

Long-term development of reservoir ecosystems - changes in pelagic food webs and their microbial component

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ABSTRACT

Reservoirs differ from lakes mostly in three aspects: (i) water residence times usually are not longer than several months, (ii) horizontal heterogeneity induced by the inflowing river water is more pronounced, and (iii) they are historically much younger than lakes. As a consequence, seasonal and long-term dynamics of pelagic food webs reflect the changes in the catchment and hydrological variations more significantly than in lakes, and an ageing and “maturing” of the reservoir ecosystem might affect the pelagic biomass even several decades after filling. Using long-term data sets on pelagic biomass components from canyon-shaped reservoirs of different residence time, the following topics are discussed: (1) changes of pelagic bacteria-phytoplankton - zooplankton abundances during ageing as well as longitudinal changes from the river inflow downstream to the lacustrine part of a reservoir, (2) long-term changes of pelagic bacteria-phytoplankton-zooplankton abundances and seasonal changes of microbial loop in two reservoirs of different residence times. Periods with relative prevalence of bacterial above zooplankton biomass were detected, mostly coinciding with (or following after) the periods with low phytoplankton to zooplankton ratios.

Keywords: reservoirs, pelagic food webs, microbial loop, plankton

RESUMEN

Los embalses difieren de los lagos principalmente en tres aspectos: (i) el tiempo de residencia del agua no suele ser superior a varios meses, (ii) la heterogeneidad horizontal inducida por la entrada de agua fluvial es más marcada, y (iii) son históricamente mucho más jóvenes que los lagos. Como consecuencia de todo ello, las dinámicas estacional y a largo plazo de las redes tróficas pelágicas reflejan los cambios en la cuenca y las variaciones hidrológicas más significativamente que en los lagos, y el envejecimiento y “madurez” del ecosistema del embalse podría afectar a la biomasa pelágica incluso varias décadas después de su llenado. Mediante el análisis de largas series de datos sobre la biomasa de componentes pelágicos en embalses con sección en forma de cañón y diferentes tiempos de residencia, se discuten los siguientes aspectos: (1) cambios en las abundancias de bacterias-fitoplancton-zooplancton pelágicos durante el envejecimiento del embalse, así como cambios longitudinales desde la entrada de los ríos hasta la zona lacustre del embalse, (2) cambios a largo plazo en las abundancias de bacterias-fitoplancton-zooplancton pelágicos y cambios estacionales del bucle microbiano en dos embalses con diferentes tiempos de residencia. Se detectaron periodos con un predominio relativo de la biomasa bacteriana sobre la biomasa de zooplancton, coincidiendo principalmente con (o justamente después de) los periodos con bajas relaciones fitoplancton / zooplancton.

Palabras clave: embalses, redes tróficas pelágicas, bucle microbiano, plancton

PELAGIC MICROBIAL FOOD WEBS IN RESERVOIRS – DIFFERENT FROM THOSE IN LAKES?

Reservoirs differ from natural lakes though they have very much in common. What are the specific features of reservoirs compared to lakes and can they effect pelagic food webs structure and function directly or indirectly?

Reservoirs are geologically much younger than natural lakes. After filling a new reservoir, a complex process of reservoir ageing starts (Purcell, 1939) with a rate depending on the residence time. A “mature” stage is achieved first after stabilization of all components and processes within the ecosystem – from abiotic to biotic ones and from microorganisms and primary producers to the highest trophic link. Fish

assemblages, as the highest trophic link, were shown to develop for decades of years in reservoirs of temperate region until they reach a stage of dynamic equilibrium (Pivnička, 1992; Kubečka, 1993). Higher trophic links, however, exert a feed-back effect on lower levels and the resultant succession of events is effected by mutual interactions (Straškraba *et al.*, 1993). During several decades after filling a reservoir, interannual changes (or trends) in pelagic food web structure and function are expected to be faster than those occurring during long-term development of natural lake ecosystems. While evaluating pelagic food webs dynamics during ageing of a reservoir, possible effects of top down control and cascading effects should be considered, even when dealing with the “lowest” microbial level.

Reservoirs mostly have shorter water residence times than lakes – usually not longer than several months. This means that the loading from catchment is relatively more important than in most lakes and its effects upon the in-reservoir processes and pelagic assemblages might be more direct and faster (Kennedy, 1999). The interannual fluctuations of meteorological and hydrological conditions influence water residence time, which is the “key factor in reservoir limnology” (Straškraba *et al.*, 1993; Straškraba, 1998). A temporary decrease in residence time would exert a negative effect on pelagic organisms with slower growth rates (e.g. metazoic plankton - possible wash-out) whereas it might enhance phytoplankton, pelagic microbes and rotifers by an increased nutrient loading and, consequently, increased production. Microbial loop was effected both directly (by a changed loading) and indirectly (via changes in higher trophic levels). The indirect effect might be both via bottom up effect (changes in primary production, which is an important food source for pelagic bacteria) and via top down control (changes in grazers assemblages). The result of these complex interactions in the reservoir ecosystem is hard to be predicted unless we can use a modelling approach (Straškraba, 1999).

Longitudinal heterogeneity and transition from a riverine to a lacustrine zone is the characteristic feature especially of canyon-shaped reservoirs constructed in narrow river valleys. Development of pelagic assemblages in the upper part proceeds together with changes of chemistry, especially of the limiting nutrient concentration (Hejzlar & Vyhnálek, 1998; Armengol *et al.*, 1999). The most pronounced changes were found in the succession of microbial assemblages and their activities in the transition zone below the river inflow (Šimek *et al.*, 2001; Comerma *et al.*, 2001; Lind, 2002). In the riverine zone, bacteria (and partly also phytoplankton) are mostly bottom up controlled, whereas in the transition zone with an increasing protozoan development the top down control becomes to prevail. At the end of transition zone, crustaceoplankton from the lacustrine zone exerts a strong grazing pressure upon all the members of microbial loop.

