Ekológia (Bratislava) Vol. 26, No. 4, p. 409–429, 2007

APPLICATION OF THE PEG MODEL TO TWO RESERVOIRS WITH DIFFERENT TROPHIC LEVELS

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Abstract

Ostojić A.M., Ćurčić S.S., Čomić L.J.R., Topuzović, M.D.: Application of the PEG model to two reservoirs with different trophic levels. Ekológia (Bratislava), Vol. 26, No. 4, p. 409–429, 2007.

Many hydrobiological investigations of lakes and reservoirs for the most part involve study of certain components of the biocoenosis, and it is often the case that separate groups are examined independently of other components of the biocoenosis and sometimes independently of environmental conditions. A great shortcoming of many investigations is that certain data are lacking, with the result that the complexity of the problem remains inadequately or incompletely explained. In the course of the last decades, increasing attention has been paid to the given problem in the professional literature. In this context, attempts have been made to devise generally applicable models that can be used to explain or predict changes in the plankton community. Application of the PEG model to the Grošnica and Gruža Reservoirs turned out to be fully justified, even without complete data. Many of the changes observed in the plankton community can be successfully explained in terms of the PEG model.

Key words: eutrophication, phytoplankton, zooplankton, nutrients

Introduction

The PEG (Plankton Ecology Group) model was suggested at the end of the 20th century to explain seasonal changes in the plankton community (Sommer et al., 1986). The model was established on the basis of research on Lake Constance (Bodensee) in Germany and involved formulation of 24 premises permitting prediction of changes in the composition and structure of plankton throughout the year. The main premise was that those changes occur in a cause-effect way, are not accidental, and can be predicted with high probability. Many tests of this model were conducted in the period following its inception. In addition to numerous corroborations of the model, deviations were also observed from time to time, for example in the case of behavior of the phytoplankton in Lake Geneva during the summer period (Anneville et al., 2002). Chapman and Green (1999) observed pronounced deviations from the PEG model in Lake Rotorua (New Zealand), such deviations primarily consisting of the fact that there were no regularities in seasonal changes of the lake's plankton. Correct interpretation of those deviations would result in improvement and more successful application of the PEG model.

In Serbia and Montenegro, little has been done so far to test the PEG model. The most frequent reason for this is that investigations have been of a partial nature treating separate components of the plankton community. It is not always possible to interpret the obtained results correctly in this way. The first and so far the most detailed use of the PEG model in Serbia and Montenegro was performed on the example of the swamp Obedska Bara (Martinović-Vitanović, 1996), where each of the 24 premises was precisely elaborated. Certain premises of the model were also tested on the example of the Vlasina Reservoir (Laušević, Cvijan, 1997).

On the basis of our extensive investigations of zooplankton in the Grošnica and Gruža Reservoirs and the data of other authors on the remaining components of the biocenosis (Ranković et al., 1999; Ranković, Simić, 2005; Milošević, 1999; Simović, 2001; Ćurčić, 2003), we attempted to apply the PEG model to these two reservoirs.

Study site

The city of Kragujevac (in the central part of Serbia) is supplied with water from the Grošnica and Gruža Reservoirs. The Grošnica Reservoir is the oldest reservoir for water supply on the territory of Serbia and was formed on the river of the same name. The dam was constructed during the period of 1931–1937, and the reservoir was filled in 1938. The system supplied the city with an adequate amount of water up until 1950. However, from that period on, the volume of the lake has undergone significant reduction due to increased consumption and filling with sediments. During the period of 1960–1962, the dam was raised by 7.3 m. During the warm period of the year, thermal stratification is observed from May to the end of September.

The Gruža Reservoir was formed on the Gruža River. Construction of the dam began in 1979, and the reservoir was filled with water in 1985. The reservoir is located at an altitude of 238–269 m a.s.l. Its total volume is 64.6×10^6 m^3 and surface area is 934 ha. Gruža Reservoir has a drainage basin of 318 km^2. The maximum depth was 31 m, and fluctuations of water level were 3–5 m. The large surface in relation to the small volume favours eutrophication. The reservoir is surrounded by farmland, and receives waste water from neighbouring settlements.

Characteristics of both reservoirs are given in Table 1.

T a b l e 1. Some characteristics of the Grošnica and Gruža Reservoirs.

	The Grošnica Reservoir	The Gruža Reservoir
Surface area (ha)	22	934
Volume (m^3)	$3.53x10^6$	$64\ x10^6$
Catchment area (km^2)	30	318
Lenght (m)	1750	10.000
Minimum width (m)	150	200
Maximum width (m)	250	1.500
Maximum depth (m)	23	31
Altitude (m a.s.l.)	312	238
Protection zone (ha)	180	1.450
Number of domestic economy in protection zone	10	93

Material and methods

Monthly sampling was carried out during the period from October of 1996 to September of 1998. Because of bad weather conditions, it was impossible to conduct field investigations from January to April of 1997 and in April of 1998. Also, it was impossible to take samples from the shallowest part of the lake during December of 1997 and January of 1998. In order to gain as accurate as possible a picture of the state of affairs in this artificial ecosystem, three permanent sampling points were selected for qualitative and quantitative sampling: I – directly beside the dam as the deepest part of the lake, where its depth varied (from 16 to 23 m in the Grošnica Reservoir and from 25 to 31 m in the Gruža Reservoir), depending on the water level; II – the central part of the lake (with a depth from 6 to15 m in the Grošnica Reservoir and from 14 to 17 m in the Gruža Reservoir); and III – the shallowest part of the lake, about 200 m from its end, which is under water even when its level is lowest (with a depth from 0.8 to 5 m in the Grošnica Reservoir and from 5 to 9 m in the Gruža Reservoir). Samples of plankton were taken at every 3 m of depth during stagnation and at every 5 m during circulation.

Qualitative samples of plankton were taken with a plankton net (mesh size 25 µm), while quantitative samples were collected with 2-liter Ruttner hydrobiological bottles and then filtered across a plankton net. Samples were preserved with 4% Formalin at the collection site.

The content of chlorophyll *a* was determined by the spectrophotometric method using 90% acetone as the extracting agent (Creitz, Richard, 1955).

The biomass of zooplankton was calculated on the basis of tabular values (Morduhay-Boltovskoy, 1954; Ulomskiy, 1958).

Analyses of chemical parameters were performed by standard methods (APHA, 1985).

Results

Analysis of parameters of the trophic state (total P, chlorophyll *a*, and transparency) indicated that the Grošnica Reservoir belongs to the category of mesotrophic waters occasionally approaching the eutrophic state, whereas the Gruža Reservoir belongs to the category of eutrophic waters on the basis of total phosphorus and even hypertrophic waters on the basis of chlorophyll *a* content and transparency (Table 2) (Ostojić, 2000).

T a b l e 2. Average values of trophic parametres and Trophic State Index (TSI) in the period October 1996-September 1998 in the Grošnica and Gruža Reservoirs (SD = Secchi disc, Chl-a = chlorophyll *a*, TP = total phosphorus).

