõges et al. (2003) and Padisák and Koncsos (2002) stressed the increase of internal nutrient loading during low water levels. Similarly, long-term investigations of Lake Peipsi showed a link between high phytoplankton density with periods of low water level, which can be explained by the increase in activity of bacteria, causing a higher uptake of oxygen and an intensive release of phosphate and ammonium from sediment to water (Laugaste et al., 2001).

In general, the seasonal succession of phytoplankton in Lake Skadar was complex, as often happens in many shallow lakes, especially those with a high surface area (Wetzel, 2001). Peaks of phytoplankton abundance did not appear at the same time at different parts of the lake, and phytoplankton succession showed distinct spatial heterogeneity (Fig. 4).

In general, the highest phytoplankton abundance characterized localities T_1, T_4 and T_5. Beside spatial differences in phytoplankton abundance, there were also evident differences as regards the dominant taxonomic groups of algae. Thus, localities T_7 and T_8 were characterized by a domination of diatoms during the majority of the year, even during the summer months. Localities T_1 and T_2 had a higher abundance of blue greens, and localities T_4 and T_{10} had a higher abundance of dinoflagellates in comparison with the other stations. Locality T_5 had the highest abundance of greens, which dominated during the entire warm period of the year (May–October).

Bacillariophyta dominated the phytoplankton community during spring and winter at most localities, with a peak in March. Exceptions were the pelagic localities T_7 and T_8, where Bacillariophyta had their peak of abundance during summer (June). During spring, the main diatoms in the phytoplankton community were pennate species: *Fragilaria capucina*, *Fragilaria ulna* var. *acus*, *F. ulna* var. *ulna* and *Synedra acus* var. *angustissima*. The summer months were characterized by centric species of diatoms, mostly *Cyclotella glomerata* and *Cyclotella ocellata*. Although centric diatoms were poor in number of species, they were much more abundant as individuals than the pennate forms and other algae in Lake Skadar. Centric diatoms are one of the best-adapted algal groups to turbulent and turbid systems (Reynolds, 2006), whereas pennate diatoms are regarded as benthic forms. A high abundance during the summer months of Bacillariophyta, especially small *Cyclotella* species, can also be explained by selective grazing by zooplankton, which is mostly based on size (Stoermer and Julius, 2003). Small algae have larger absorptive surfaces than larger algae, and the small size means that the settling rate is lower and that predation by some grazers may be lessened (Reynolds, 2006). Former investigations (Petković, 1981) showed that diatoms dominated the phytoplankton community in the sense of abundance during the whole year. At present, their domination is observed mostly during the period October–May in the majority of investigated localities (exceptions were the pelagic localities T_7 and T_8, with a summer domination of diatoms).

Chlorophyta developed mainly from late spring to early autumn and attained their peak in abundance in summer (mostly in June). Exceptions were the river zones, T_3, T_6 and T_9, where peak of abundance was recorded in autumn (September–October). Locality T_5 (Vučko blato) had the highest abundance of greens during the whole investigated period. The most abundant greens were Chlorococcales (*Pandorina morum*, *Crucigeniella pulchra*, *Oocystis* spp., *Scenedesmus* spp.) and the filamen-