In some respect, the phenomena observed along the longitudinal profile of the transition zone are similar to a time-succession of pelagic biota during the initial period of reservoir ageing. However, the changes in the transition zone of a mature reservoir are uncomparably faster than those occurring in a young ageing reservoir (i.e. the successive development of a “lacustrine” assemblage from an “inoculum” in the inflow). The “lacustrine” pelagic assemblage is already developed in a mature reservoir and the inflowing river water is “inoculated” from the lacustrine part by longitudinal mixing. In shallow (“non-canyon-shaped”) reservoirs of semi-arid and arid regions, characteristic short-term heterogeneity pattern were found close to the inflow during storm-driven pulses (An & Jones, 2002; Lind & Barcena, 2003).

In lacustrine parts of reservoirs the seasonal dynamics of pelagic assemblages is likely to be similar to this observed in lakes (PEG model - Sommer *et al.*, 1986). Various interactions among the components of pelagic food web are described in lake (e.g. Arndt & Nixdorf, 1991; Geller *et al.*, 1991). Even the interactions between bacteria and heterotrophic protozoans on

one side and crustaceoplankton on the other side (which have not been referred in PEG model) are mentioned in different aquatic systems (Pace & Orcutt, 1981; Güde, 1988; Gellert *et al.*, 1991; Kalff, 2002). Any specificity of such phenomena in reservoirs, and especially in behaviour of microbial loop, might be expected at low retention times, which might effect thermal stratification, higher trophic levels and/or higher input of allochthonous organics.

These effects are complex and difficult to identify, since they are usually accompanied by the changes of human activities in catchment, climate effect etc. A complex effect of climate drivers was indicated by coherent interannual changes in lakes not directly connected together (Kratz *et al.*, 1998) and in reservoirs of different retention time and size (Straškrábová, 1991; Straškrábová *et al.*, 1998).

In the following paper, several case studies dealing with the above referred topics will be presented from different Czech Reservoirs of various residence times, loading and size, however, of a

similar shape – narrow, canyon-shaped with steep banks and with a low surface to volume ratio, i.e. with a rather stable thermal stratification.

CHANGES DURING RESERVOIR AGEING AND DURING TRANSITION FROM RIVER TO RESERVOIR

The initial phases of reservoir ageing are documented with the data from Římov Reservoir, a canyon-shaped reservoir with three months average residence time, meso- to eutrophic. The filling started in 1979 and pelagic assemblages were analyzed each three weeks. Figure 1 shows changes during the first seven years after filling. Bacterial abundances and chlorophyll *a* concentrations were representative for epilimnetic layers, whereas the zooplankton biomass (protein N) was sampled from the whole column (25 m). In the first year of flooding bacterial abundances were extremely high, whereas the second year they were rather low with quite irre-

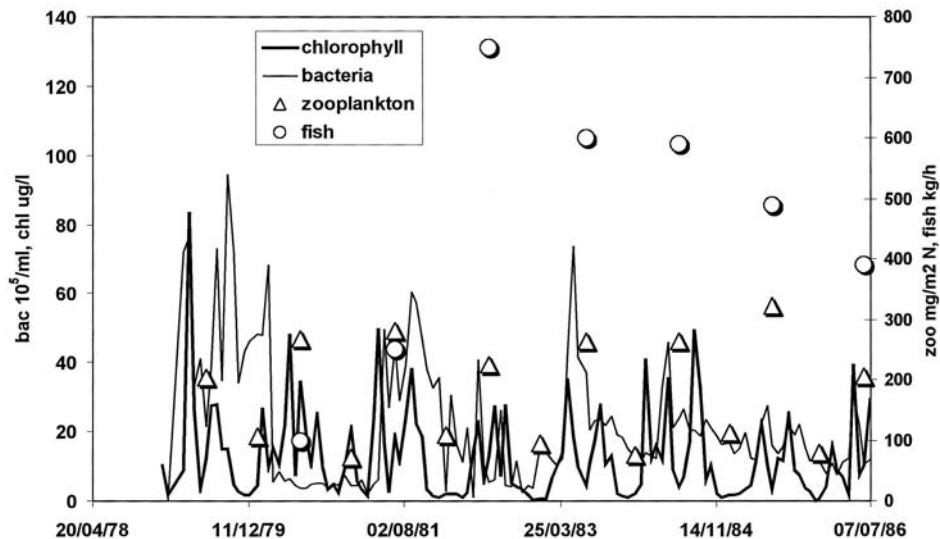


Figure 1. Changes in plankton and fish during the ageing of Římov Reservoir in the period 1979 – 1986 (6 years after filling the reservoir). Data for bacteria and chlorophyll from epilimnion - three weeks' interval, zooplankton from whole water column – averages from warm (April – September) and cold (October – March) periods, fish – yearly estimates. Chlorophyll, zooplankton and fish by the authors Komárková & Vyhánek, 1998, Brandl, 1994, Kubečka *et al.*, 1990, respectively. *Cambios en el plancton y en peces durante el envejecimiento del embalse Římov en el período 1979-1986 (6 años después de llenado el embalse). Datos de bacterias y clorofila del epilimnion – intervalos de 3 semanas, para el zooplancton de la columna de agua completa, – medias de los períodos cálido (abril-septiembre) y frío (octubre-marzo) peces – estimas anuales. Clorofila, zooplancton y peces según los autores Komárková & Vyhánek (1998), Brandl (1994) y Kubečka *et al.* (1990), respectivamente.*

gular seasonal changes. Chlorophyll concentrations also were quite high the first year and then decreased, but they showed regular seasonal pattern with two peaks (spring and summer) from the very beginning. Zooplankton biomass (averages for warm and cold half-year periods) did not show extreme peaks after flooding as observed earlier in other reservoirs (see Straškrábová & Pivnička, 2001). Zooplankton biomass was not adversely affected even in the year with the maximum fish biomass estimate (1982) and the following fish biomass decrease by biomanipulation was not connected with an increase of zooplankton. The only clear effect after filling and flooding soils in the catchment, apparently, was an enhanced phytoplankton development (bottom up effect of released nutrients) and increased bacterial abundances (bottom up effect of released organics and of phytoplankton production).

