

Brief history of long-term ecological research into aquatic ecosystems and their catchments in the Czech Republic

Part I: Manmade reservoirs





Research vessels mostly used for a research into fish ecology in reservoirs. Above is a new boat, named after Norwegian adventurer Thor Heyerdahl, and designed to conduct advanced hydroacoustical surveys and pelagic trawling (photo by Jaroslava Frouzová). Below is an older one Ota Oliva.



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Part I: Manmade reservoirs

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Jaroslav Hrbáček and Viera Straškrábová, photo from the archive of Viera Straškrábová

Dedication:

This book is dedicated to the founders of the Czech reservoir limnology school and initiators of long-term ecological research of reservoirs: Jaroslav Hrbáček, Pavel Blažka, Zdeněk Brandl, Blanka Desortová, Pavel Javornický, Jiří Popovský, Lidmila Procházková, Milan Straškraba, Viera Straškrábová, and many others.

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Long-term ecological research in the Czech Republic

Long-term ecological research provides valuable insights that can be obtained from other approaches only with difficulty. It facilitates testing of general ecological principles that are essential for understanding the complexity of ecosystems and allows future environmental changes to be predicted. The Czech long-term ecological research (LTER) network emerged during the early 1990s, following an initiative of US LTER scientists, and coordinates efforts among many scientists investigating ecological processes over long temporal and broad spatial scales. The network was formally established from six UNESCO Biosphere Reserves and two reservoir sites in 1996 and has gradually evolved into the current network, which consists of more than twenty LTER sites covering various temperate forests, grasslands, wetlands, and freshwaters in the Czech Republic (Fig. 1). Long-term data series have indicated changes in land use,

eutrophication, atmospheric sulphur and nitrogen deposition, and climate. In addition, the Czech LTER network includes a post-mining area to study soil formation and early succession, as well as an exterritorial LTER tropical rain forest site in Papua-New Guinea. Here we present two manmade reservoirs listed among the LTER sites and investigated by the Institute of Hydrobiology BC CAS for decades, and also present our major findings from these long-term and site-based studies. The first, Římov Reservoir, serves as a good example of a medium-sized headwater reservoir with no cascade effect from upstream reservoirs, while the Slapy Reservoir is a good example of downstream cascade reservoir. The Slapy catchment covers almost the entire region of South Bohemia for which statistical data regarding anthropogenic pressure are available and can be compared with time series of water-quality parameters.

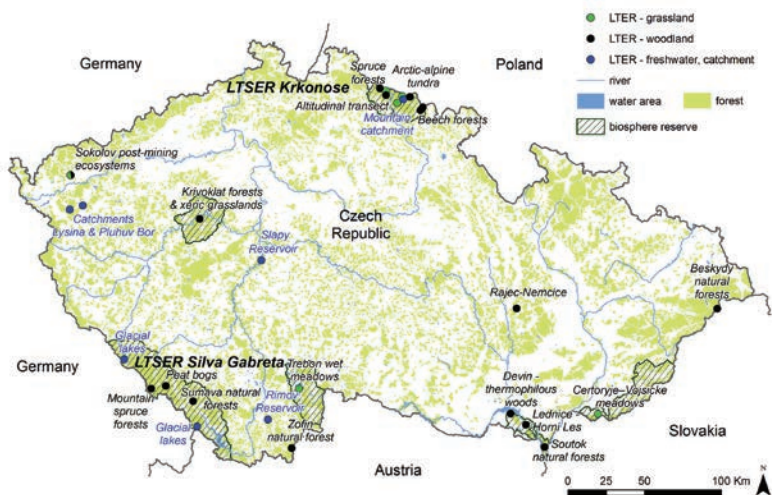


Figure 1: Map of all sites included in the Czech LTER network (except for Wanang, Papua-New Guinea).

Freshwater planktonic food webs

Freshwater plankton are among the most important components of aquatic food webs. In lakes and reservoirs, the planktonic food chain is responsible for most of the autochthonous production. Planktonic organisms have adapted to spend a part or all of their lives in the open water. The plankton can be divided into several functional groups, the major groups of which are phytoplankton, zooplankton and bacterioplankton.

Phytoplankton represent the base of aquatic food webs and consist of photosynthesizing microscopic algae and cyanobacteria ranging in size from 1 μm to macroscopically visible particles of up to few centimetres that float in the water column. Their role in aquatic ecosystems is to form organic matter by assimilating dissolved inorganic carbon, absorbing light as a pri-

mary source of energy. For their growth they also require inorganic nutrients (mainly phosphorus and nitrogen), which are taken up in dissolved forms. Their composition and biomass vary on both temporal and spatial scales. Seasonal succession of freshwater phytoplankton has been described as an annually repeated process of community assembly driven by both external factors and internal interactions. Among the phytoplankton, diatoms are one of the most important components of pelagic food webs, tending to dominate in spring when water column mixing and nutrient availability allow for the building of a vernal peak of biomass. After a mid-season phytoplankton minimum (so called “clear-water phase”, induced by intensive zooplankton grazing), various algal groups can dominate the summer phytoplankton (**Fig.2**), depending on

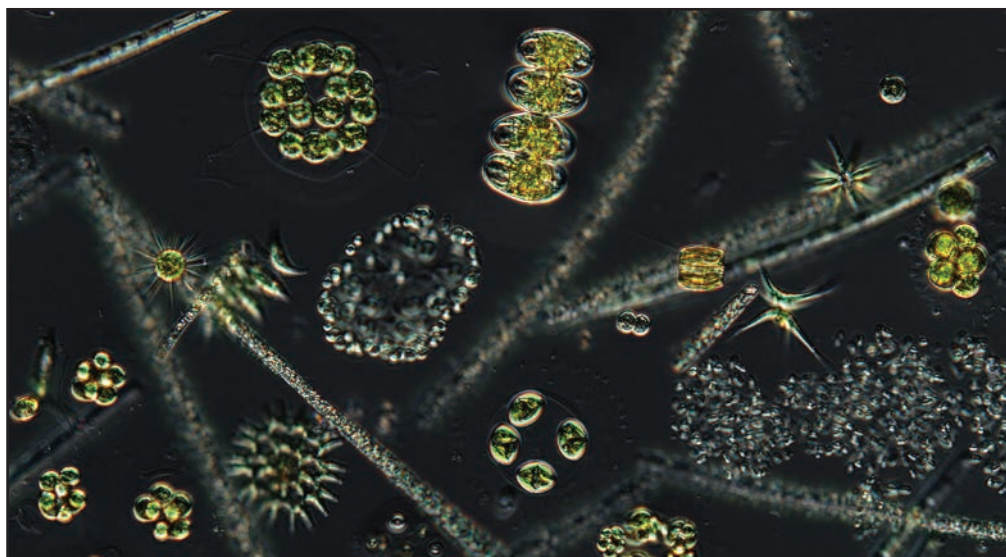


Figure 2: Species-rich summer phytoplankton consisting of cyanobacteria, green algae, desmids and diatoms.

the environmental conditions that favour a particular ecophysiological trait.

Zooplankton are a vital component of freshwater food webs and encompass a wide range of both unicellular and multicellular animals. The biggest are only few millimetres long, and the smallest are just one thousandth of this size. Zooplankton graze on bacteria, phytoplankton and suspended detrital particles at the same time; the smallest are eaten by the larger zooplankton which, in turn, are eaten by fish. Freshwater zooplankton (**Fig. 3**) are dominated by protists, rotifers, and two subclasses of the Crustacea, the cladocerans and copepods. Filtration of particles is the dominant way rotifers and cladocerans collect food. Filtering rates tend to increase

with increasing body length, and the size of particles ingested is generally proportional to body size. The effectiveness of zooplankton grazing varies greatly seasonally and among sites. At certain times of the year (especially in spring), grazing can remove large portions of algae, leading to the clear-water period. At this time herbivorous zooplankton become food-limited and their numbers decline due to both reduced fecundity and increased predation pressure from planktivorous fish.

Fish (**Fig. 4**) are the top consumer and the key component that structures aquatic food webs. Fish communities are less dynamic than plankton, so the recommended temporal resolution of basic fish standing stock surveys is at one year, with one extensive survey

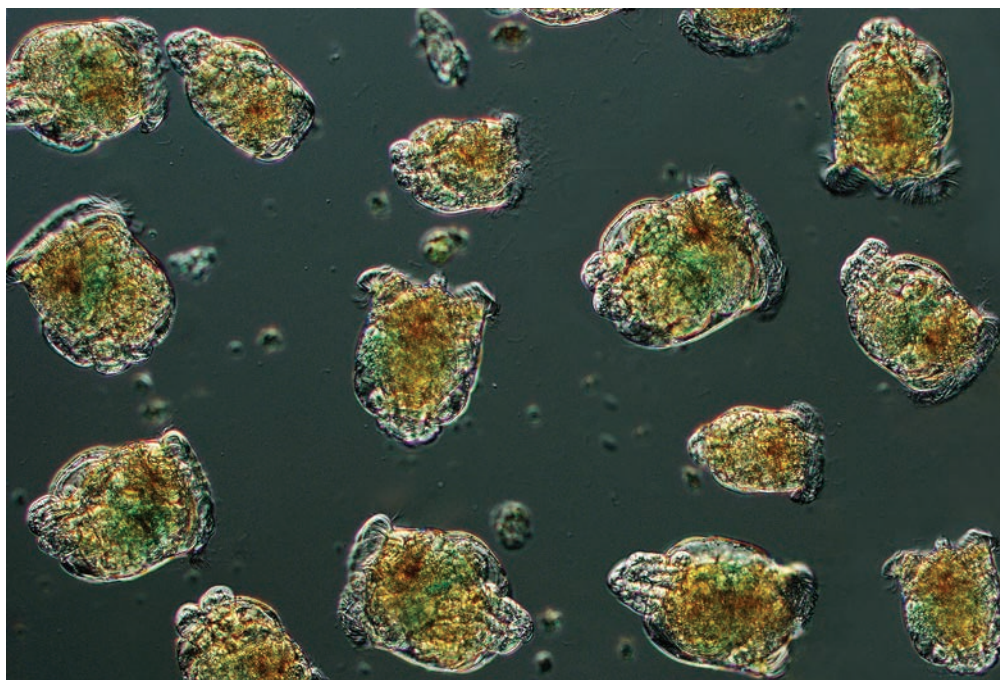


Figure 3: Planktonic rotifers. Green colour comes from ingested algae.