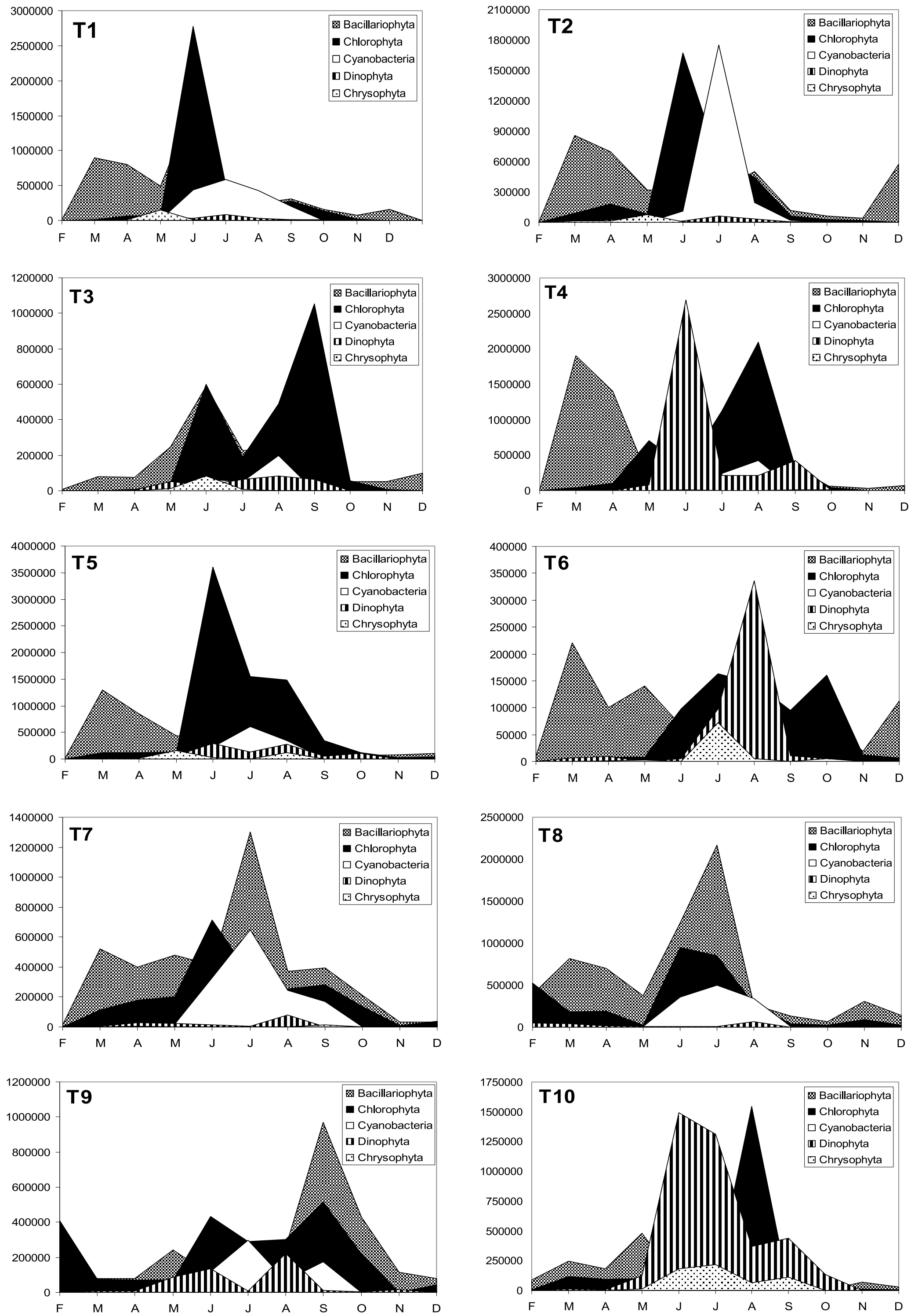

Fig. 4. Seasonal succession of main phytoplankton groups in Skadar Lake during investigated period (February – December 2004) at 10 sampling localities (T_1 – T_{10}; monthly abundance expressed as cells/l)

tous alga, *Planktonema lauterbornii*. Being almost entirely deprived of self-motility, Chlorococcales are completely dependent on water turbulence to keep them suspended in the water column. Consequently, they exhibit their greatest population net growth rates and abundance in turbulent waters (Happey-Wood, 1988; Reynolds, 2006), like the polymictic Lake Skadar. *Planktonema lauterbornii* was also abundant in the lake during summer, especially at station T_5. This species usually dominates the phytoplankton assemblage in highly eutrophic lakes (Jensen et al., 1994; Laugaste et al., 2001; Chen et al., 2003). Comparing a large number of Danish lakes of different trophic levels, Jensen et al. (1994) concluded that cyanobacteria were often replaced by green algae when total phosphorus in the lake water reached values above 1000 mg/m^3. In Lake Skadar, however, the filamentous green alga *Planktonema lauterbornii* dominated the phytoplankton assemblage already at a total phosphorus level of 50 mg/m^3, and there is no explanation for its high abundance under such trophic conditions. It might be considered as a separate 'stable state' within phytoplankton, depending on the nature and latitude of the lake (Scheffer, 1998). Previous investigations of the phytoplankton in Lake Skadar did not detect this species as significantly abundant.

The maximal abundance of Cyanobacteria was recorded during late summer, with a peak in August at all localities and with the highest density at the pelagic localities (T_2, T_7, T_8). At locality T_2, a slight bloom of filamentous alga *Anabaena variabilis* was recorded in August (1x10^6 cells/l) and in addition to this locality, *A. variabilis* dominated the community of blue-greens at stations T_1, T_3 and T_5. These algae are capable of storing phosphorus and fixing atmospheric nitrogen, thus enabling them to survive in systems with different trophic levels. Temperatures above 20°C and a decrease in transparency (Reynolds, 2006) also contribute to the maximum competitiveness and subsequent increase of blue greens' density in the system. During the summer (dry) period, the water temperature varied between 24.9 and 31°C, and water transparency dropped to about 50% compared to that of the rainy period. Beside *Anabaena variabilis*, the contribution of Cyanobacteria was mainly due to colonial species *Merismopedia punctata*, *Merismopedia glauca* and *Microcystis incerta* that dominated the community of blue-greens at stations T_4, T_7, T_8 and T_9. In shallow lakes, where suspended particles influence underwater light, algal species with gas vesicles, such as *Microcystis*, can either float up when underwater light conditions are poor or move down to avoid the high light intensity at the water surface (Brookes and Ganf, 2001). A summer peak of blue-greens in the phytoplankton community has also been recorded in many literature data (Fabbro and Duivenvoorden, 2000; Huszar et al., 2003; Mischke and Nixdorf, 2003; Albay and Akcaalan, 2003; Chen et al., 2003).