In 1999, i.e. 20 years after filling, transects from the inflow of the Malše River through transition zone towards the dam (lacustrine part) were investigated in meso- to eutrophic Římov Reservoir 7 times from April to October (Mašín *et al.*, 2003; Jezbera *et al.*, 2003). Seasonal averages of all pelagic components studied (chlorophyll, bacteria, heterotrophic

nanoflagellates, ciliates and crustaceoplankton) showed increases from the values in river towards those in the first station of transition zone (Fig. 2). The most conspicuous increase appeared in the mean abundance of crustaceoplankton, up to values more than 5 times higher compared to those in the lacustrine part, apparently as a consequence of an increased water residence time at the beginning of impoundment. The inflowing river is not rich in phytoplankton (light limited in forest), but it contains $30 \mu\text{g l}^{-1}$ of reactive phosphorus (average), which then allows phytoplankton growth under better light conditions in a broader canyon and at slower flow. All components of microbial loop were thus “bottom up” controlled, similarly like in the first stage of reservoir ageing.

In the following stations of the transition zone towards the dam, all pelagic biota were decreasing in abundance, especially zooplankton and phytoplankton. First then, the top down control of microbial loop is apparent. Quite a different situation occurred in the riverine and transition zone of another reservoir – eutrophic Orlík (Mašín *et al.*, 2003; Jezbera *et al.*, 2003). There the inflowing river contains high concentrations of phytoplankton (by one order higher

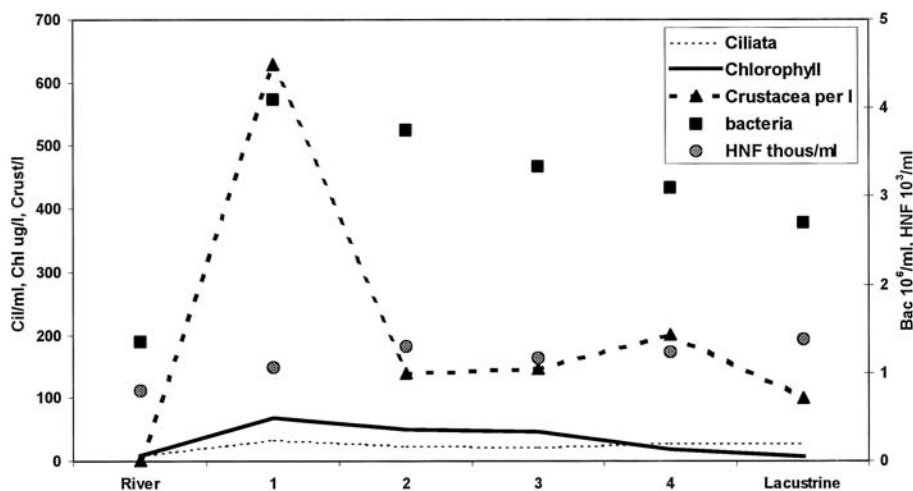


Figure 2. Longitudinal transect in the riverine and transitional part of canyon-shaped reservoir Římov (surface layer, averages from 7 transects) in 1999. Data by Mašín *et al.*, 2003 and Jezbera *et al.* 2003. *Transecto longitudinal en la parte fluvial y de transición del embalse Římov con perfil de cañón (capa superficial, medias de 7 transectos) en 1999. Datos según Mašín et al. (2003) y Jezbera et al. (2003).*

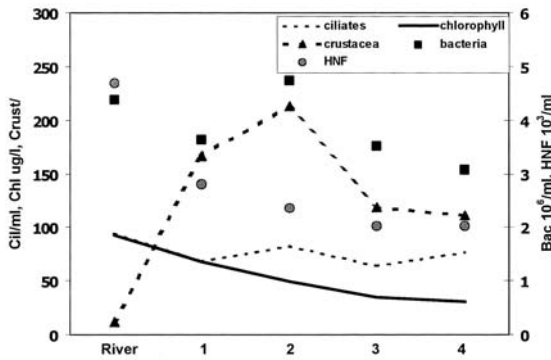


Figure 3. Longitudinal transect in the riverine and transitional part of one Vltava river branch in Orlik Reservoir (surface layer, averages from 7 transects) in 2000. Data by Mašín *et al.*, 2003 and Jezbera *et al.* 2003. *Transecto longitudinal en la parte fluvial y de transición de un ramal del río Vltava en el embalse Orlik (capa superficial, medias de 7 transectos) en 2000. Datos según Mašín et al. (2003) y Jezbera et al. (2003).*

compared to the Římov inflow), and, in accordance, also bacterial and protozoan abundances are 5 to 10 times higher (Fig.3). Crustaceoplankton abundances, however, showed quite similar pattern of development like in the Římov transect, with a slower increase (apparently due to higher flow in the Orlik transition zone). From the first station of transition zone, microbial loop, especially its protozoan component, were top-down

controlled and their abundances decreased (mostly those of heterotrophic flagellates) simultaneously with the increase of crustaceoplankton.