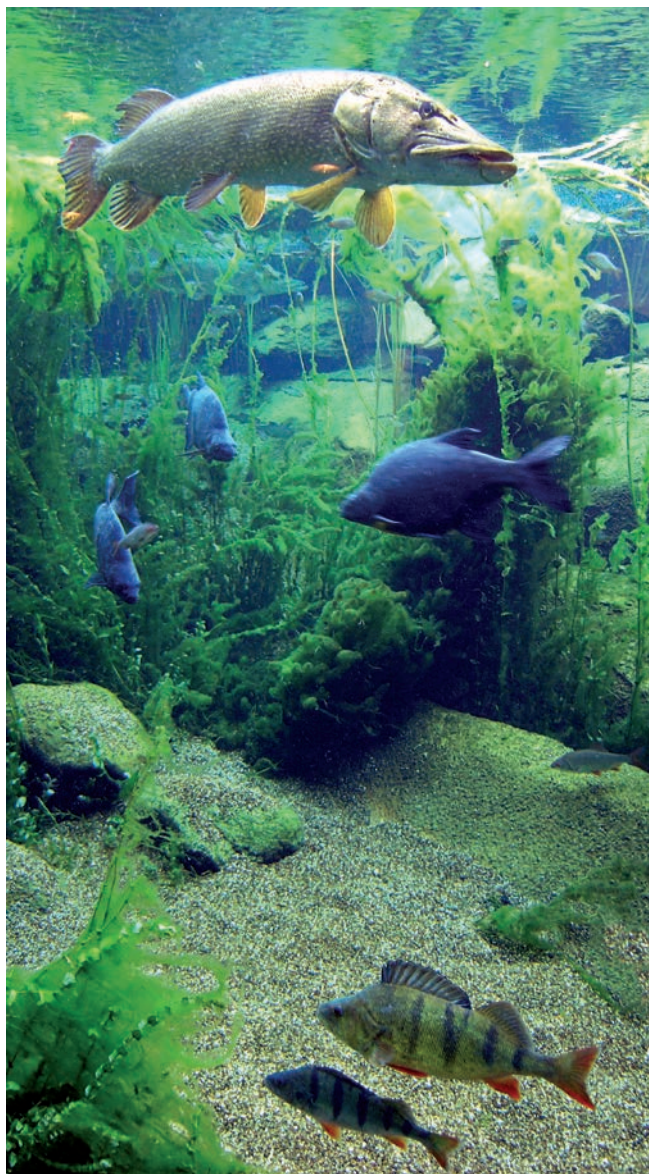


Figure 4: Common freshwater fish, pike (above), bream (centre) and perch (below). Photo by Jiří Peterka.

separately for age-0 fish (young-of-the-year) and all older individuals (both predatory and non-predatory).

Bacterioplankton play the prominent role in transforming organic matter within aquatic food webs and in driving global biogeochemical cycling of elements essential for life. The main role of bacterioplankton is to recycle dissolved and particulate organic matter (DOM and POM) formed in aquatic ecosystems during processes such as phytoplankton growth, viral lysis, or incomplete digestion of food grazed by zooplankton, which makes both DOM and POM available to higher trophic levels via their incorporation into bacterial cells that can be grazed. The most important grazers on bacteria are small colourless flagellated cells, called heterotrophic nanoflagellates (HNF). Ciliates, rotifers, and other (smaller) zooplankton may, however, be important for brief periods. Bacteria also use

done each August or September. For methodical and practical reasons, the fish data are usually expressed

allochthonous dissolved organic matter (mainly of terrestrial origin), and they can grow on detrital particles.

Basics of reservoir limnology

Most of our studies addressing plankton ecology were done at reservoirs, since natural lakes are virtually absent from the Czech Republic. In their place, several tens of thousands of manmade ponds and reservoirs are scattered across the land. Freshwater reservoirs are water bodies of special interest, as they provide various ecosystem services such as the supply of drinking water, agricultural irrigation, industrial and cooling water supplies, power generation, flood control and recreation. Reservoirs share many features with natural lakes but differ from them in several important aspects, particularly the very common canyon-shaped reservoirs, constructed by damming a river valley (**Fig. 5**), and which repre-

sent a transition between running and standing waters. Compared to natural lakes, these reservoirs often have elongated morphology, shorter water residence times, pronounced water-level fluctuations and irregular water withdrawal, often from various strata. As such, reservoirs have complex hydrodynamic characteristics that affect aquatic biota and that have specific implications for water quality.

The mixing regime and thermal structure of aquatic systems have a profound effect on ecosystem functioning because they strongly influence the availability of nutrients, light and oxygen. Most of the deep temperate reservoirs show a dimictic



Figure 5: Aerial view of the concrete dam of the Slapy Reservoir.

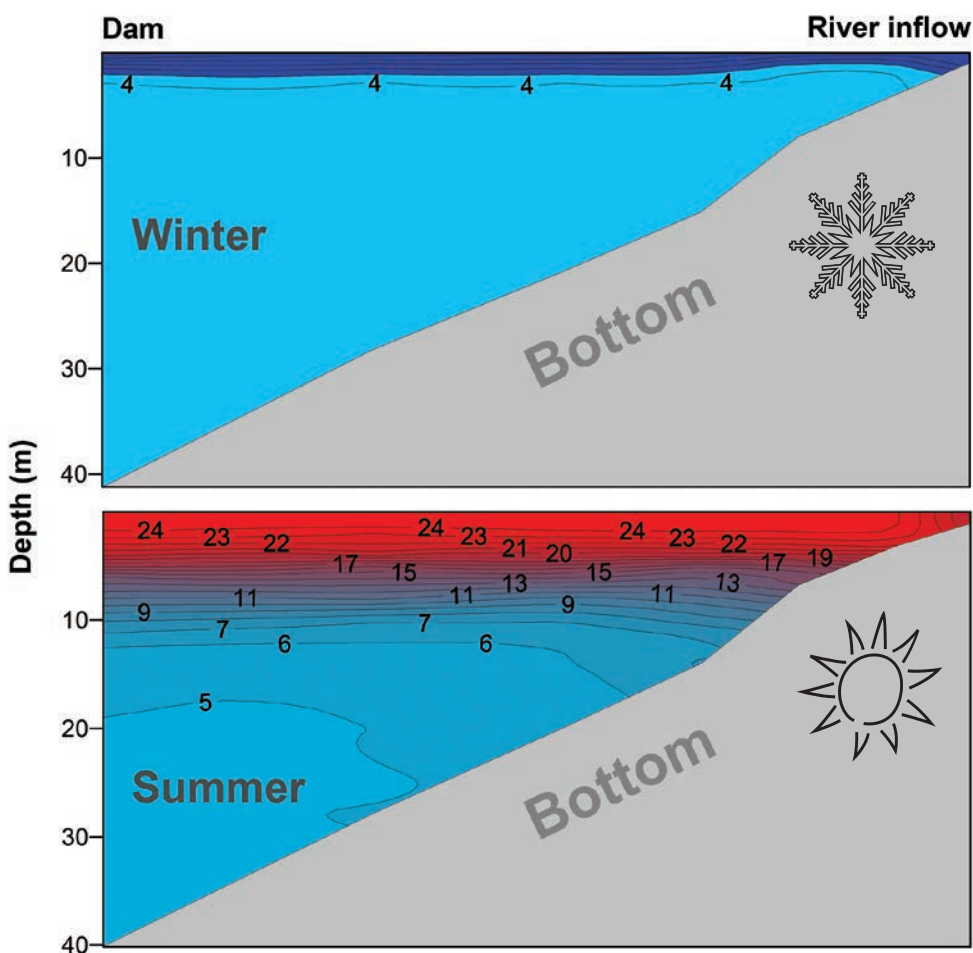


Figure 6: A scheme of typical temperature profiles of a reservoir. Numbers indicate temperature ($^{\circ}\text{C}$), lines isotherms. Upper panel depicts the inverse thermal stratification in winter, where the cold water (dark colour) is at the surface. Lower panel illustrates the summer stratification of the water column, where the epilimnion and hypolimnion are indicated by red and blue, respectively.

pattern in the water column. Dimictic reservoirs mix twice a year, in spring and autumn, while typically stratifying during summer and winter (Fig. 6). In summer, three layers can be recognized in the water column. At the surface, there is a warm upper layer (epilimnion) between the surface and the thermocline (metalimnion) which forms the boundary between the epilimnion and the cold waters of

the lower depths (hypolimnion). Water in the epilimnion is less dense than in the hypolimnion, homothermous and mixed by wind actions. Stratification in canyon-shaped reservoirs is often influenced by insertion of inflows through different layers of the water column and by the depth of outflow. Discharging of water from deep layers supports short-circuiting water flow through the reservoir and modifies

the seasonal stratification pattern. Reservoirs with deep discharging accumulate more heat than natural lakes, which always have surface outflows. The thermal and mixing regime in cascades of reservoirs can have even more complicated seasonal patterns.