	Total P mg L^{-1}	Chl-a average µg L^{-1}	Chl-a max µg L^{-1}	Secchi average m	Secchi min m	TSI_{SD}	TSI_{TP}	TSI_{Chl-a}
Grošnica	32.2[3]	4.3[3]	10.5[3]	2.1[2]	1.0[2]	48.55[3]	54.24[3]	44.87[3]
Gruža	54.0[2]	29.1[1]	99.2[1]	1.1[1]	0.5[1]	58.62[3]	61.70[2]	63.34[2]

Notes: [1]hypertrophic, [2]eutrophic, [3]mesotrophic

Ostojić (2000) summarized detailed results of analysis of the composition and structure of zooplankton in the Grošnica and Gruža Reservoirs. Figures 1 and 2 show the dynamics of changes in average values of zooplankton abundance and biomass in the investigated reservoirs.

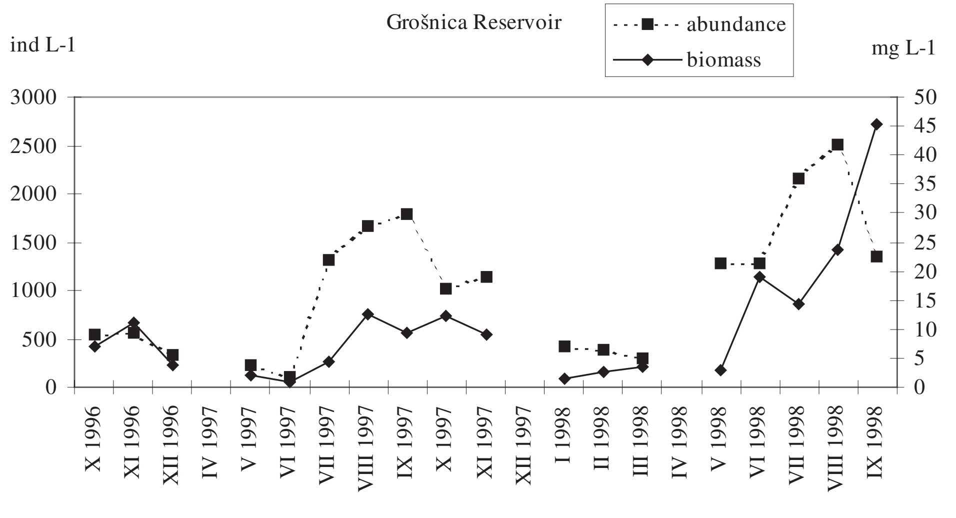


Fig. 1. Average values of abundance and biomass of zooplankton in the Grošnica Reservoir.

The dynamics of average abundance and biomass of each of the investigated groups exhibited certain characteristics in keeping with their ecological peculiarities (Figs 3–4). In interpreting changes in the total abundance of zooplankton and each group separately with all its specificities, different abiotic and biotic factors must be taken into account.

On the basis of extensive research on zooplankton in the Grošnica and Gruža Reservoirs and using the data of authors who investigated other components of the biocenosis in both reservoirs during the same period of time (chlorophyl-*a* – Milošević, 1999; Ćurčić, 2003;

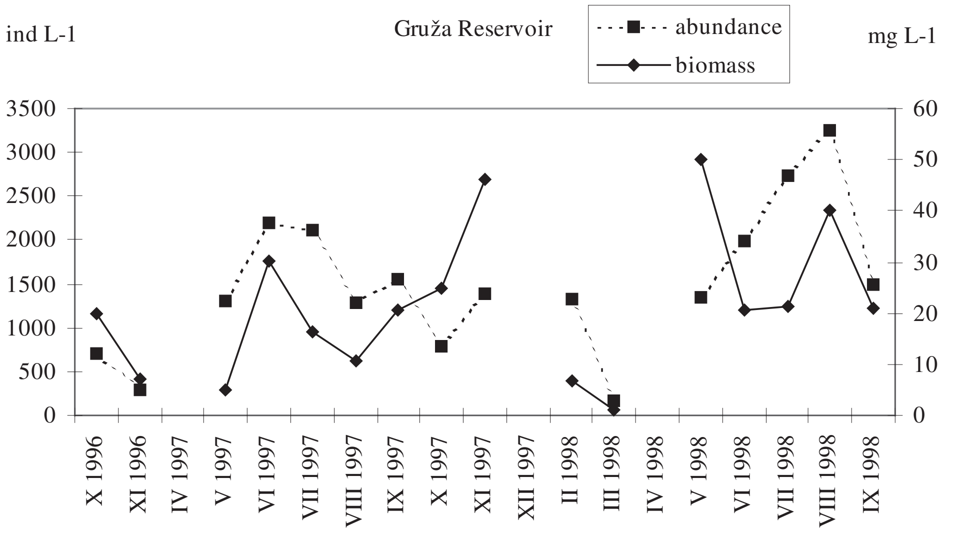


Fig. 2. Average values of abundance and biomass of zooplankton in the Gruža Reservoir.

phytoplankton – Ranković et al, 1999; Ranković, Simić, 2005; ichthyofauna – Simović, 2001), we attempted to apply the PEG model to these two reservoirs

Renewal of nutrients occurs during the winter period, with the result that conditions for development of smaller algae are created in early spring if a favorable light regime is present (Kerfoot et al., 1988). At the beginning of spring, small Bacillariophyta are dominant with respect to abundance in both reservoirs. In the Grošnica Reservoir Bacillariőphyta constitute as much as 76.2% of total phytoplankton and 81.4% of total phytoplankton in the Gruža Reservoir. Thus, the first maximum in the development of phytoplankton occurs in the spring, which is in keeping with the first point of the PEG model.

Adequate amounts of edible algae should serve as a good basis for development of phytophagous zooplankton (point 2), first of all ones with a short generational period, such as Protozoa and Rotatoria, and later on those with a longer cycle, such as Cladocera and Copepoda (point 3). Forms characteristic of the cold-water complex appear in greater numbers in the course of the spring period, such forms including *Kellicottia longispina*, species of the genus *Synchaeta*, and *Conochilus unicornis*. This phenomenon was observed in the Grošnica Reservoir in the spring of 1997, when the species *Kellicottia longispina* took part with more than 90% in the abundance of Rotatoria and with more than 60% in the abundance of all zooplankton. A somewhat different situation prevailed in the spring of 1998, when participation of *K. longispina* was minimal (about 4% of all Rotatoria) and the clearly dominant species were *Synchaeta kitina* (about 36%) and *Keratella cochlearis* f. *macracantha* (about 26%), a form that is characteristic of the colder season of the year. Participation of the nauplius stage of Copepoda was insignificant during this period in