LONG-TERM CHANGES OF BACTERIOPLANKTON AND SEASONAL DYNAMICS OF PELAGIC MICROBIAL LOOP

Two reservoirs, Slapy and Římov, have been investigated in regular three weeks intervals for decades of years. The Slapy Reservoir is a part of the Vltava River cascade, located below the large Orlik Reservoir. It was impounded in 1954, the mean residence time is 38 days, mean depth 20.7 m and volume $270 \times 10^6 \text{ m}^3$. The other reservoir, Římov, was impounded in 1979 and its inflows are two small rivers. The mean residence time is 96 days, mean depth 16.5 m and volume $34.3 \times 10^6 \text{ m}^3$. The Slapy Reservoir is more trophic, with higher concentrations of total phosphorus, total nitrogen and dissolved organic carbon than Římov. Figures 4 and 5 show changes in bacterial abundances, chlorophyll concentrations and cladoceran biomasses during 1992 – 2001 in Římov and Slapy

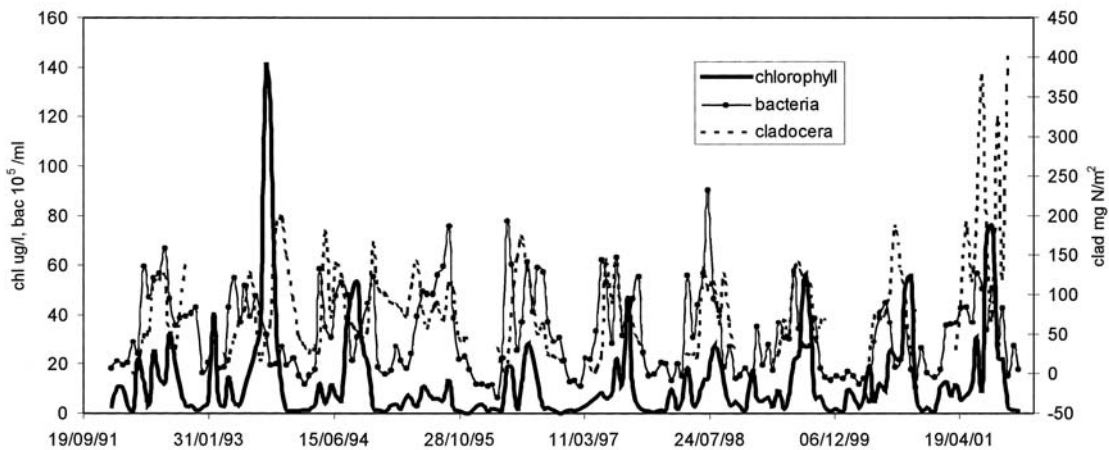


Figure 4. Long-term changes in plankton of Římov Reservoir (1996 – 2000). Bacteria and chlorophyll in epilimnion, cladocera – whole column. Sampling intervals every three weeks (zooplankton in winter less frequently). Data on chlorophyll and zooplankton by Komárková, 1993, Brandl, 1994 and from databases of Hydrobiological Institute CAS. *Cambios a largo plazo en el plancton del embalse de Římov (1996-2000). Bacterias y clorofila en epilimnion, cladocera – columna de agua completa. Intervalos de muestreo cada tres semanas (zooplankton en invierno menos frecuentemente). Datos de clorofila y zooplankton según Komárková (1993), Brandl (1994) y de las bases de datos del Hydrobiological Institute CAS.*

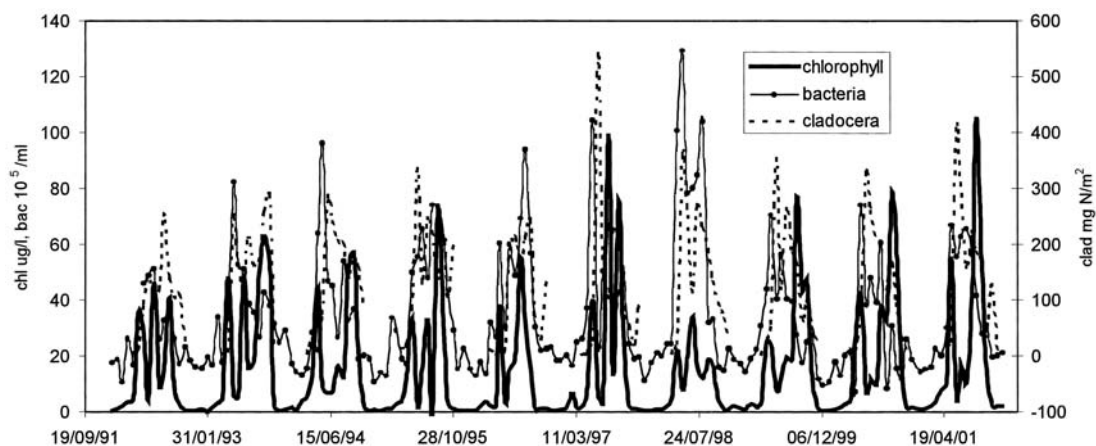


Figure 5. Long-term changes in plankton of Slapy Reservoir (1996 – 2000). Bacteria and chlorophyll in epilimnion, cladocera – whole column. Sampling intervals every three weeks, zooplankton in winter less frequently). Data on chlorophyll and zooplankton by Komárková, 1993, Brandl, 1994 and from databases of Hydrobiological Institute CAS. *Cambios a largo plazo en el plancton del embalse de Slapy (1996-2000). Bacterias y clorofila en epilimnion, cladocera – columna de agua completa. Intervalos de muestreo cada tres semanas (zooplankton en invierno menos frecuentemente). Datos de clorofila y zooplankton según Komárková (1993), Brandl (1994) y de las bases de datos del Hydrobiological Institute CAS.*

reservoirs, respectively. Bacteria were determined in surface layer as DAPI stained counts in epifluorescent microscope. Chlorophyll was analyzed in mixed samples from 3 meters (in Římov 4 meters) long tube and it is representative for euphotic layers. Cladocerans were sampled by nets from the whole column, separated by narcotization and protein N was determined as a measure of biomass. Methods are described in details by Straškrábová *et al.* (1998), Komárková (1993) and Brandl (1994).