One important parameter affecting phytoplankton growth is the depth of the euphotic zone. The euphotic zone extends from the surface down to the depth of compensation point where light intensity falls to one percent of that at the surface. At the compensation point, primary production is equal to phytoplankton respiration. A useful measure of light availability is the ratio between mixing and euphotic depths. If the thermocline is below the euphotic zone, the phytoplankton will

spend at least part of their life in the deeper aphotic zone where there is not enough light for photosynthesis. On the other hand, when the euphotic zone is deeper than the epilimnion, phytoplankton may form pronounced subsurface peaks of biomass due to enhanced growth at the thermocline, where nutrients are often being replenished from the hypolimnion. It is noteworthy that phytoplankton maxima at the thermocline can be also formed due to biomass accumulating at the density gradient.

In numerous water bodies, harmful (toxic, food-web altering, hypoxia-generating) phytoplankton blooms (Fig. 7) recurrently threaten the ecological integrity and sustainability of those systems. Traditionally, the term



Figure 7: Cyanobacterial blooms accumulated in the upstream part of the Římov Reservoir.

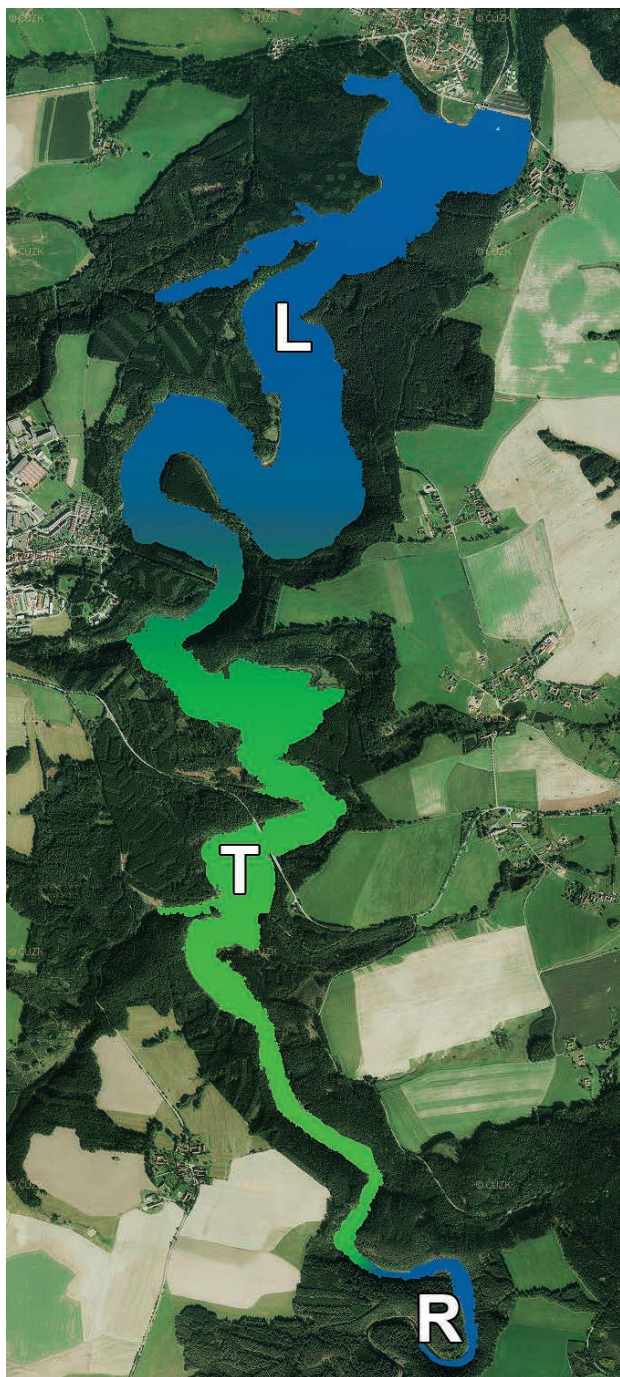
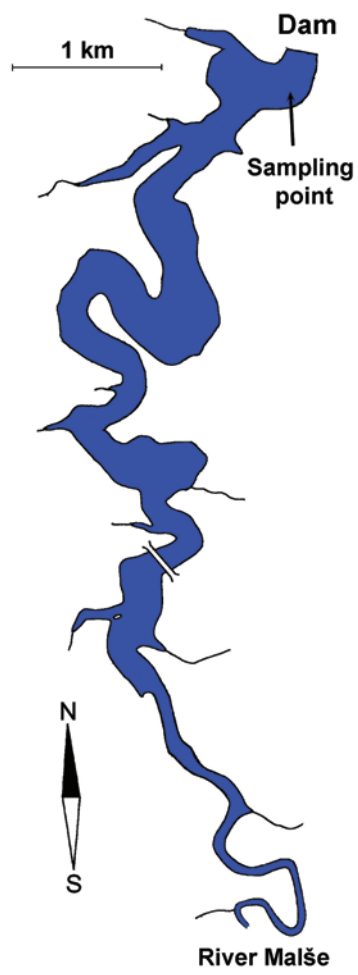


Figure 8: A map of the Řimov Reservoir. The reservoir is highlighted by false colours indicating the riverine (R), transition (T) and lacustrine (L) zones.

phytoplankton bloom is applied to a rapid increase or accumulation of algal or cyanobacterial biomass. The increasing incidence of blooms is considered to be a consequence of anthropogenic nutrient enrichment, i.e. eutrophication. The most important sources of nutrients are external sources situated in the catchment, which mainly include domestic sewage and agricultural waste in the form of manure or artificial fertilizers. However, internal loading from sediment and recycling of accumulated nutrients, especially of phosphorus, can contribute significantly to eutrophication and may continue to hamper recovery from eutrophication even after catchment sources are controlled. While eutrophication in reservoirs is subject to the same rules as in lakes, many specific issues affect the growth of phytoplankton, such as stratified flows and short-circuiting of tributaries, mixing regime and water-level fluctuations. Eutrophication effects in elongated reservoirs can be also highly variable spatially, for example on a gradient from hypertrophy to oligotrophy across the inflow/transition/lacustrine parts of the water body (**Fig. 8**).

Římov Reservoir

| | |
|---|---|
| Ecosystem type | Manmade freshwater reservoir |
| Site coordinator/contact | Petr Znachor/znachy@gmail.com |
| Institution | Institute of Hydrobiology, Biology Centre CAS |
| Address | Na Sádkách 7, České Budějovice, CZ-37005, Czech Republic, more details on www.hbu.cas.cz |
| Site characteristics | |
| Surface area / volume | 2.06 km ² / 34.5 × 10 ⁶ m ³ |
| Maximum / average depth | 43 / 16.5 m |
| Latitude / longitude / water level maximum altitude | 48°49'58"N / 14°29'30"E / 471 m a.s.l. |
| Mean air temperature / annual precipitation | 7.1°C / 659 mm |
| Annual / long-term mean retention time | 31–122 / 77 days |



The Římov Reservoir (**Fig. 9**) is a dimictic, deep-valley reservoir built in 1974–1979 to store drinking water by damming a 13.5 km long section of the River Malše, the main reservoir tributary accounting for 90% of the water inflow. The reservoir is filled by headwaters from a medium-sized hilly catchment (489 km²) covered mostly by forests and partly with arable land, pastures and meadows. The dam is 47 m high and 290 m long at its crest and is equipped with multilevel outlet and withdrawal structures. Water is discharged into the river via (i) a gated spillway (466.1 m a.s.l.), (ii) two bottom outlets (430.5 m a.s.l.) and (iii) a small shaft outlet with adjustable spot height of intakes from 440.5 to 471 m a.s.l. and a capacity of 3.6 m³ s⁻¹, which is also used by a small hydropower plant with a maximum capacity of 1 MW. Raw water for the drinking water plant (approx. 7 km downstream from the dam) is withdrawn at different elevations (444.5, 450.5, 457 and 463.5 m a.s.l.) in a tower situated near the dam

Figure 9: A map of the Římov Reservoir.



Figure 10: Aerial view of the dam area of the Římov Reservoir.

(**Fig. 10**). The reservoir became fully operational in 1979, when it was filled to the elevation of 464.5 m a.s.l. The monitoring program has been conducted by the Institute of Hydrobiology BC CAS (based in the nearby town

of České Budějovice) regularly at three-week intervals since 1979. At a fixed sampling site near the dam, and above the maximum depth of 40–42 m, the water is sampled for physical, chemical and biological parameters (**Table 1**).