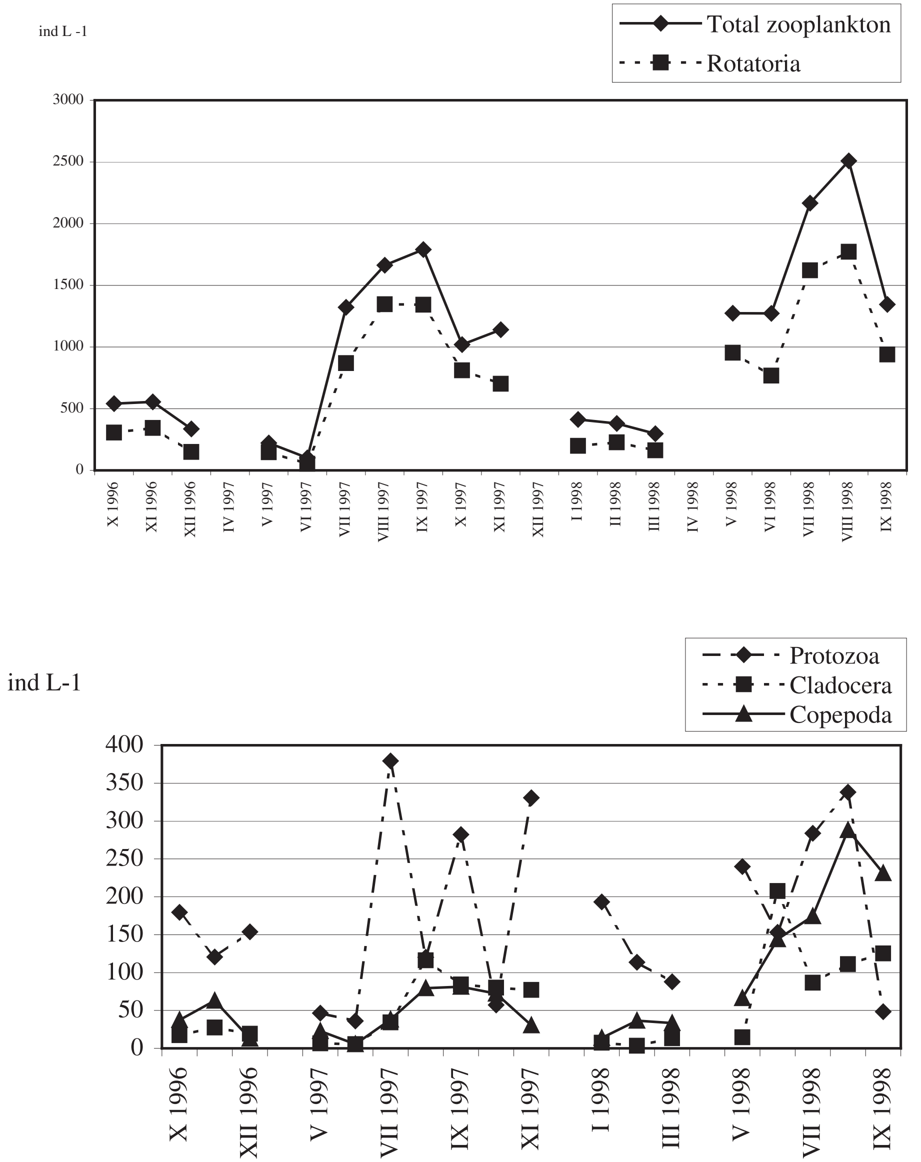
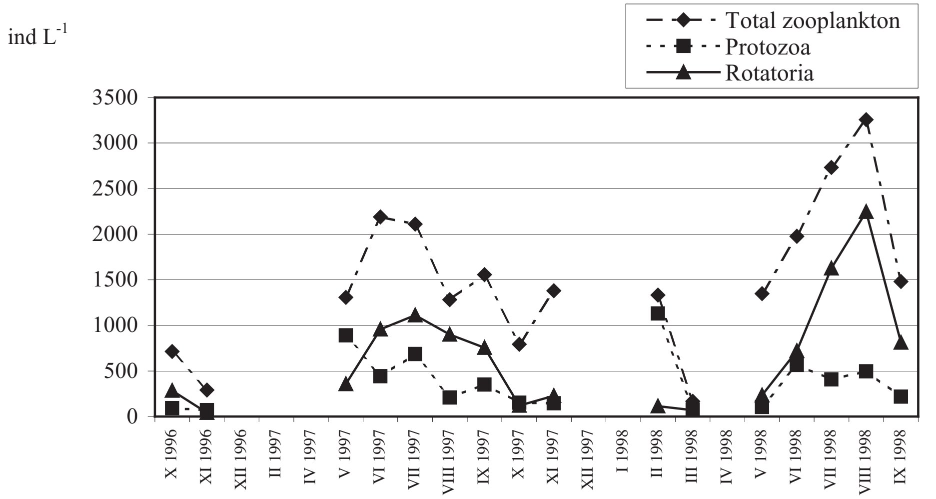


Fig. 3. Dynamics of the investigated groups of zooplankton in the Grošnica Reservoir.



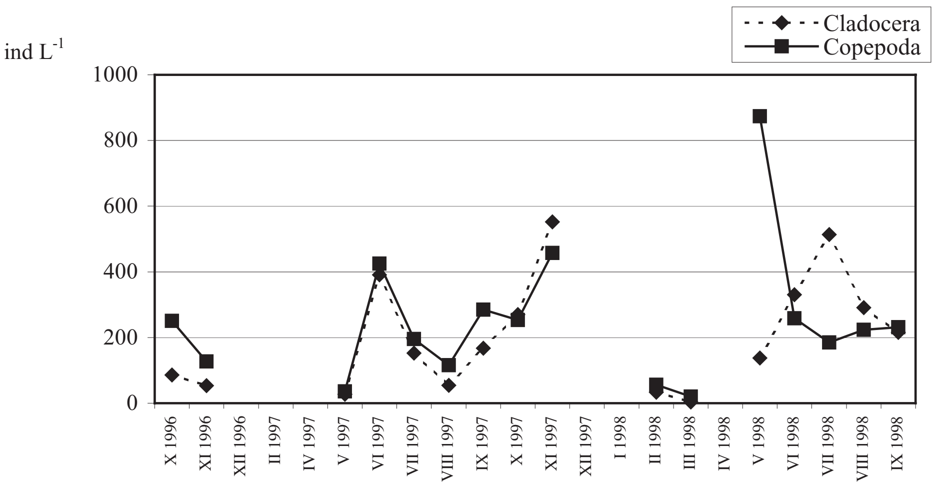


Fig. 4. Dynamics of the investigated groups of zooplankton in the Gruža Reservoir.

the Grošnica Reservoir, while the presence of large planktonic Crustacea was negligible, a fact reflected in the low values of biomass (2.045 mg L^{-1} in May and only 0.833 mg L^{-1} in June of 1997; and 2.996 mg/l in May of 1998) (Fig. 1). In the Gruža Reservoir, *Kellicottia longispina* and *Keratella cochlearis* f. *macracantha* were most abundant in the early spring (March) of 1997, whereas *K. cochlearis* and *K. quadrata frenzeli* were clearly dominant in May. *Conochilus unicornis* appeared only in the Gruža Reservoir, exclusively in the spring. *Filinia longiseta* was in both reservoirs the most abundant form during the spring of 1997, as well as during the winter months of 1998 in the Gruža Reservoir. The participation of planktonic Crustacea was minimal, so that a second minimal value of zooplankton biomass (5.071 mg L^{-1}) was recorded in May of 1997. The situation was completely different in the spring of 1998. By far the most abundant forms in the composition of zooplankton were larval (nauplius and copepodid) stages of Copepoda, which accounted for more than 50% of the total abundance of zooplankton. This produced a spring biomass maximum of 50.145 mg L^{-1} (Fig. 2) (which was at the same time the greatest recorded value).