During the years 1992 – 2001 the yearly averages of total phosphorus concentrations in the surface layer fluctuated in the range of 47.5 $\mu\text{g l}^{-1}$ P (in 1999) to 71.8 $\mu\text{g l}^{-1}$ P (in 1997) in Slapy and in the range of 26.4 $\mu\text{g l}^{-1}$ P (in 1994) to 35.3 $\mu\text{g l}^{-1}$ P (in 1992) in Římov Reservoir. Average yearly concentrations of total nitrogen (surface) also fluctuated, being 2520 – 4740 $\mu\text{g l}^{-1}$ N in Slapy and 2210 – 3350 $\mu\text{g l}^{-1}$ N in Římov. Dissolved organic carbon (yearly averages, surface) was in the range of 5.25 – 8.2 mg l^{-1} C in Slapy (maximum in 1996) and 4.8 – 5.8 mg l^{-1} C in Římov (maximum in 1994). Chlorophyll concentrations showed in Figs 4 and 5 correspond with a difference in trophic chemical indices – every year they are higher in Slapy than in Římov

(yearly averages 9.58 – 19.42 $\mu\text{g l}^{-1}$ in Slapy and 4.69 – 28.01 $\mu\text{g l}^{-1}$ in Římov), but neither the interannual variations in each reservoir nor the variations between reservoirs for each year correlated with total phosphorus concentrations. It seems that chlorophyll increase (or decrease) occurs with a delay of one or more years after a change in phosphorus concentration (if the change is longer lasting than one year). This is more pronounced in Římov, where the two years of the highest phosphorus concentrations (1993 and 2001) also show the highest chlorophyll values.

When comparing long-term seasonal dynamics of the two reservoirs, the most conspicuous difference is the higher amplitude of fluctuations in Římov (max/min is >3) than in Slapy (max/min is ~2.5), in spite of higher yearly averages in Slapy.

Then we tried to construct a generalized model of seasonal changes in the two reservoirs, which includes phytoplankton, two groups of zooplankton (copepods and cladocerans) and microbial loop (bacteria, heterotrophic flagellates and ciliates). An average seasonal course of pelagic components was calculated from the years 1992 – 2001, based on sampling in three weeks' intervals. Differences

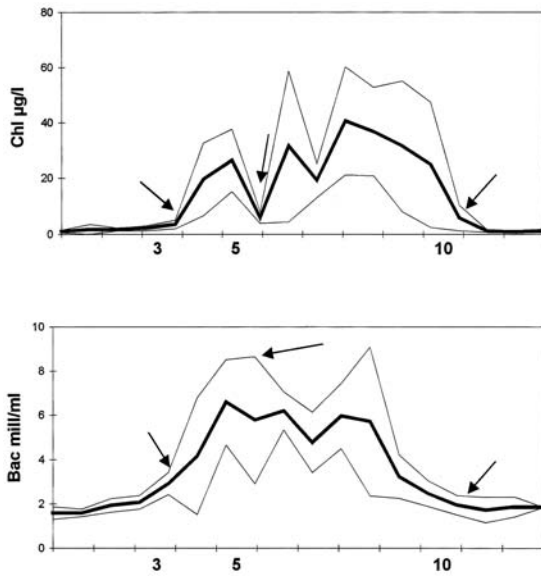


Figure 6. Normalized average seasonal dynamics of chlorophyll and bacteria in Slapy Reservoir for the period 1992 – 2001. Average values and average deviations (plus and minus) are plotted. Three arrows show the start of spring chlorophyll peak (end of 3rd month), clear water phase (end of 5th month) and end of summer chlorophyll peak(s) (end of 10th month). Based on databases of Hydrobiological Institute CAS. *Media normalizada de la dinámica estacional de la clorofila y bacterias en el embalse de Slapy durante el periodo 1992-2001. Se representan los valores medios y desviaciones medias (positiva y negativa). Tres flechas indican el inicio del pico de clorofila de primavera (finales del 3^{er} mes), la fase de agua clara (finales del 5^o mes) y final del pico(s) de clorofila estival (finales del 10^o mes). Basado en datos del Hydrobiological Institute CAS.*

between individual years due to meteorological conditions were excluded by “normalizing” seasonal events of each year according to the chlorophyll changes, i.e. the sampling in clear water phase (a decrease between spring and summer peaks) was compared for all years – this means shifting the whole-year sampling by one sampling interval forwards or backwards.

Figures 6 and 7 show the average curves in the two reservoirs for chlorophyll and bacteria together with average deviations. Important periods of plankton dynamics were distinguished according to the chlorophyll changes and marked by arrows: spring peak of phytoplankton starts with the increase of chlorophyll above $5 \mu\text{g l}^{-1}$, then clear water phase below $7 \mu\text{g l}^{-1}$