Dinophyta showed low occurrence. They were mostly represented by *Peridiniopsis beroliense* and *Peridiniopsis cuningtonii*. Exceptions were localities T_4 and T_{10} where Dinophyta had a distinctly higher abundance and even dominated in the phytoplankton community (June). One reason for this may be the clear-water phase due to nutrient limitations in the case of station T_{10}. The high grazing resistance, ability of dinoflagellates to migrate vertically and to take up nutrients in deeper layers of the lake, and their mixotrophic abilities at times enable their dominance in the phytoplankton community (Reynolds, 2006). However, localities T_4 (Virpazar) and T_{10} (Karuc) had very different nutrient concentrations: T_4 had the highest and T_{10} the lowest TP and TN values in comparison with the other investigated stations. Apart from this, these localities were very similar in the abundance of Dinophyta (e.g. explosion of *Peridiniopsis beroliense* in June). Both localities are quite isolated from the main water mass of the lake and protected from wind influence, which probably enables a stable stratification formation, at least for a certain time. Consequently, motile species like *Peridiniopsis* spp. gain a competitive advantage under such stable conditions.

Chrysophyta also exhibited low occurrence and were represented only by *Dynobryon divergens* and *Dynobryon bavaricum*. Maximal abundance of this group was recorded at locality Karuč (T_{10}). This is probably a consequence of the low water temperature and extremely low nutrient concentration near this sublacustrine spring, considering that Chrysophyta are well adapted to such environmental conditions (*Dynobryon* species are mixotrophic, which gives them more opportunities under nutrient limitation; Sandgren, 1988; Reynolds, 2006; Forsstrom et al., 2007).

A pattern found in shallow lakes is a constant wind action promoting the resuspension of sediment particles. Sediment resuspension can affect the underwater light climate, nutrient concentrations and phytoplankton density (Wiedner et al., 2002). The shortage of light associated with turbidity and wind-promoted turbulence in the Lake Skadar could be an important species-selection factor. Strong wind is a frequent summer occurrence at Lake Skadar and these irregularly occurring mixing events are the predominant disturbance to the succession of phytoplankton, disabling stratification and consequently steady-state formation. Wind is also indirectly the power factor that pushes other physical and chemical factors in the system to act more directly on the phytoplankton community. As expected, plankton responds to wind-generated hydrodynamics with changes in the community structure, as many studies of shallow lakes have documented (Wiedner et al., 2002; Chen et al., 2003; Lopes et al., 2005; Markensten and Pierson, 2007). In a general sense, the horizontal heterogeneity of phytoplankton comes from the spatial heterogeneity of some limiting factors for phytoplankton growth (i.e., local concentration of nutrients, light availability) or from water movement induced by the surface wind shear or by inlets, which can lead to highly heterogeneous spatial patterns (Blukacz et al., 2009). Thus, it is clear that a close relationship exists between hydrodynamics and phytoplankton patchiness. For that reason, it can be said that both spatial and temporal distribution of the main groups of phytoplankton in Lake Skadar are mostly connected to meteorological and hydrological factors. Results from this investigation are further proof that the seasonal succession of phytoplankton in shallow polymictic lakes shows significant deviations from plankton-succession trajectories consistent with the PEG-model.

The central, open part of Lake Skadar exhibited similarity with previously established phytoplankton data (Petković, 1981): diatoms still dominate the phytoplankton community during a majority of the year and monitoring of the phytoplankton community at this part of the lake can actually be reduced to the monitoring of diatoms. On the other hand, in the western and especially northwestern parts of the lake, which are more isolated and more affected by rivers and springs, there were evident differences in comparison with previous phytoplankton data. These differences are mostly reflected in the fact that diatoms (which previously dominated in terms of abundance during a whole annual cycle), are nowadays replaced with greens and/or blue-greens during almost the whole warm period of the year. Additionally, in both parts of the lake a higher total abundance of phytoplankton is registered in comparison with old data (at several orders of magnitude). The shift from diatoms to greens and blue-greens may be connected with the higher TN/TP ratio, which has increased from 6 to 21 during the last 30 years. Nydick et al. (2004) reported a similar trend: taxa that increased with nitrogen enrichment were small colonial Chroococcales (Cyanobacteria) and Chlorococcales (Chlorophyta), whereas taxa that diminished in relative importance were Chrysophyta.

All mentioned changes indicate that the trophic level of Lake Skadar has increased in the last 30 years and that the lake has generally deteriorated, especially its shallow, northwestern part. In order to protect Lake Skadar, it is necessary to utilize procedures capable of assessing whether nutrient enrichment is under control, especially regarding the influx of untreated sewage water and use of fertilizers in the lake's environment.

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