Table 1. Major long-term data available for the Římov Reservoir. Unless stated otherwise, physical and chemical variables have been measured regularly at the dam at three-week intervals since 1979.

| Measured variables | |
|-----------------------------|--|
| Physical environment | transparency, vertical profiles of water temperature and dissolved oxygen concentration, inflow and outflow rates |
| Hydrochemistry | alkalinity, conductivity, pH, major ions, nutrients (various forms of C, N, P) |
| Hydrobiology | chlorophyll <i>a</i> ; phytoplankton biovolume and abundance (since 1983); zooplankton size structure and protein biomass; fish biomass, abundance and species composition*; bacterial abundance (and biomass since 1996); HNF (abundance since 1990); species composition, abundance and biomass of ciliates (since 1987) |

* measured once a year in the whole reservoir since 1985

Overview of long-term ecological research into the Římov Reservoir

The history of limnological research into the Římov Reservoir (**Fig. 11**) began soon after its filling in the early 1980s and was closely associated with monitoring of basic hydrochemical, physical and biological parameters that had implications on water-quality management. Most of the early results have been published as scientific reports and conference proceedings written in Czech, which are not available online. Searching for rel-

evant papers on the Web of Science (<http://apps.isiknowledge.com>) turns up 190 studies in total (July 2016, search string “Římov”, all databases). These studies have received 3,137 citations, which achieves a quite decent “site” Hirsh index of 32 (32 papers were cited at least 32 times). Altogether, this clearly illustrates the importance of the research for our understanding of reservoir limnology. The first paper to be internationally recognized (65 citations by July 2016) was published in 1990 and has dealt with possible food-chain relationships between bacterioplankton, protozoans and cladocerans (**Fig. 12**) in the reservoir (Šimek et al. 1990). This paper represents the pioneering study that studied different trophic levels of aquatic food chains and showed new avenues for future research into aquatic microbial ecology. In the early 1990s the scope of limnological research into the Římov Reservoir was significantly extended and addressed important questions on ecosystem functioning.

The most relevant early findings on reservoir hydrology, water quality, phytoplankton, zooplankton and fish community during the first years of the reservoir



Figure 11: Aerial view of the Římov Reservoir.



Figure 12: A representative of filter-feeding crustacean zooplankton – *Ceriodaphnia* sp.

were summarized in the book “Ichthyofauna of the River Malše and the Římov Reservoir” (Kubečka 1990), which was, however, published only in Czech, with English abstracts, and indexed by Web of Science. As time passed, new methods and techniques have been adopted to assess, for example, diagnostics of phosphorus deficiency for phytoplankton growth (Nedoma et al. 1993), in-vivo chlorophyll *a* fluorescence for estimation of phytoplankton biomass (Vyhnálek et al. 1993), and activity- or enzyme-based assays for estimating nutrient transformation by plankton communities (Vrba et al. 1992, 1993). Our understanding of reservoir limnology benefited from the holistic approach to the ecosystem, allowing for syntheses based on numbers of narrowly targeted studies; the most important will be described in detail later.

In general, reservoirs undergo great changes in water quality during the early stages of their formation whilst a new ecological balance is being established. In the early 1990s the first attempts were made to evaluate long-term changes in nutrient loading and aquatic biota composition. Hejzlar et al. (1993) used a simulation model of reservoir hydrodynamics to quantify epilimnion phosphorus loading in the spring-summer period between 1984 and 1991. Due to the inflow temperature-density currents, through those years the fraction of total P entering the upper layers of the water column varied from 12 to 31%. That clearly illustrates that nutrients brought by the river inflow usually form a persistent intrusion at the thermocline. Occasionally, due to the wind action, nutrients are mixed, drawn to the upper

layer and transported along the reservoir to the dam, which in turn results in increased phytoplankton biomass. In a short data set (1984–1990), phytoplankton summer biomass was found to be negatively correlated with average river flow rates, supporting the previous assumption that nutrients remain mostly inaccessible to phytoplankton in deeper strata of the water column (Komárková 1993). Using an extended time series (1980–1993), Komárková & Hejzlar (1996) elaborated on previous findings postulating that in dry years, phytoplankton growth at the dam is maintained by internal P cycling in the water column, since phosphorus entering the reservoir is exhausted upstream. Interestingly, the relative proportion of cyanobacteria

(Fig. 13) in summer phytoplankton was correlated with average epilimnion temperature, which has since been repeatedly observed elsewhere. From 1980–1996, the mean annual concentration of total phosphorus at the dam significantly decreased; however, it was not followed by a decreasing trend in the overall phytoplankton biomass (Komárková & Vyhánek 1998). No systematic trend was found in phytoplankton composition. Using multivariate analyses, Komárková et al. (2003) attributed the occurrence of diatom-dominated phytoplankton to summer disturbances (high inflow episodes), while cyanobacteria prevalence was associated with stable thermal stratification.



Figure 13: Coiled filaments of a bloom-forming cyanobacterium *Dolichospermum flos-aquae*.



Figure 14: Aerial view of the Římov Reservoir. Brown water colour is caused by both diatom bloom and high concentration of dissolved organic carbon.

The Římov Reservoir is one of many localities in Europe and North America where concentration of dissolved organic matter (DOM) increased during the last three decades, leading to browning of water (Fig. 14) with important ecological consequences. Among these are the provision of ecosystem subsidies in the form of nutrients and organic carbon for bacteria, the microbial loop and zooplankton, and the effects of shading in the water column. Hejzlar et al. (2003) analyzed long-term and seasonal DOM changes in the main reservoir's tributary, the River Malše, during 1969–2000. Two periods have been detected within

this data set: years with a decreasing trend in DOM concentration until the middle of 1980s, and then years with increasing DOM concentration until 2000. Temperature, the hydrological regime of runoff from the catchment (namely the amount of interflow), and changes in atmospheric deposition of acidity coincided with variations in DOM.

Based on the analysis of the twelve-year data set (1979–1990), Brandl (1994) characterized the mean seasonal dynamics of zooplankton community as a pronounced spring peak of copepods followed by a cladocer-

an maximum three weeks later. A remarkable experiment manipulating the trophic structure of pelagic food webs in the reservoir was conducted in 1985–1992 (Seda & Kubečka 1997). Soon after the reservoir was flooded came a huge increase in the biomass of planktivorous fish, which in parallel with high nutrient loading led to lower water quality. A decision was therefore made to take remedial biomanipulative measures, which involved three strategies. (i) The spawning success of cyprinids was controlled by increasing the water level before the spawning period, to encourage spawning in flooded terrestrial vegetation, and then at the end of spawning period by lowering the level by ~ 0.5 m. This measure destroyed 95% of the eggs laid in the littoral zone. (ii) Undesirable fish species like perch, roach (Fig. 15), bream, and rudd were captured and

removed using various approaches such as electroshocking, fyke-nets and shore seines. (iii) Finally, the population of piscivorous fish was supported by regular stocking and by prohibiting any angling on predatory fish. Combining all the aforementioned strategies, fish biomass decreased from 650 kg ha^{-1} to 100 kg ha^{-1} . Despite the effort, the improvement in water quality was negligible. Nonetheless, Seda & Kubečka (1997) confronted this failure with data from similar biomanipulative experiments and eventually were able to construct a quantitative model showing that to induce a desirable effect on the structure of the pelagic food web, i.e. to lower the phytoplankton biomass, fish biomass must be reduced to below 60 kg ha^{-1} . It is noteworthy that, in response to biomanipulation, and despite no significant change in the overall phytoplankton

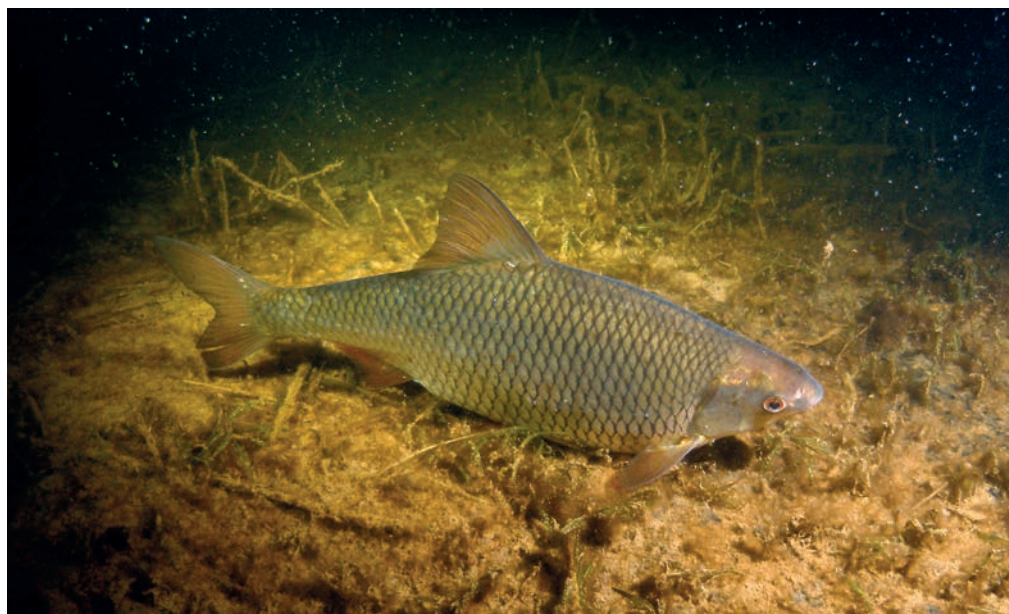


Figure15: An example of zooplanktivorous fish – roach (*Rutilus rutilus*). Photo by Jiří Peterka.