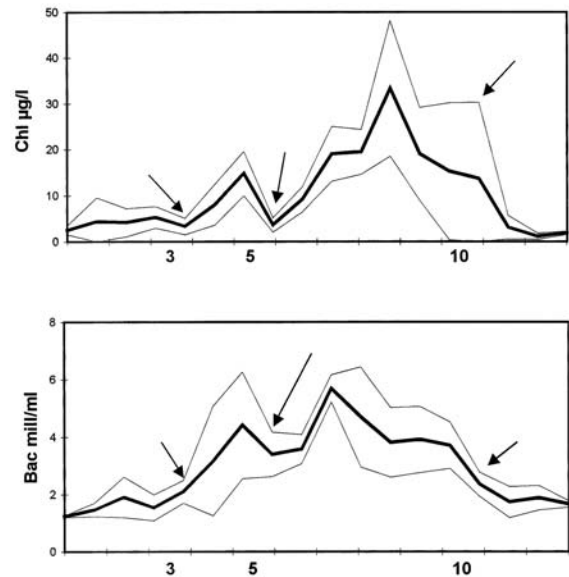


Figure 7. Normalized average seasonal dynamics of chlorophyll and bacteria in Římov Reservoir for the period 1992 – 2001. Average values and average deviations (plus and minus) are plotted. Three arrows show the start of spring chlorophyll peak (end of 3rd month), clear water phase (end of 5th month) and end of summer chlorophyll peak(s) (end of 10th month). Based on databases of Hydrobiological Institute CAS. *Media normalizada de la dinámica estacional de la clorofila y bacterias en el embalse de Římov durante el periodo 1992-2001. Se representan los valores medios y desviaciones medias (positiva y negativa). Tres flechas indican el inicio del pico de clorofila de primavera (finales del 3^{er} mes), la fase de agua clara (finales del 5^o mes) y final del pico(s) de clorofila estival (finales del 10^o mes). Basado en datos del Hydrobiological Institute CAS.*

only appeared in one sampling, which is the end of spring peak and also the start of summer phytoplankton peak and, finally, the end of summer phytoplankton peak(s) when chlorophyll falls below $10 \mu\text{g l}^{-1}$. The most pronounced differences between the two reservoirs are in chlorophyll concentrations during winter – they were very low in Slapy, but in Římov they were variable at the end of summer and in late winter they increased to a low late winter peak. Two more or less separated summer peaks of phytoplankton were found in Slapy, but not in Římov. A decrease in bacterial abundances during the clear water phase was only observed in Římov, but in Slapy no separate peaks of bacteria occurred from spring to autumn.

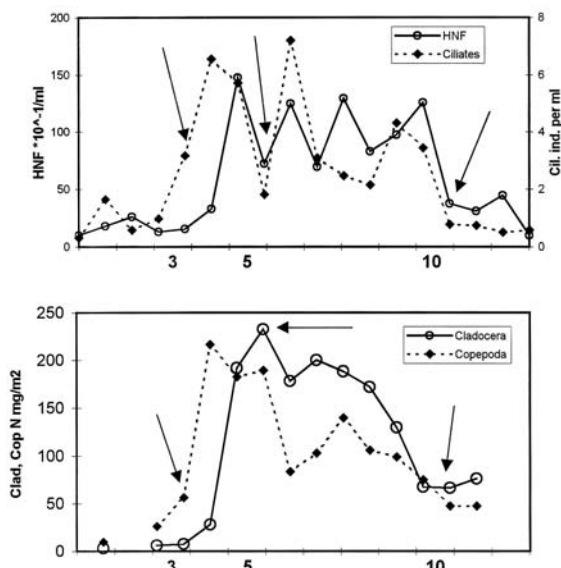


Figure 8. Normalized average seasonal dynamics of heterotrophic nanoflagellates (HNF) and ciliates (upper part) and cladocerans and copepods (lower part) in Slapy Reservoir for the period 1992 – 2001. Three arrows show the start of spring chlorophyll peak (end of 3rd month), clear water phase (end of 5th month) and end of summer chlorophyll peak(s) (end of 10th month). Based on databases of Hydrobiological Institute CAS. *Media normalizada de la dinámica estacional de los nanoflagelados heterotróficos (HNF) y ciliados (fracción superior), y cladóceros y copépodos (fracción inferior) en el embalse de Slapy durante el periodo 1992-2001. Tres flechas indican el inicio del pico de clorofila de primavera (finales del 3^o mes), la fase de agua clara (finales del 5^o mes) y final del pico(s) de clorofila estival (finales del 10^o mes). Basado en datos del Hydrobiological Institute CAS.*

The protists and metazoic zooplankton were shown in figures 8 and 9. The time of the spring copepods increase is different in both reservoirs – in Slapy it started from very low values earlier than in Římov and reached the maximum before the clear water phase, i.e. before the cladoceran maximum. In summer they showed another smaller peak. In Římov, on the other hand, copepods already were found to increase in late winter, peaked in clear water phase and decreased to lower values without the other peak. In concordance with this, cladocerans in Římov increased later and were far lower than in Slapy. And also the protists (upper parts of figures) developed accordingly. Though all components of plankton were higher in Slapy than in Římov,

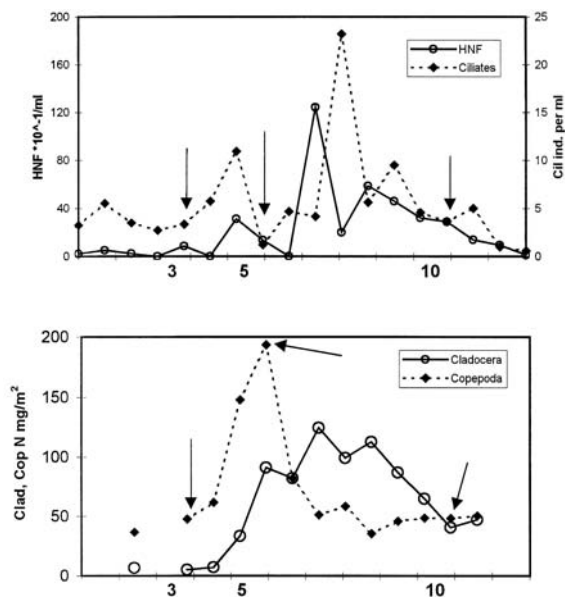


Figure 9. Normalized average seasonal dynamics of heterotrophic nanoflagellates (HNF) and ciliates (upper part) and cladocerans and copepods (lower part) in Římov Reservoir for the period 1992 – 2001. Three arrows show the start of spring chlorophyll peak (end of 3rd month), clear water phase (end of 5th month) and end of summer chlorophyll peak(s) (end of 10th month). Based on databases of Hydrobiological Institute CAS. *Media normalizada de la dinámica estacional de los nanoflagelados heterotróficos (HNF) y ciliados (fracción superior), y cladóceros y copépodos (fracción inferior) en el embalse de Římov durante el periodo 1992-2001. Tres flechas indican el inicio del pico de clorofila de primavera (finales del 3^o mes), la fase de agua clara (finales del 5^o mes) y final del pico(s) de clorofila estival (finales del 10^o mes). Basado en datos del Hydrobiological Institute CAS.*