To judge from available data on the concentration of chlorophyll *a* and the abundance and biomass of zooplankton, the "clear water phase" in the Grošnica Reservoir was distinctly expressed in mid-summer of the year 1997 (when chlorophyll *a* concentration was halved in relation to its value at the end of spring – from 3.8 to 2.0 µg L^{-1}), which was also manifested in increased transparency (Fig. 5). Such regularities were not clearly discernible in 1998, although the detected deviations do not greatly contradict the stated rule. In the Gruža Reservoir, when a pronounced decrease of primary production was clearly discernible at the end of spring, together with simultaneous increase of transparency (Fig. 5). From 42.20 µg L^{-1} in February of 1999, the average value of chlorophyll *a* content decreased to only 15.95 µg L^{-1} in May and 13.07 µg L^{-1} in June, which is in agreement with what has been said. These data are largely in keeping with the predictions of Sommer et al. (1986) expressed in points 4 and 5.

According to point 6 of the model, the density and biomass of zooplankton decline due to decrease in available amounts of food. At the same time as decrease in available food, an increase occurs in predatory activity of planktivorous fish (point 7), with the result that the biomass of planktonic Crustacea declines (Goldyn et al., 1997). The expected decrease in density and biomass of zooplankton at the beginning of summer was only partially recorded in the Gruža Reservoir. To be specific, contrary to the model, an increase in density and biomass of zooplankton was recorded during this period in 1997. Moreover, an increase of abundance also occurred in 1998 (due to massive development of *Bosmina*), whereas a decline of biomass occurred at the same time (Fig. 2) (as predicted by the model) due to considerable decrease in the abundance of Copepoda (Fig. 4) and their participation in the total mass of zooplankton (Fig. 6).

According to the given model, a decline of fecundity also occurs, which in the Gruža Reservoir is evident in a marked decrease in abundance of the nauplius and copepodid stages (Fig. 7).

This situation was not very expressed in the Grošnica Reservoir, which can be linked with a lower trophic level characterized by less pronounced oscillations of biomass. An

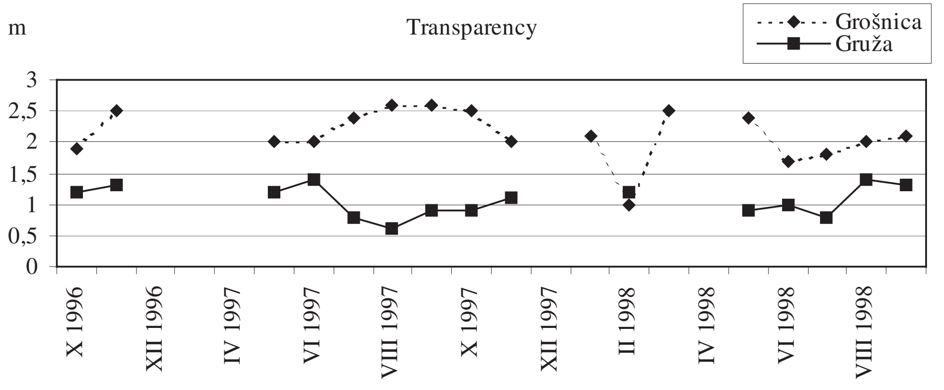


Fig. 5. Average values of transparency in the Grošnica and Gruža Reservoirs.

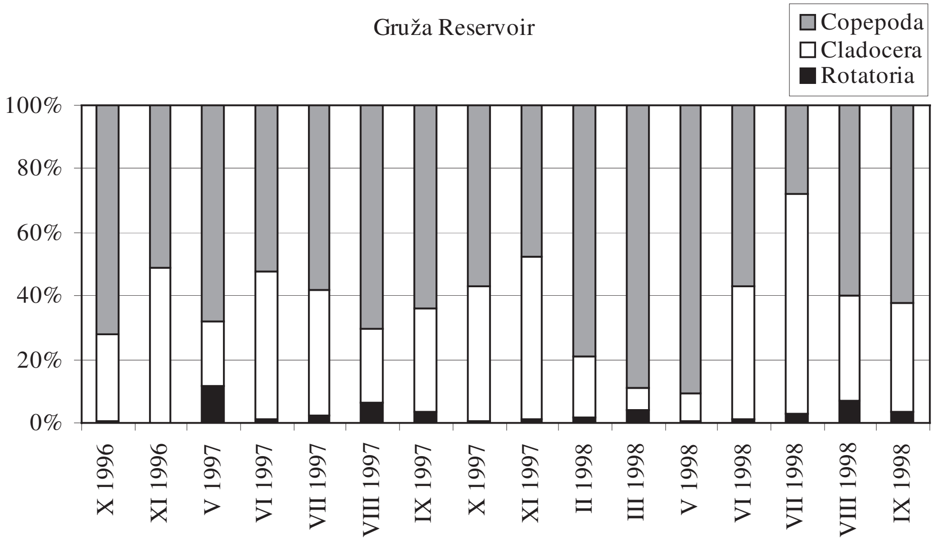


Fig. 6. The percentage of the investigated groups in the total biomass of zooplankton in the Gruža Reservoir.

insignificant decrease in abundance of Cladocera and Copepoda occurred at the beginning of summer in 1997 (Fig. 3), and it was reflected in minimal values of total biomass, in which planktonic Crustacea continued to represent the most important component due to the low abundance of Rotatoria (Fig. 8). In the year 1998, a decrease in abundance at the beginning of summer occurred only in the group Cladocera, but not in the group Copepoda (Fig. 1).