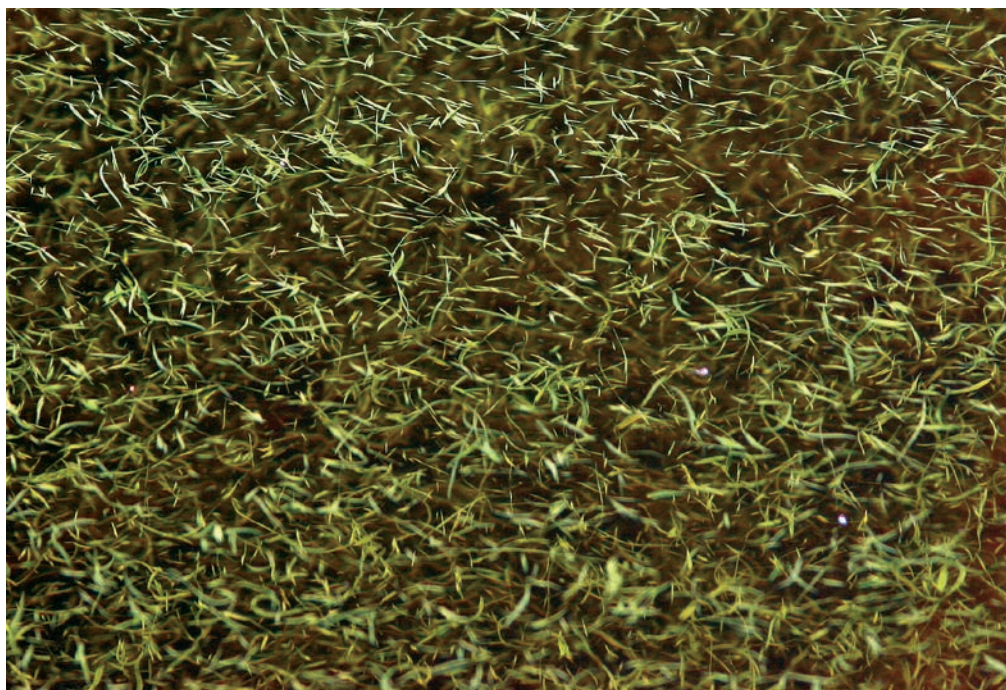


Figure 16: Macroscopic colonies of *Aphanizomenon flos-aquae* floating near the surface.

biomass, the composition of the phytoplankton assemblage shifted towards the dominance of large filamentous cyanobacterium *Aphanizomenon flos-aquae* (Fig. 16, Komárková et al. 1995).

Long-term changes in structure and composition of fish community were evaluated by Říha et al. (2009) using a 21-year data set (1985–2006). There was a decreasing trend in the overall fish abundance and biomass (Figs. 17, 18). During the existence of the reservoir, perch, roach and bream were the dominant species, accounting for over 70% of the total fish abundance. In terms of fish community composition, the 1984–1988 period represented a highly dynamic phase dominated by perch. In 1988, the

perch population collapsed and since 1989 it has been replaced by roach and bream. During the cyprinid phase (1989–2006 and beyond), abundance of both species oscillated and the amplitude decreased with time (Fig. 17). Many finer aspects of fish community development were recorded and still wait to be properly evaluated and published. The construction of the reservoir also significantly influenced the fish assemblage in the river upstream (Hladík et al. 2008). Fish species that had successfully colonized the reservoir soon after its impoundment also expanded into the river. During the cyprinid-dominated phase, roach became the most abundant species both in the reservoir and in the river, outnumbering the indigenous river species.

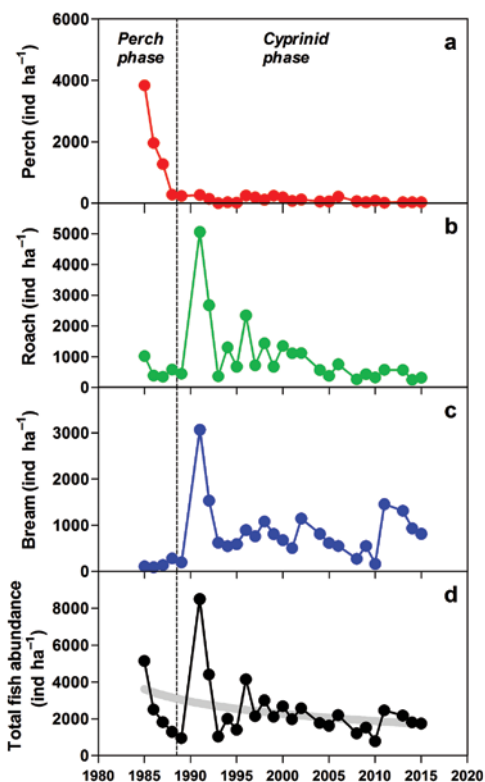


Figure 17: Long-term trends in perch (a), roach (b), bream (c), and total fish abundance (d).

The most comprehensive study of the long-term development of reservoir ecosystems including the Římov Reservoir (Straškrabová et al. 2005) pointed out several important aspects of reservoir limnology. Compared to natural lakes, reservoirs are geologically much younger and have shorter water residence times. This means that the loading from the catchment is relatively more important than in most lakes and its effects upon the in-reservoir processes and pelagic assemblages can be detected at much shorter time scales. Due to the short life span of plankton communities,

the succession of those communities is highly dynamic, which makes plankton a sensitive indicator of a changing environment. Straškrabová et al. (2005) intuitively summarized the process of reservoir ageing; that study suffers, however, from the absence of thorough statistical analysis.

Here we would like to present in a popular form the latest findings of long-term ecological research into the Římov Reservoir and its catchment using the 32-year time series (1983–2014).

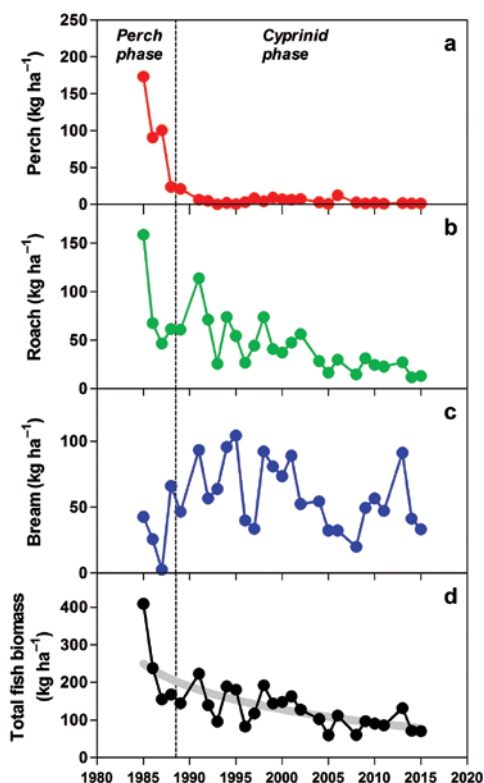


Figure 18: Long-term trends in perch (a), roach (b), bream (c), and total fish biomass (d).

Long-term changes in environmental conditions of the Římov Reservoir and its catchment

Long-term monitoring program and data analyses

Data from the regular three-week monitoring program were supplemented with additional daily data on hydrology and climate, provided by the Vltava River Authorities and the Czech Hydrometeorological Institute. To evaluate long-term trends, we analysed annual averages based on 17 samplings per year from **1983** to **2014**. In the first step, we analysed trends in individual variables. We then grouped these variables into a few categories characterizing changes in agricultural practice and land-use in the catchment, meteorological conditions, reservoir hydrochemistry and hydrodynamics, and composition of plankton communities. For each category we used Principal Component Analysis (PCA) to reduce the high number of correlated variables into two uncorrelated principal components (PC1 and PC2), which allowed a general conclusion to be drawn about long-term changes that the reservoir had undergone. In general, variables show several distinct time trends. The most common is the monotonic increasing or decreasing **linear** trend. Sometimes **two different linear relationships** in the data with a change in directionality (**breakpoint**, Fig.19c) can be distinguished statistically.

When a time series is described as a discontinuous constant function that abruptly changes its value at shift-points analogous to breakpoints, we term it **regime shift** (Fig. 20d).

Meteorological conditions and agricultural activities in the catchment

Meteorological data were obtained from the climatic station in České

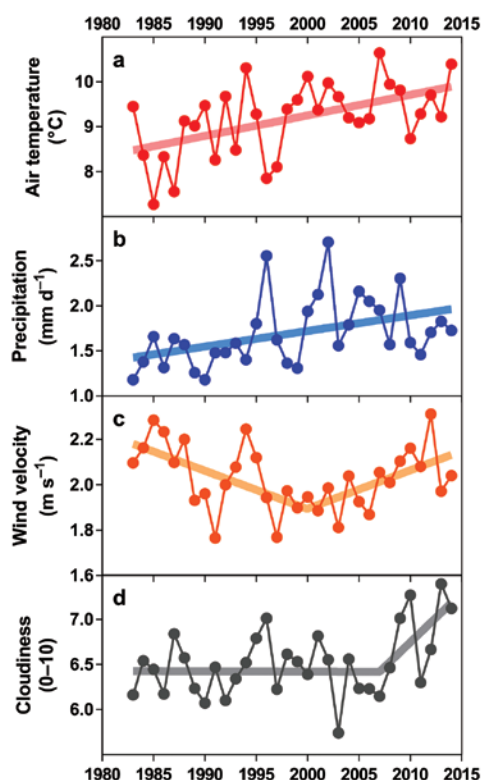


Figure 19: Long-term trends in air temperature (a), precipitation (b), wind velocity (c), and cloudiness (d).