ciliates were lower – apparently due to predation by copepods. In Římov, where no summer peak of copepods occurred, ciliates formed a high summer peak. In both reservoirs, a deep decrease of both protozoan groups was observed during clear water. When comparing seasonal courses of bacteria and protozoans, it seems that bacterivory of protists has not a direct effect upon a decrease in bacterial abundances (though it might exert a selective pressure on particular bacterial groups and enhanced their growth rates – Šimek *et al.*, 2001). An effect of cladocerans and even copepods on both protozoan and bacterial abundances was more pronounced.

In this study no attempt was made to assess interannual variations in amplitudes, periods

and timing of particular phases of plankton seasonal development. Interannual variations were excluded by normalizing among years.

SUMMARY

Special features of reservoirs compared to lakes were documented in two case studies: reservoir ageing and longitudinal changes in the upper transition zone of canyon-shaped elongated reservoirs.

Microbial assemblages together with phytoplankton are the first developed in high abundances after flooding a new reservoir. The following succession depends on development of higher trophic levels. After zooplankton development bacteria and phytoplankton are controlled. Ageing depends on residence time of the reservoir.

In some respect, the changes in the transition zone from a river to lacustrine part of reservoir are similar to ageing. In opposite, however, the lacustrine pelagic assemblages (even the higher trophic levels) are already developed in the reservoir and inoculate the inflowing water masses. Longitudinal succession of microbial assemblages mostly depends on zooplankton development.

When comparing the long-term changes of pelagic biota in two reservoirs of different trophy and different residence time, the reservoir with a higher trophy and shorter residence time showed higher average values of all investigated pelagic components except of ciliates, but a generally lower amplitude of yearly variations. Seasonal changes of the higher trophic level – zooplankton, apparently determined the changes in seasonal variation of microbial loop – both protozoans and bacteria.

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REFERENCES

- AN, K. & J. JONES. 2002. Reservoir response to the Asian monsoon with an emphasis on longitudinal gradients. *J. Freshwater Ecol.*, 17: 151-160.
- ARNDT, H. & B. NIXDORF. 1991. Spring clear-water phase in a eutrophic lake: Control by herbivorous zooplankton enhanced by grazing on components of the microbial web. *Verh. Internat. Verein. Limnol.*, 24: 879-883.
- ARMENGOL, J., J. C. GARCIA, M. COMERMA, M. ROMERO, J. DOLZ, M. ROURA, B. P. HAN, A. VIDAL & K. ŠIMEK. 1999. Longitudinal processes in canyon type reservoirs: The case of Sau (N. E. Spain). In: *Theoretical reservoir ecology and its applications*. J. G. Tundisi & M. Straškraba (eds.): 313-345. International Institute of Ecology, Brazilian Academy of Sciences, Backhuys Publishers, Leiden, The Netherlands.
- BRANDL, Z. 1994. The seasonal dynamics of zooplankton biomass in two Czech reservoirs: a long-term study. *Arch. Hydrobiol. Beih., Ergebn. Limnol.* 40: 127-135.
- COMERMA, M., J. C. GARCÍA, J. ARMENGOL, M. ROMERO & K. ŠIMEK. 2001. Planktonic food web structure along the Sau Reservoir (Spain) in summer 1997. *Int. Rev. Hydrobiologia*, 86: 195-209.
- DESORTOVÁ, B. & J. KOMÁRKOVÁ. 2001. Phytoplankton of the Klíčava Reservoir during 1959-1970. *Acta Universitatis Carolinae Environmentalica*, 15 (1/2): 33-55.
- GELLER, W., R. BERBEROVIČ, U. GAEDKE, H. MÜLLER, H. R. PAULI, M.M. TILZER & T. WEISSE. 1991. Relations among the components of autotrophic and heterotrophic plankton during the seasonal cycle 1987 in Lake Constanz. *Verh. Internat. Verein. Limnol.*, 24: 831-836.
- GÜDE, H. 1988. Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constanz. *Hydrobiologia*, 159: 63-73.
- JEZBERA, J., J. NEDOMA & K. ŠIMEK. 2003. The role of protistan bacterivory along longitudinal transects of two canyon-shaped reservoirs. *Hydrobiologia*, 504: 115-130.