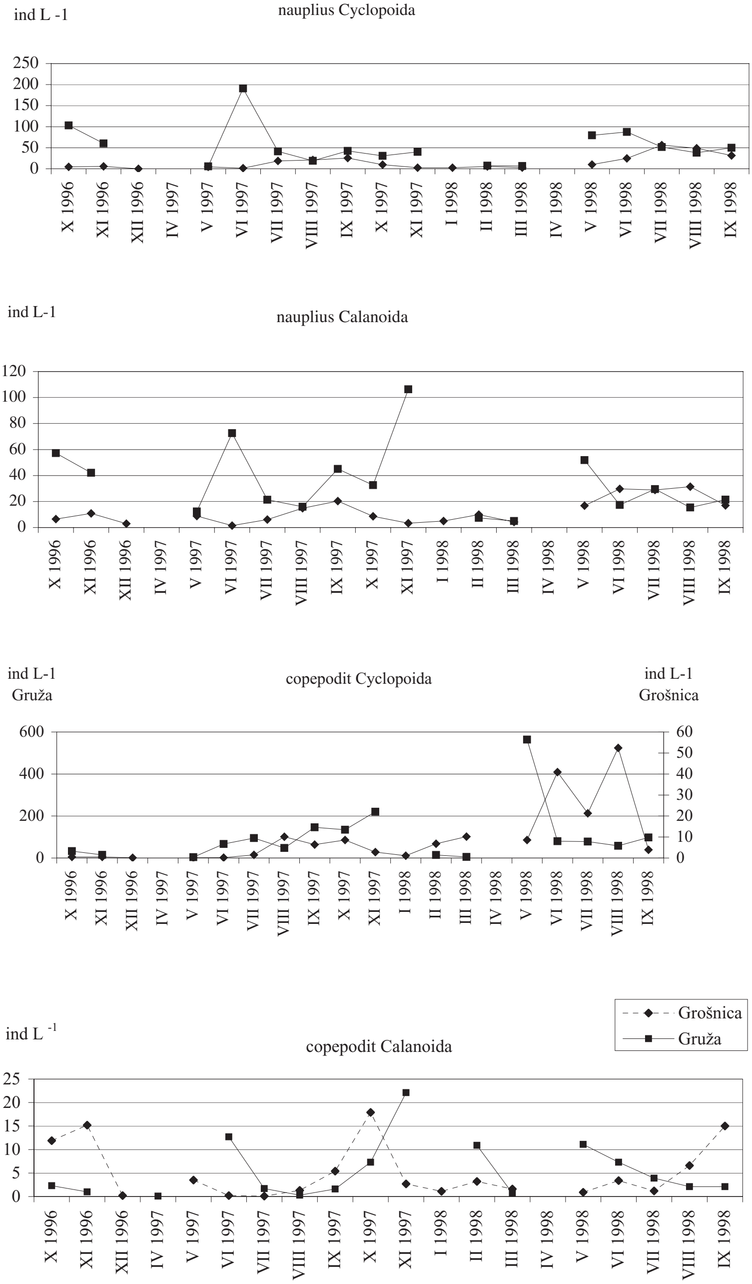


Fig. 7. Dynamics of the larval stages of Copepoda in the Grošnica and Gruža Reservoirs.

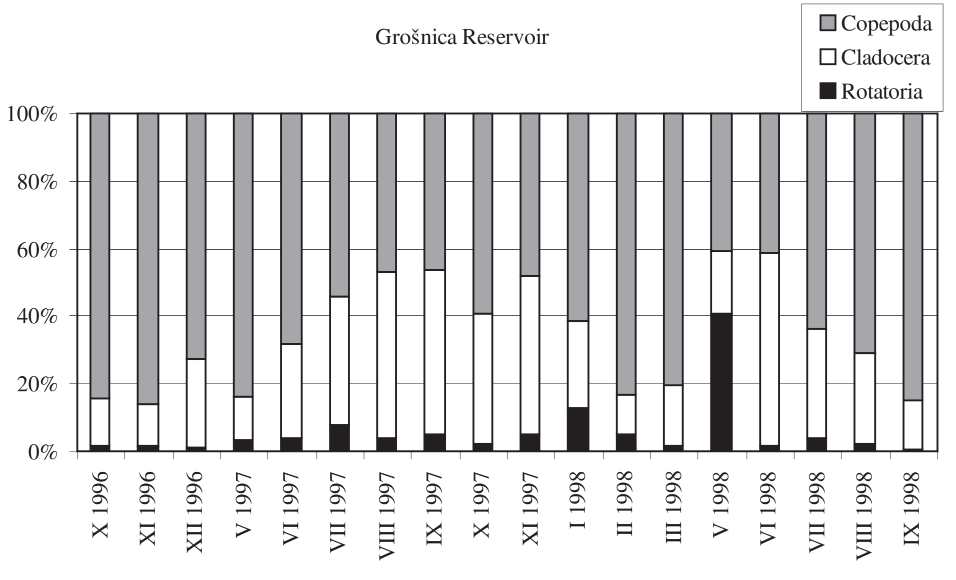


Fig. 8. The percentage of the investigated groups in the total biomass of zooplankton in the Grošnica Reservoir.

However, a decrease of biomass still occurred (Fig. 1) because nauplius stages were then prevalent, while the abundance of copepodids declined (Fig. 7).

It is known that planktovorous fih exert predator influence on zooplankton. According to the data of Simović (2001) on feeding of common wild goldfish (*Carassius auratus gibelio*) and roach (*Rutilus rutilus*), zooplankton represents an important component in the food of these fish in certain stages of development, although it is not the only one, since the presence of diverse food is discernible in their intestines (in addition to zooplankton, phytoplankton, bottom fauna elements, and parts of macrophytes are also utilized as food). There are no data on the ichthyofauna of the Grošnica Reservoir, so it is impossible to speak clearly of its influence on the dynamics of zooplankton. In the Grošnica Reservoir, the abundance of large copepods (*Eudiaptomus*) declined during the period of investigation, whereas that of small ones (*Thermocyclops*) increased. In the Gruža Reservoir, the abundance of small cladocerans (*Bosmina longirostris*) increased (in May of 1998 average abundance 46 ind L^{-1}, in June same year average abundance 491 ind L^{-1}), while that of large ones (*Daphnia*) decreased (in May of 1998 average abundance 35 ind L^{-1}, in June same year average abundance 3 ind L^{-1}).

Due to incompleteness of the data on phytoplankton, it is possible to discuss points 8–13 only partially and indirectly. With decrease in pressure from phytophagous species of zooplankton and simultaneous increase in the amount of nutrients in the water of both reservoirs (Fig. 9), conditions are created for summer development of phytoplankton. Dur-

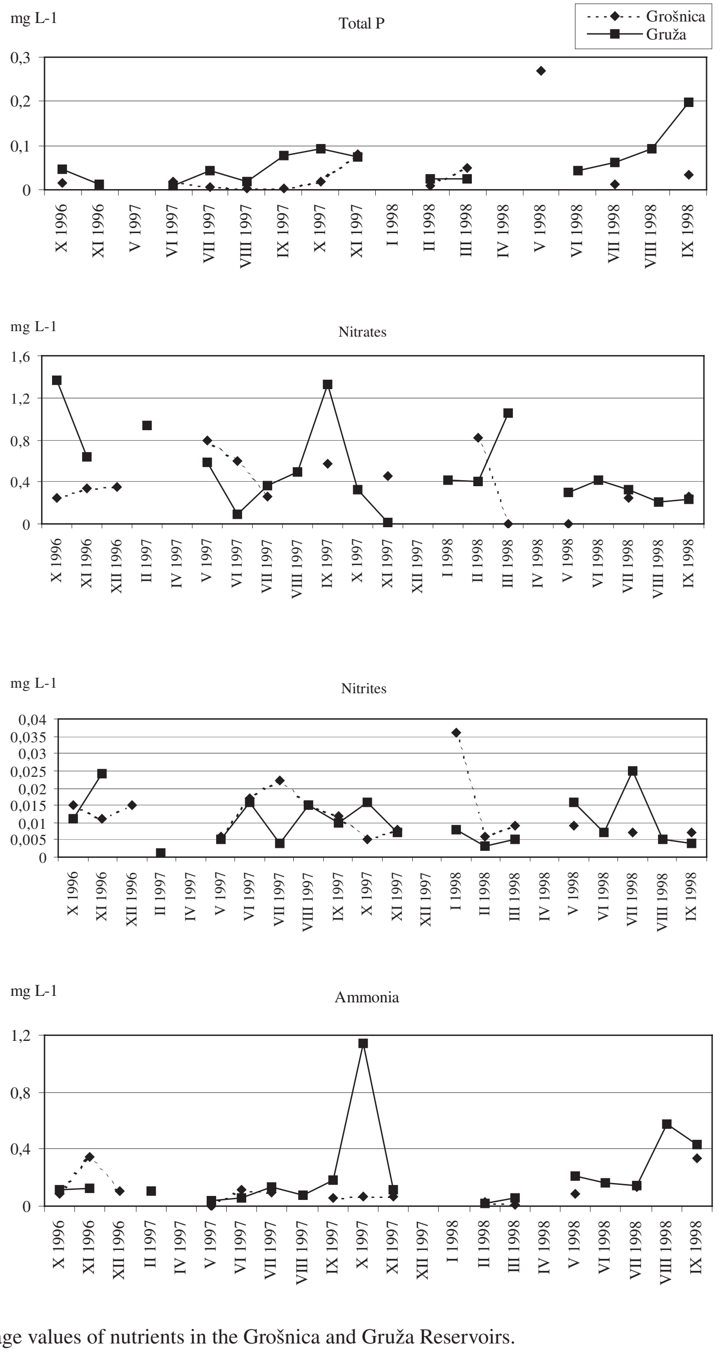


Fig. 9. Average values of nutrients in the Grošnica and Gruža Reservoirs.