Budějovice approx. 20 km north of the reservoir. From 1983–2014 a significant increasing linear trend in precipitation and air temperature occurred, the latter amounting to $\sim 0.5^{\circ}\text{C}$ per decade (Fig. 19a,b). Trends in wind velocity and cloudiness show breakpoints in 2000 and 2007 (Fig. 19c,d), respectively, but are difficult to interpret. To illustrate socio-economic changes in the reservoir catchment, we analysed data on annual average application rate of mineral and organic fertilizers per hectare of farmland,

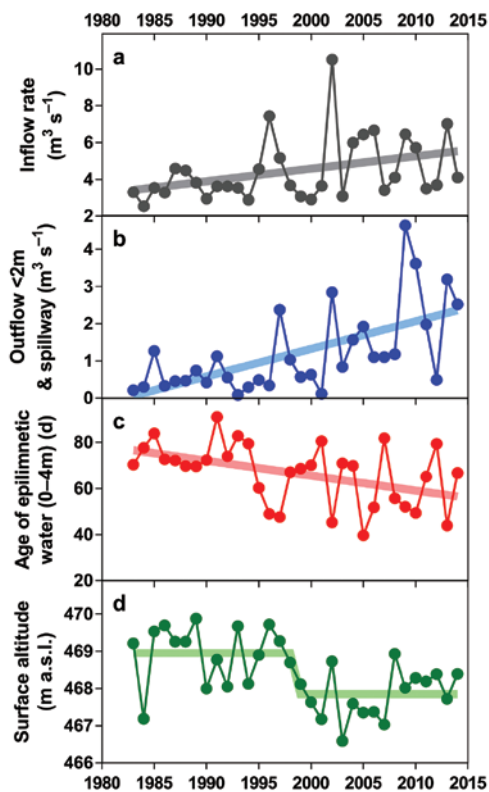


Figure 20: Long-term trends in inflow (a) and outflow (b) rates, epilimnetic water age (c), and surface altitude (d).

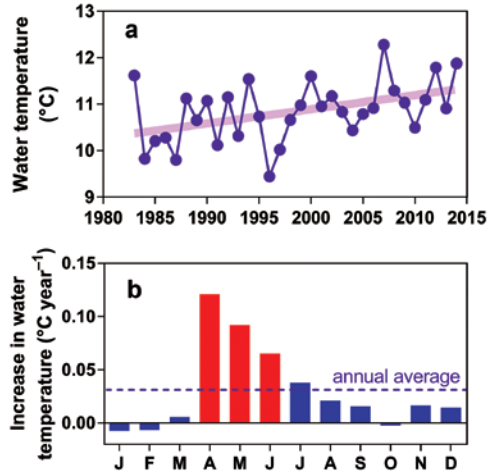


Figure 21: Long-term changes in surface water temperature (a) and mean month temperatures (b). Red columns indicated statistically significant increasing trends.

annual per hectare production of major agricultural products (cereals, potatoes and fodder), and numbers of cattle and pigs. All these indicators of land use and agricultural activities in the catchment show an abrupt decrease in the early 1990s, which can be classified either as breakpoint or regime shift (not shown).

Reservoir hydrodynamics

Hydraulic conditions in the reservoir show the most dramatic changes. As a consequence of increasing precipitation, inflow and outflow rates significantly increased (Fig. 20a,b). While in the 1980s and 1990s water was discharged from deeper strata, the water outflow from upper layers and via the spillway significantly increased in the following period (Fig. 20b). Consequently, water age in the epilim-

nion has markedly decreased and has recently shown high interannual fluctuations (Fig. 20c). The stability of the water column, which reflects the thermal regime of the reservoir, shows a continuously increasing trend. Annual surface water temperature increased by $\sim 1^\circ\text{C}$ during the study period (Fig. 21a). Interestingly, the most pronounced warming trend occurred in spring (April–June, $0.4\text{--}1.2^\circ\text{C}$ per decade) while it was not significant in other months (Fig. 21b). After a series of heavy rains in the late 1990s, the surface water level fell by $\sim 1\text{ m}$ following an administrative decision to increase the flood-retention volume of the reservoir and reduce flood damage downstream. The remarkable shift in water level in the reservoir after the 1990s (Fig. 20d) thus primarily reflects this management measure.

Reservoir hydrochemistry

Many distinct and even contrasting trends occur in the data on hydrochemical variables. Concentrations of dissolved organic carbon (Fig. 22a) and total organic nitrogen increased by 50 and 30%, respectively, from 1983 to 2014, clearly corresponding with elevated terrestrial export of humic matter to the river system (Hejzlar et al. 2003). The resulting increase in the yellow-brown colour of the water contributed to decreasing water transparency (Secchi depth, Fig. 22b). Time series of concentrations of major cations (calcium, magnesium, sodium, potassium) and strong acid anions (sul-

phate, chloride, nitrate, Fig. 22c,d) exhibit breakpoints around 1995 when a hydrologically unstable period with elevated frequency of increased flows began. Concentra-

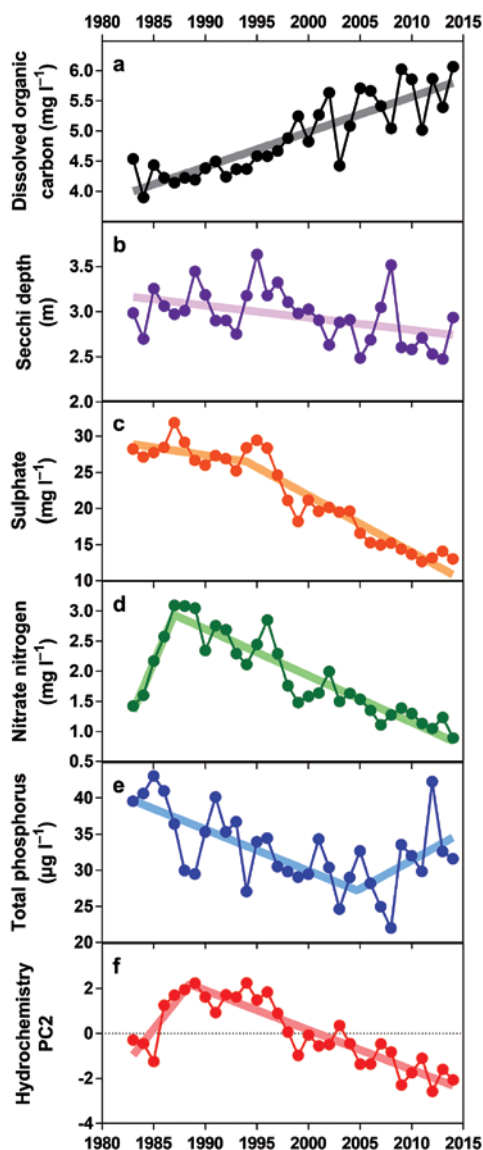


Figure 22: Long-term changes in dissolved organic carbon (a), transparency (b), sulphate (c), nitrate nitrogen (d), total phosphorus (e), and hydrochemistry (f).

tions of most ions (e.g. sulphate, nitrate, and calcium) started to rapidly decline, while trends of others (chloride, potassium) merely levelled off. These trends reflected socio-economic changes in the Czech Republic after a shift from the planned to the market economy after 1989. The most important changes in the reservoir catchment that affected water chemistry occurred concurrently during the 1990s and included a reduction in atmospheric pollution and in the intensity of farming. The latter change included (i) a drastic reduction in the application rate of synthetic fertilisers, (ii) rapidly decreasing numbers of cattle and pigs (and reduced application rate of organic fertilizers), and (iii) a conversion of a significant part of the arable land to extensive grassland. Total phosphorus concentrations decreased till 2008, but then increased again and neared their original values from the 1980s (**Fig. 22e**). The most likely reasons for this negative trend are phosphorus releases from ponds formerly used for wastewater treatment and phosphorus leaching from catchment soils after heavy precipitation. Principal component analysis confirmed that reservoir hydrochemistry significantly changed in the 1990s, as indicated by PC2 (**Fig. 22f**). The year-to-year variability in lake water concentration of bicarbonate was large throughout the study period, but concentration of this anion started to grow consistently in the last decade (not shown). The cause of this trend is not yet clear.

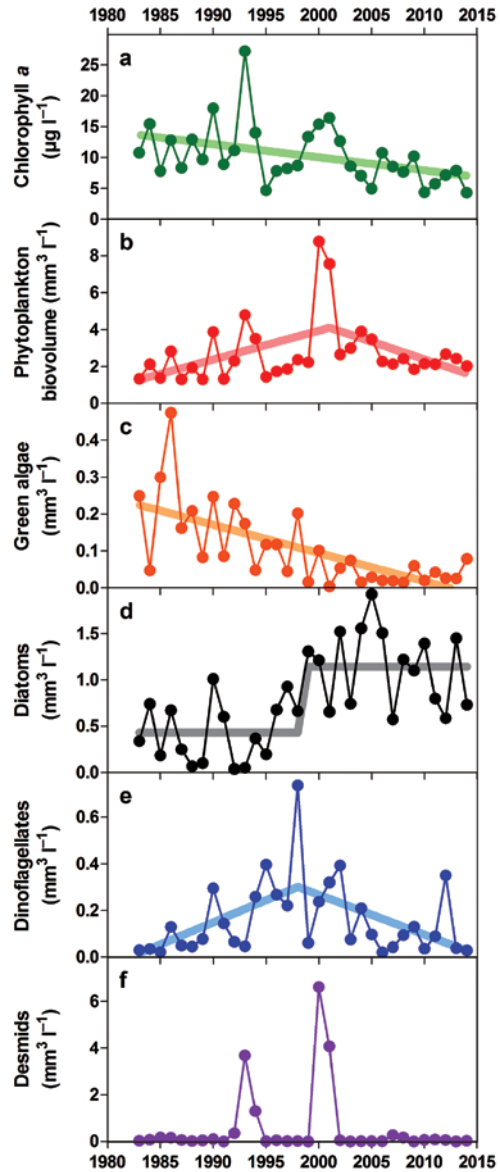


Figure 23: Long-term changes in total chlorophyll a (a), phytoplankton biovolume (b), green algae (c), diatoms (d), dinoflagellates (e), and desmids (f).