- HEJZLAR, J. & V. VYHNÁLEK. 1998. Longitudinal heterogeneity of phosphorus and phytoplankton concentrations in deep-valley reservoirs. *Int. Rev. Hydrobiol.*, 83 (Special issue): 139-146.
- KALFF, J. 2002. *Limnology: Inland water ecosystems*. Prentice-Hall Inc., Upper Saddle River, NJ, 592 pp.
- KENNEDY, R. H. 1999. Reservoir design and operation: limnological implications and management opportunities. In: *Theoretical reservoir ecology and its applications*. J. G. Tundisi & M. Straškraba (eds.): 1-28. International Institute of Ecology, Brazilian Academy of Sciences, Backhuys Publishers, Leiden, The Netherlands.
- KOMÁRKOVÁ, J. 1993. Cycles of phytoplankton during long-term monitoring of Římov and Slapy Reservoirs (Czech Republic). *Verh. Internat. Verein. Limnol.* 25: 1187-1191.
- KOMÁRKOVÁ, J. & V. VYHNÁLEK. 1998. Long-term changes in chlorophyll concentration and phytoplankton structure in two canyon-type reservoirs. *Int. Rev. Hydrobiol.*, 83 (Special issue): 421-430.
- KRATZ, T. K., P. A. SORANO, S. P. BAINES, B. J. BENSON, J. J. MAGNUSON, T. M. FROST & R. C. LARTHROP. 1998. Interannual synchronous dynamics in north temperate lakes in Wisconsin, USA. In: *Management of lakes and reservoirs during global climate change*. D. G. George *et al.* (eds.): 273-287. NATO ASI Series 2: Environment vol. 2 Kluwer Academic Publishers.
- KUBEČKA, J. 1990. The quantity of fish populations in the Římov Reservoir in 1985 and the attempt of its evaluation in the previous years (In Czech). In: *Ichthyofauna řeky Malše a nádrže Římov (Ichthyofauna of the Malše River and the Římov Reservoir)*. J. Kubečka (ed.): 66-71. Jihočeské museum v Č. Budějovicích.
- KUBEČKA, J. 1993. Succession of fish communities in reservoirs of Central and Eastern Europe. In: *Comparative reservoir limnology and water quality management*. M. Straškraba, J. G. Tundisi & A. Duncan (eds): 153-168. Kluwer Academic Publishers
- LIND, O. 2002. Microbial production and reservoir zone trophic states. *Lake and Reservoir Management*, 18: 129-137.
- LIND, O. T. & E. BARCENA. 2003. Riverine and transition zone bacterioplankton community dynamics in response to pulsed river inflow. *Hydrobiologia*, 504: 79-85
- MAŠÍN, M., J. JEZBERA, J. NEDOMA, V. STRAŠKRÁBOVÁ, J. HEJZLAR & K. ŠIMEK. 2003. Changes in bacterial community composition and microbial activities along the longitudinal axis of two canyon-shaped reservoirs with different inflow loading. *Hydrobiologia*, 504: 99-113.
- PACE, M. L. & J. D. ORCUTT Jr. 1981. The relative importance of protozoans, rotifers and crustaceans in a freshwater zooplankton community. *Limnol. Oceanogr.*, 26: 822-830.
- PIVNÍČKA, K. 1992. The Klíčava Reservoir, Czechoslovakia: a 30 year study of the fish community. *Fisheries Research*, 14: 1-20.
- PURCELL, L. T. 1939. The ageing of reservoir waters. *J. Amer. Water Works Assoc.*, 31: 1775-1806.
- ŠIMEK, K., J. ARMENGOL, M. COMERMA, J. C. GARCIA, P. KOJECKÁ, J. NEDOMA & J. HEJZLAR. 2001. Changes in the epilimnetic bacterial community composition, production and protist-induced mortality along the longitudinal axis of a highly eutrophic reservoir. *Microb. Ecol.*, 42: 359-371.
- SOMMER, U., Z. M. GLIWICZ, W. LAMPERT & A. DUNCAN. 1986. The PEG model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.*, 106: 433-471.
- STRAŠKRABA, M. 1998. Limnological differences between deep valley reservoirs and deep lakes. *Int. Rev. Hydrobiol.*, 83 (Special issue): 1-12.
- STRAŠKRABA, M. 1999. Self-organization, direct and indirect effects. In: *Theoretical reservoir ecology and its application.s* J. G. Tundisi & M. Straškraba (eds.): 29-51. International Institute of Ecology, Brazilian Academy of Sciences, Backhuys Publishers, Leiden, The Netherlands.
- STRAŠKRABA, M., J. G. TUNDISI & A. DUNCAN. 1993. State-of-the-art of reservoir limnology and reservoir management. In: *Comparative reservoir limnology and water quality management*. M. Straškraba, J.G. Tundisi & A. Duncan (eds.): 213-288. Kluwer Academic Publishers.
- STRAŠKRÁBOVÁ, V. 1991. Periodic interannual oscillations in bacterial numbers and activity related to meteorological cycles. *Verh. Internat. Verein. Limnol.*, 24: 1332-1335.
- STRAŠKRÁBOVÁ, V., Z. BRANDL, J. HRBÁČEK, J. KOMÁRKOVÁ, J. SEĎA, M. STRAŠKRABA & K. ŠIMEK. 1998. Long-term changes of bacteria, phytoplankton and zooplankton: temporal coherence between deep stratified reservoirs. *Int. Rev. Hydrobiol.*, 83 (Special issue): 21-30.
- STRAŠKRÁBOVÁ, V. & J. KOMARKOVÁ. 1979. Seasonal changes of bacterioplankton in a reser-

- voir related to algae. I. Numbers and biomass. *Int. Rev. Hydrobiol.*, 64: 285-302.
- STRAŠKRÁBOVÁ, V. & K. PIVNIČKA. 2001. Long-term development of the Klíčava Reservoir ecosystem. *Acta Universitatis Carolinae Environmentalica*, 15 (1/2): 149-154.
- STRAŠKRÁBOVÁ, V., K. ŠIMEK & J. NEDOMA. 1999. Importance of pelagic bacteria in lakes and reservoirs of different trophic – implications for long-term monitoring. In: *Lake 99, Sustainable lake management*, 8th Internat. Conf. on the Conserv. and Management of Lakes, Vol. II, S7C, 4pp, Copenhagen.
- STRAŠKRÁBOVÁ, V., M. STRAŠKRABA & L. PROCHÁZKOVÁ. 2001. Limnology of the Klíčava Reservoir – 11 years' study. *Acta Universitatis Carolinae Environmentalica*, 15 (1/2): 13-32.