ing the summer period, the qualitative composition of phytoplankton is characterized by its greatest diversity. In both reservoirs were more than 50 taxa in composition of phytoplankton, which indicates that environmental conditions (above all the amounts of nutrients available) are then favorable and ensure the survival and development of various groups of phytoplankton, as well as its considerable diversity. Janković (1965) studied plankton community in the Grošnica Reservoir during the period 1950–52 and she observed the greatest diversity of phytoplankton during the summer period too.

In late spring to early summer, there is a decrease in the abundance of Bacillariophyta and increase in that of Chlorophyta, which constitute as much as 37.7% of total phytoplankton in the Grošnica Reservoir and more than 50% of total phytoplankton in the Gruža Reservoir. Apart from them, two species appear with increasing abundance at the outset of spring in the Grošnica Reservoir, namely *Dinobrion divergens* (Chrysophyta), which accounts for 39.8% of total phytoplankton in the surface layers, and *Trachelomonas volvocina* (Euglenophyta), while in the Gruža Reservoir representatives of other genera of Euglenophyta (*Euglena*, *Phacus*) also appear at this time. Dinophyta (mainly *Ceratium hirundinella* and species of the genus *Peridinium*) occur in great numbers somewhat later and by the end of summer attain 61.5% of total phytoplankton in the Grošnica Reservoir and 38.8% of total phytoplankton in the Gruža Reservoir.

Even though development of phytoplankton, primarily Chlorophyta, is intensive during this period, phosphates are not completely consumed in the water of either reservoir (Fig. 9). And since there is also enough silicon, Bacillariophyta as well appears in the summer. They occur in great numbers during the summer months in the Grošnica Reservoir thanks to mass development of the species *Asterionella formosa*, which represents a superior competitor at high values of the Si:P ratio (Sommer et al., 1986). At the same time, *A. formosa* is resistant to “grazing” by daphnias (Horn, Horn, 1995).

During the summer months in the Gruža Reservoir, a marked increase is observed in the abundance of Cyanobacteria (more than 40% of total phytoplankton), some of which owing to their capacity for nitrogen fixation become competitively superior under conditions of reduced amounts of nitrogen salts. As a result, this reservoir is characterized by intensive development of *Anabaena flos-aquae*, *Microcystis aeruginosa*, and (especially) *Aphanisomenon flos-aquae*, which in certain periods during the summer causes “blooming” of water in the surface layers.

At the same time, Cyanobacteria are an insignificant group in the composition of phytoplankton of the Grošnica Reservoir, where they are represented by only one species, *Oscillatoria limnetica*, which occurs only sporadically and always with a small number of individuals. Same situation found Janković (1965). The significant presence of Cyanobacteria in the Gruža Reservoir (35–40% of total phytoplankton during the summer) is in keeping with assumptions of the model and indicates strong human influence.

Such pressure favors the development of smaller forms, which in summer attain their greatest diversity and occur in large numbers (their mortality is lower and fecundity greater than in larger species), which indicates their successful coexistence (points 14 and 15). The influence of microzooplankton on bacterio- and phytoplankton increases during this period

(Kozak, Goldyn, 2004). During the summer months, both the diversity and density of the investigated zooplankton increase in each of the reservoirs, attaining maximal values in mid-summer. Clearly dominant with respect to abundance are Rotatoria, which in summer invariably take part with more than 50% of both the total number of taxa and total abundance (Figs 3 and 4). The dominant members of the group Rotatoria during summer are smaller species such as *Keratella cochlearis*, *K. c.* var. *hispida*, *Polyarthra dolichoptera*, *Pompholyx sulcata*, *Synchaeta kitina*, and *Trichocerca similis*, together with the somewhat larger *Kellicottia longispina*, in the Grošnica Reservoir; and *K. cochlearis*, *K. c.* var. *tecta*, *Polyarthra dolichoptera*, *P. major*, *Pompholyx sulcata*, and *Trichocerca pusilla* in the Gruža Reservoir. Mass development of the species *Anuraeopsis fissa* – which is a distinctly thermophilic species – also occurs during summer in the latter reservoir. The summer period is characterized as well by an increase in the abundance of Protozoa (*Difflugia limnetica*, *Epistylis rotans*, *Tintinnidium fluviatile*, and *Tintinnopsis lacustris*). An insufficiency of data on the participation of Protozoa in summer production of zooplankton is a shortcoming of many investigations (Sommer et al., 1986).

During the summer period, large species of planktonic Crustacea (*Daphnia cucullata* f. *kahlbergensis*, *Eudiaptomus gracilis*, and occasionally *Cyclops vicinus* as well in the Gruža Reservoir) appear in the reservoirs, but with a small number of individuals, whereas their abundance increases with decline of predatory pressure from fish in the fall, when they achieve maximal production and are dominant with respect to both abundance (Figs 3 and 4) and biomass (Figs 6 and 8). The main representatives of planktonic Crustacea in summer are small forms such as *Bosmina longirostris* (especially in the Gruža Reservoir) and *Diaphanosoma brachyurum*, a species that appears exclusively in summer, which is in keeping with data of Tifnouti et al. (1993) indicating that the given species usually does not occur at temperatures lower than 15 °C and does not reproduce at temperatures below 25 °C. There is an increase during the summer in abundance of juvenile stages of Cladocera, adult specimens of *Acanthocyclops vernalis* (only in the Gruža Reservoir) and *Thermocyclops crassus* (only in the Grošnica Reservoir), as small representatives of Copepoda as well. The nauplius stages of Cyclopoida and Calanoida and the copepodid stage of Cyclopoida are abundant, whereas the abundance of Calanoida copepodids is low (Fig. 7), which may be a consequence of the fact that they are larger than Cyclopoida copepodids and thereby more exposed to pressure from predatory fish.

During the summer months, even when environmental conditions are favorable, there are minor fluctuations in the abundance of zooplankton, such fluctuations varying as a function of locality and specific ecological conditions. With decline of temperature at the end of summer and beginning of autumn, changes occur in the composition and abundance of zooplankton (Figs 3 and 4), which is in agreement with point 16 of the model.