Changes in plankton communities

Plankton communities were found to respond sensitively to changes to their environment. Phytoplankton biomass expressed in terms of chlorophyll *a* concentration (main photosynthetic pigment used for phytoplankton quantification) shows a monotonic decrease (Fig. 23a). However, phytoplankton biovolume, which is another commonly used measure of algal biomass, shows a distinct time trend with a peak around 2000 (Fig. 23b). Changes in phytoplankton composition (dominated mostly by diatoms, cyanobacteria, cryptophytes, dinoflagellates and desmids) are far more conclusive. Over the last three decades there has been a significant decrease in biomass of green algae (Fig. 23c). In contrast, diatom biomass significantly increased, showing a regime shift in 1997 that coincided with the shift in the hydraulic regime of the reservoir (Fig. 23d). The colonial species *Fragilaria crotonensis* is the most abundant diatom of the summer phytoplankton. Dinoflagellates, dominated by *Ceratium hirundinella*, increased their biomass till 1998 and then fell back to their initial biovolume (Fig. 23e). No systematic trend was found for cryptophytes and cyanobacteria. Temporal changes in the biomass of desmids (Fig. 23f) are marked by remarkable peaks in 1993 and 2000, which were formed exclusively by a single species, *Staurastrum planktonicum*.

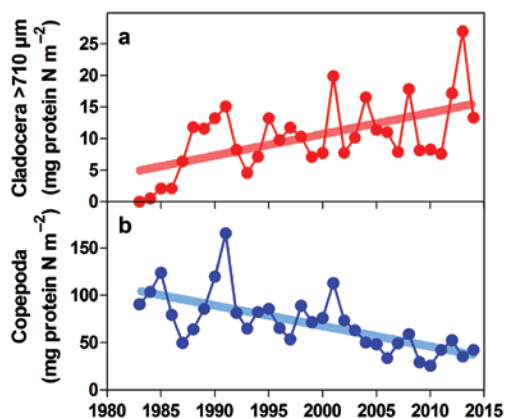


Figure 24: Long-term trends in biomass of large cladocerans (a) and copepods (b).

Long-term trends in zooplankton are characterized by changes in their size structure. The most conspicuous is an increasing trend in biomass of large filter-feeding cladocerans (>710 µm, Fig. 24a), which may be related to an inverse trend in planktivorous fish (Figs. 17, 18; Říha et al. 2009). On the other hand, we cannot exclude the effect of algal food, as the phytoplankton composition has changed and recently their nutritive value appears to be improving.

In contrast to large daphnids, copepods have become less abundant (Fig. 24b). In terms of protein nitrogen, the copepod decrease represents ~50 mg over the whole study period, while cladoceran increase is only 10 mg. One can hypothesize that the inverse trend may reflect outcompetition of larval stages of copepods by large cladocerans that are considered more effective feed-

ers. However, the annual means are calculated by summing up the biomass of five distinct copepod species irrespective of their different seasonal patterns. For a more detailed analysis of the long-term trend, the contribution of each copepod species to the mean annual biomass should be identified individually.

Seasonal cycle of planktonic events

Temperature is the most influential driver of the reservoir seasonal cycle. In the dam area, the ice cover usually develops in January and lasts on the average for 54 days. No systematic trends in ice cover duration and ice disappearance date have been found. Mixing of the water column is most intense at the break of March and April (Fig. 25b), and stable thermal stratification is established by mid-May. The summer epilimnion extends to ~4 m. In July–August, surface temperature peaks at 20°C (Fig. 25a). In September, thermal stratification starts to erode, leading to complete autumn overturn in November–December at the temperature of ~6°C. Water transparency declines soon after the water column mixing is completed (April, Fig. 25c), as a consequence of spring phytoplankton bloom formed by small flagellated species of green algae, chrysophytes and cryptophytes. Due to fast phytoplankton growth, dissolved reactive phosphorus is quickly depleted (Fig. 25d); its concentration remains low in summer and increases

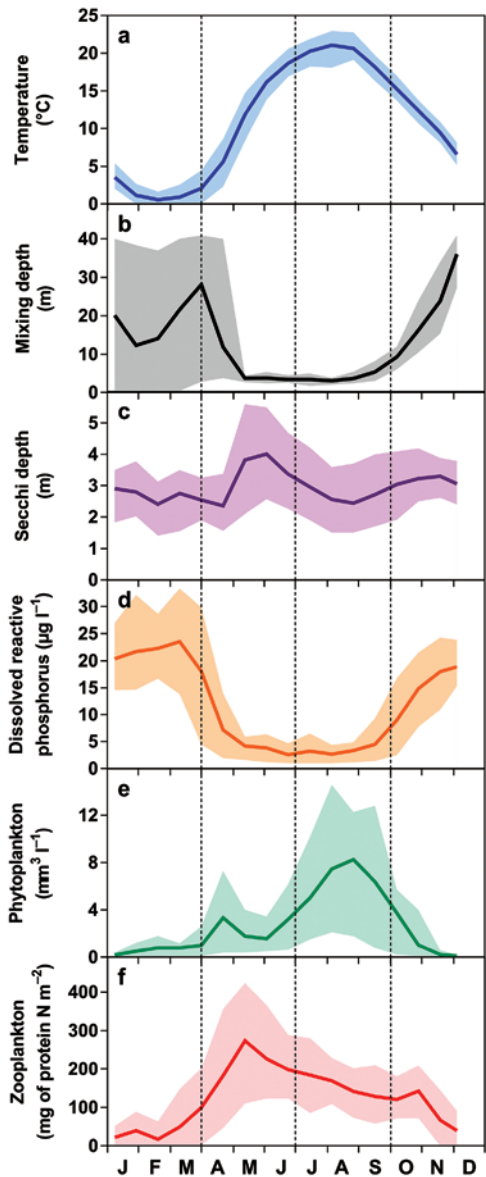


Figure 25: Mean seasonal course temperature (a), mixing depth (b), transparency (c), dissolved reactive phosphorus (d), phytoplankton biovolume (e), and zooplankton biomass (f). Shaded area depicts 10–90 percentile.

again during the autumn overturn (**Fig. 25b,d**). In May, phytoplankton biomass decreases due to enhanced grazing pressure of zooplankton reaching their seasonal maximum (**Fig. 25e**), which coincides with high water transparency ("clear-water" period; **Fig. 25c**). Other causes of phytoplankton decline can also be sedimentation and nutrient limitation. The clear-water phase usually lasts several weeks in May–June and is terminated by development of summer phytoplankton adapted to flourish

in the stratified water column. The summer phytoplankton (**Fig. 26**) is formed by diatoms, desmids, cryptophytes, dinoflagellates or cyanobacteria, switching in dominance according to ambient environmental conditions. Due to decreasing light availability, lower temperatures, and a deepening of the thermocline in autumn, phytoplankton biomass falls. This process is sometimes accelerated by the grazing pressure of zooplankton, which form the second peak of biomass in late October (**Fig. 25f**).

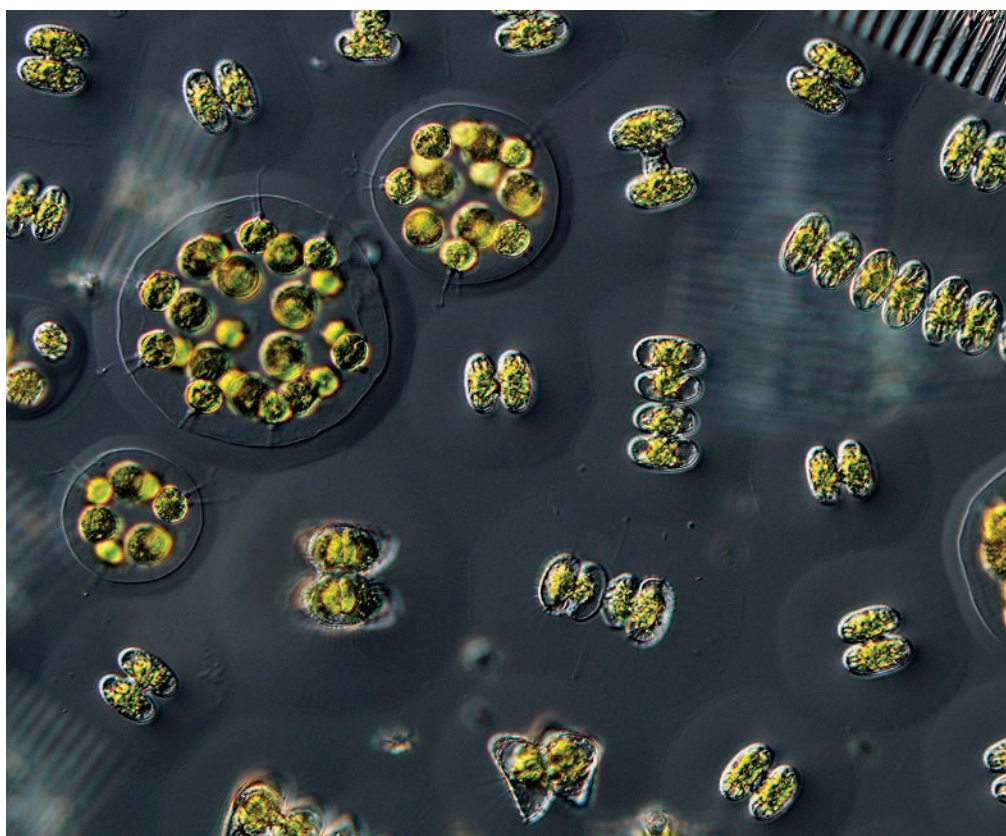


Figure 26: Mixture of flagellated green algae (*Eudorina*), desmids (*Cosmarium*), and diatoms (*Fragilaria*) commonly occurring in the summer phytoplankton of the Řimov Reservoir.