In the fall, physical factors (such as temperature and light) affected composition and structure of the phytoplankton (points 17–21). Temperature drops in the autumn, and gradual wind-assisted mixing of water layers begins at that time, circulation is established, and the water becomes less transparent (Fig. 5). Nutrients are then renewed and phosphate content increases, while the content of nitrogen salts remains on the summer level or even declines slightly (Fig. 9). The abundance of phytoplankton usually decreases at the beginning of autumn due to increased pressure of zooplankton (Hannson, 2000), which in the Gruža Reservoir is indirectly indicated by decrease in the concentration of chlorophyll *a* (from 33.6 μg L^{-1} in July to 24.7 μg L^{-1} i September of 1998). That trend is not clearly expressed in the Grošnica Reservoir, where values of chlorophyll *a* content at the beginning of autumn (4.9 μg L^{-1} in November) remain on the level of summer values (4.7 μg L^{-1} in July of 1997). An autumn peak then occurs in the development of Bacillariophyta, about 65% of total phytoplankton in the Grošnica Reservoir, and more than 86% of total phytoplankton in the Gruža Reservoir. At the same time, the abundance of Dinophyta (especially *Ceratium hirudinella*) remains high – about 65% of total phytoplankton in the Grošnica Reservoir, and about 80% of total phytoplankton in the Gruža Reservoir. During the autumn, the percentage of Cyanobacteria in the Gruža Reservoir decline, from 51% of total phytoplankton in summer to 1.3% in autumn. Percentage of Chlorophyta decline, too – from 38% in summer to 8% in autumn in the Grošnica Reservoir, and from 41% in summer to 9% in autumn in the Gruža Reservoir.

The presence of edible algae and reduced pressure from planktivorous fish lead to an autumn maximum of zooplankton (point 20), whose abundance lags behind summer peak values in both reservoirs (Figs 1–2), whereas biomass values can be even higher than at the time of the late spring to early summer maximum, which is a consequence of increase in the abundance of larger Cladocera (*Bosmina coregoni*, *Daphnia cucullata* f. *kahlbergensis*), their juvenile stages, and the species *Eudiaptomus gracilis* (both adults and nauplius and copepodid stages).

Production of phytoplankton declines with further reduction of temperature and worsening of conditions (including the light regime), which is evident in gradual decrease in the concentration of chlorophyll *a* during the colder period in the Grošnica Reservoir (3.9 μg L^{-1}). Average content of chlorophyll *a* also decreases in the Gruža Reservoir, from 28.91 μg L^{-1} in August of 1998 to the level of 7.25-9.53 μg L^{-1} during the cold period. This is accompanied by decrease in the abundance and biomass of zooplankton (Figs 1–2). Decrease in the abundance and biomass of phyto- and zooplankton is in keeping with points 21 and 22.

In the course of the colder period of the year, most species "withdraw" from the composition of zooplankton by passing over into a state of dormancy in different ways (point 23), which is reflected in significant decrease in both abundance and biomass of the zooplankton (Figs 1 and 2). But in both reservoirs the winter months are marked by the apppearance of adult copepods in addition to larval stages in composition of the zooplankton, a circumstance that contributes to faunistic diversity (point 24). Their greatest abundance (between 11 and 88 ind–L^{-1}) is in the deepest layers in both reservoirs.

Discussion

Although the investigated reservoirs differ in regard to their trophic level, the Grošnica Reservoir being mesotrophic and the Gruža Reservoir eutrophic (Table 1), the obtained results are in good agreement with predictions of the PEG model. The differences noticed are more qualitative than quantitative.

The predictions relating to the spring of the year (points 1–3) are also fulfilled in these investigations. The only difference between the two reservoirs lies in qualitative composition of the dominant zooplankton species and their abundance. Nevertheless, we are dealing here with species characteristic of cold water in both cases. A spring maximum in the abundance of larval stages has also been recorded by other authors (Ferrara et al., 2002). Such dynamics and composition of zoooplankton are largely in agreement with the stated considerations.

In establishing the PEG model, the authors attempted to view comprehensively the interrelations between phyto- and zooplankton. However, in the original paper (Sommer et al., 1986), they did not take into account one extremely important component of plankton in the food web, namely microorganisms, which are an imporrtant source of food for unicellular animal organisms (primarily heterotrophic flagellates and ciliates) (Rothhaupt, Güde, 1996). Bacteria compete seriously with algae for nutrients (Reche et al., 1997). If these components are taken into account, it becomes clear why there was a decrease in the total number of bacteria in mid-spring and late spring/early summer in the Grošnica Reservoir (Milošević, 1999), when an increase was recorded in abundance of the epizoic ciliate *Epistylis rotans* (May – average abundance 27 ind L^{-1}) in 1997 and *Tintinnidium fluviatile* (June – average abundance 70 ind L^{-1}) in 1998. In the Gruža Reservoir in May of 1997, there was mass development of the colonial ciliate *Carshesium polyspinum* (average abundance 800 ind L^{-1}), which participated with more than 60% in the total abundance of zooplankton, while abundance of the species *Tintinnopsis lacustris* was elevated in the spring of 1998 (average abundance 27 ind L^{-1}). A spring peak in the development of Protozoa would be in complete agreement with point 3 of the model.

In keeping with this period in the development of zooplankton forms, which by means of "grazing" reduce the biomass of phytoplankton (Kerfoot et al., 1988), the concentration of chlorophyll *a* in both of the investigated reservoirs declines during the months when the abundance of zooplankton starts to increase. The so-called "clear water phase" sets in as a consequence of grazing by phytophagous zooplankton (points 4 and 5). After the outset of this period, the most important role in "grazing" on phytoplankton is played by daphnias (Rothhaupt, Güde, 1996), especially in the spring and early summer in eutrophic lakes (Kasprzak et al., 1999).

The development of phytoplankton in summer is dictated both by reduced pressure from herbivorous zooplankton and by the quantity of nutrients (points 8–13). Since environmental conditions change relatively rapidly, the occurrence of competitive exclusion is prevented because species that are better competitors are unable to realize their advantage in the course of a short period of time, a fact that makes great diversity of the phytoplankton possible (Martinović-Vitanović, 1996). Theoretically, overlapping of niches should lead to competitive exclusion and domination of only one species, which Hutchinson (1961) termed the "plankton paradox".

The most obvious difference between the two investigated reservoirs in summer is the fact that Bacillariophyta are forced out by Dinophyta in the Grošnica Reservoir, but by

Cyanobacteria in the Gruža Reservoir. The dominance of Cyanobacteria in the Gruža Reservoir and their minimal participation in the composition of phytoplankton in the Grošnica Reservoir can be attributed to a greater quantity of nutrients in the former (Fig. 9) and to the fact that its trophic state is higher (Table 1) owing to considerably stronger human influence. To be specific, phosphates are not recorded in the Grošnica River, whereas the amount of phosphates in tributaries of the Gruža Reservoir varies in the range of 0.4–2.4 mg–L^{-1} (Ostojić, 2000). Also, there are many cultivated fields on which artificial fertilizers are used in direct proximity to the Gruža Reservoir. When it rains, those fertilizers enter the water of the Gruža Reservoir and become available to the phytoplankton. All of this makes possible the competitive superiority of Cyanobacteria in the Gruža Reservoir.

The flourishing of Cyanobacteria and Dinophyta during this period has been confirmed by a number of authors. Large dinoflagellates and colonial Cyanobacteria are at a selective advantage (point 12) due to their dimensions, resistance to "grazing," resistance to sedimentation, mobility or the ability to "float," and the ability to migrate vertically and better utilize nutrients and light under conditions of stratification (Sommer et al., 1986). A whole series of authors have shown that resistance of filamentous Cyanobacteria is also manifested in the fact that they are capable of producing substances that are toxic to zooplankton (Baca, Drenner, 1995). The development of daphnias can be linked with the abundance of filamentous algae of the genus *Oscillatoria*, which can inhibit survival of the daphnias (Infante, Abella, 1985, cited in Gilbert, 1988). One of the reasons for this is that they clog the filtration apparatus by forming long filaments (Edmondson, 1991).

Results of the present investigations indicate that the summer development of phytoplankton is subject to bottom-up control in both reservoirs.

At the same time, it could be said that the development of zooplankton is subject to combined bottom-up and top-down control (points 6–7 and 14–16). Decrease in the density of zooplankton (especially large phytophagous Crustacea) is in great measure influenced by changes of phytoplankton composition involving the appearance of algae that are unsuitable as food or can even damage the filtration apparatus of the given Crustacea (such a species is *Ceratium*, which during summer develops massively in both reservoirs – 62% of total phytoplankton in the Grošnica Reservoir and 38% of total phytoplankton in the Gruža Reservoir) and ones that are inedible or can be toxic (Kozak, Goldyn, 2004), as in the case of intensive summer development of Cyanobacteria in the Gruža Reservoir. Increase in abundance of *Ceratium* with simultaneous dominance of small forms of zooplankton during this period has also been observed in other stratified reservoirs (Echevarria, Rodrigez, 1994). Jungmann and Bendorf (1994) established that *Microcystis* spp. (present in the Gruža Reservoir) produce substances that are toxic to daphnias, while Horn and Horn (1995) found that the abundance of daphnias has no effect on Cyanobacteria, colonial Chlorophyta, or the species *Asterionella formosa* (the dominant alga in the Grošnica Reservoir).

Visually oriented predatory fish find larger forms of zooplankton considerably easier to detect and therefore choose them selectively as prey (Arnott, Vanni, 1993). The data of Simović (2001) indicate that zooplankton plays an important part in the feeding of wild goldfish and roach. The Gruža Reservoir is also home to other fish that feed on zooplankton, such as bream (*Abramis brama*), bleak (*Alburnus alburnus*), chub (*Leuciscus cephalus*), and perch (*Perca fluviatilis*). Their influence on zooplankton structure has been cited by many authors (Serafimova-Hadžišče, 1978; Faurot, White, 1994; Kalafatić et al., 1997; Scharf, 1999).

Larger zooplankton species are readily noticeable and therefore become prey. However, body size is not always decisive. In the course of the discussed investigations, a great disporoportion was observed in the ratio of abundance of males and females of the species *Acanthocyclops vernalis* in favor of males during the summer months. In studying the varying success of three species of Cyclopoida (*Acanthocyclops robustus*, *Cyclops vernalis*, and *Diacyclops bicuspidatus*) in settling the pelagial of eutrophic lakes, Maier (1998) established that dominance of males in many populations of *Acanthocyclops robustus* is a result of predation by fish, which is also confirmed by many other authors (see list in Maier, 1998). Experiments showed that predatory fish are responsible for the low percentage of females (Maier, 1990a, cited in Maier, 1998). According to the explanation offered by Hopp et al. (1997, cited in Maier, 1998), females of *A. robustus*, although they are of medium size, produce much larger egg sacs and in much greater numbers than is the case with *Cyclops vicinus*, *C. abyssorum*, *Mesocyclops leuckarti*, and *Thermocyclops crassus*. Moreover, they do so at a time when they feed exclusively on algae or a mixture of algae and small zooplankton. The combination of large egg sacs and small or medium body size (as in *Acanthocyclops robustus*) leads to greater "vulnerability" of females as compared with males to predation by fish, which (together with significantly smaller body size in males) causes the ratio of sexes to be disturbed (Maier, 1998). These assertions are supported by data of Nassal (1997, cited in Maier, 1998) and Svensson (1997, cited in Maier, 1998) obtained in experiments with Cyclopoida and Calanoida, the results of which indicate that large dimensions of clearly visible egg sacs increase the risk of predation more than does large body size.

In addition to planktivorous fish, zooplankton can be prey to different groups of invertebrates, such as insect larvae and the largest of Cladocera, *Leptodora kindti*, which is present in both reservoirs. This species appears exclusively in summer, when a decrease is observed in the abundance of large herbivores. Citing many authors, Wojtal et al. (1999) assert that *L. kindti* significantly affects the abundance of planktivorous zooplankton, although it predominantly feeds on juvenile stages of Cladocera, whose abundance is in the phase of decline during summer, when *L. kindti* is present (Figs 3 and 4).

During the summer period, an increase is also observed in density of the rotifer *Asplanchna* sp. in both reservoirs, a species that is an important regulator of the abundance of small Rotatoria (Gilbert, 1980).

All predictions of the PEG model linked with the coldest period of the year (points 21–24) were completely fulfilled in both reservoirs. The small number of species in composition of the zooplankton and low values of abundance and biomass during the winter period (Figs 1 and 2) indicate that most species passed over into a stage of dormancy or formed durable (latent) eggs. Although point 24 predicts the appearance of certain species of Cyclopoida as a result of their "awakening" from the dormant phase, adults of Cyclopoida were only sporadically recorded, whereas fairly great abundance of Calanoida adults was registered. Thus, adults of *Eudiaptomus gracilis* were found during the winter months in the discussed investigations, especially in deeper layers. Other Copepoda and certain species of Cladocera occurred with a small number of individuals in the composition of winter zooplankton in both reservoirs (point 24) (Ostojić, 2000).

Conclusion

Even though 20 years have passed since the PEG model was conceived, it is still not possible to assert with complete certainty that all phenomena in dynamics of the plankton community can be explained by this model. Results of the present investigations are in large measure in keeping with predictions of the model. Certain differences between the two investigated reservoirs are evident in the presence of fairly pronounced oscillations of zooplankton density and biomass in the Gruža Reservoir, which is characteristic of other eutrophic aquatic ecosystems as well. Moreover, minor differences are also discernible in the species composition and dominance of different species during certain periods of the year, but they do not affect agreement of the results in both reservoirs with the PEG model.

Nevertheless, there are certain deviations from the PEG model. In the Grosnica Reservoir, which is mesotrophic, the greatest deviation is the almost total absence of Cyanobacteria, while the pattern of zooplankton dynamics at the beginning of summer represents a smaller deviation. At the same time, in the eutrophic Gruža Reservoir, enhanced production of zooplankton at the beginning of summer can be attributed to increased pressure of piscivorous fish with consequent decline in the number of planktophagic species, which enables zooplankton to develop.

However, for a more correct interpretation of the PEG model, it would perhaps be well to include some other components of the biocenosis. It should be noted that the mentioned model primarily explains successions in terms of *nutrients-algae-zooplankton* relations and that little is known about the influence of aquatic bacteria on successions of eukaryotic planktonic organisms (Chrost, 1991). The dynamics of bacterioplankton can more clearly explain changes in the abundance of some zooplanktonic organisms (above all Protozoa), as was evident in the present investigations.

Only a good understanding of different abiotic factors in combination with awareness of the interactions between organisms (predation, grazing, competition) can explain variations in their abundance, biomass, and successions (Hannson, 2000).

Translated by the authors

Acknowledgements

We are deeply grateful to anonymous referee for his valuable critique and suggestions.

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Received 8. 9. 2005