Summary of the long-term development of the Římov Reservoir

The existence of the Římov Reservoir can be divided into three distinct periods, determined by a breakpoint in water chemistry (1989) and a regime shift in the reservoir hydraulic conditions (1999). The early period (1983–1989) is characterized by high concentrations of ions and major nutrients (nitrogen and phosphorus) and high phytoplankton biomass. The environmental conditions in the latest period (2000–2014) differed markedly from those in the early period. Lower nutrient concentrations and higher water tempera-

tures along with the shift in reservoir's hydrological regime resulted in changes in biotic components of the reservoir ecosystem. The contribution of green algae to phytoplankton biomass decreased, while diatoms showed the opposite trend. Total zooplankton biomass decreased due to a significant shrinkage of the copepod (Fig. 27) population. On the other hand, the population of large cladocerans vulnerable to fish predation increased along with the continuously decreasing biomass of planktivorous fish. The succession of the fish stock shows that even in highly variable conditions of a man-made reservoir, relatively stable fish species composition can develop.



Figure 27: Planktonic copepods of the genus *Thermocyclops* sp.

Selected highlights of multidisciplinary research into the Římov Reservoir

Role of protists and viruses in shaping bacterioplankton community composition

Over the last three decades remarkable advances have been made in unveiling the role of bacteria in aquatic ecosystems and their interactions with other planktonic organisms, mainly bacterial grazers, host-specific viruses, and phytoplankton. Some of the pioneering studies in this area were done in the Římov Reservoir and provided answers to fundamental questions, such as ‘who eats whom’, how mortality factors of bacterioplankton can co-act, and how these mortality factors influence the

bacterioplankton community dynamics and overall carbon flow to higher trophic levels.

In spring, small heterotrophic nanoflagellates (HNF) are the dominant grazers of bacteria, capable of consuming up to 50% of the total free-living bacteria per day (Šimek et al. 1990, 2014; Šimek & Straškrabová 1992), while in summer, ciliates are frequently more important bacterial grazers. Although ciliates are usually 10–100-times less numerous than the flagellates, some of them have immense grazing capabilities (**Fig. 28**). *Vorticella aquadulcis*, for example, can take up 4200 bacterial and 560

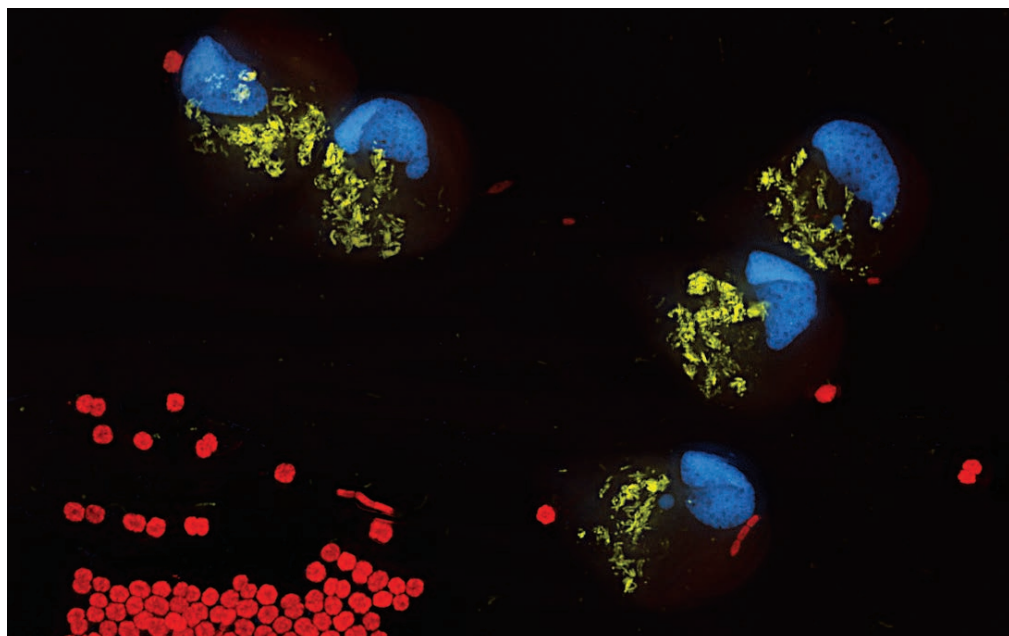


Figure 28: Fluorescence composite image of peritrichous planktonic colonial ciliates with ingested bacteria stained by yellow. Blue are DAPI-stained nuclei; red is autofluorescence of photosynthetic pigments of cyanobacteria. Photo by Karel Šimek and Jiří Nedoma.

picocyanobacterial (cyanobacteria slightly bigger than bacteria, i.e. 1–2 μm) cells per hour (Šimek et al. 1995). Some of the ciliates were found to be highly specialized in feeding exclusively on small pelagic bacteria and picocyanobacteria (Šimek et al. 1996, 1997). In the reservoirs, the most important ciliate bacterivores in order of importance were ciliate groups called oligotrichs, primarily the bacterivorous *Halteria* spp., peritrichs, and scuticociliates. Correspondingly, a revised concept of planktonic ciliate bacterivory was suggested, where the principal role is attributed to small omnivorous filter-feeding oligotrichous ciliates (Šimek et al. 1995, 1996, 1998, 2000).

Until the late 1990s freshwater bacteria were treated as a “black box”, characterized by bulk parameters of numbers, biomass and activities, while the community composition and ecophysiological traits remained largely unknown. Identification of individual bacterial taxa and their metabolic pathways was based mainly on cultivation techniques, which has often been shown to fail, since most of the bacteria dominating in freshwaters simply did not grow on nutrient-rich media. However, with the advent of new culture-independent molecular techniques, many of these techniques were successfully applied in nutrient-poor planktonic samples. In particular, development of fluorescence probes

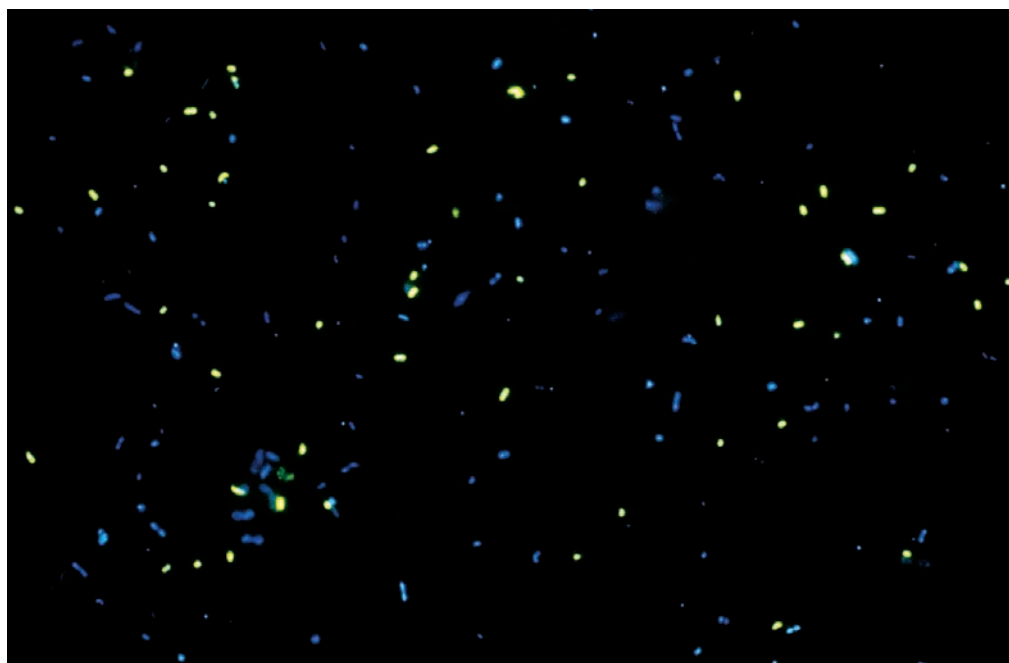


Figure 29: Fluorescence composite image of DAPI-stained bacterioplankton. All bacteria are stained with DAPI (blue), yellow ones are targeted by a specific FISH probe for particular bacterial taxa. Photo by Jiří Nedoma.

(**Fig. 29**) specific for certain groups of bacteria (Fluorescence In Situ Hybridization – FISH) allowed for identification of the key taxa involved in carbon fluxes in the ecosystem. It was found that grazing pressure of protists (i.e. HNF and ciliates) induced pronounced changes in bacterioplankton community composition and morphology (Šimek et al. 1999). When bacteria were subjected to heavy predation pressure in experiments, they started to form large filaments and flocks and thus became grazing-protected and in fact inedible to the small protistan predators (**Fig. 30**). The undisputed importance of applying modern molecular techniques for improving our understanding of bacterial composition and dynamics in natural systems is illustrated in the paper of Šimek et al. (2001). This outstanding study benefiting from sophisticated experimental design has received 236 citations (WOS, All databases, Sep 2016) and is the most cited paper in the whole history of research into the Římov Reservoir. It is also one of the pioneering studies investigating effects of viruses on natural bacterial communities under different grazing pressures. The paper brought quite new insights into possible interactions of two key bacterial mortality factors, prey-selective bacterivorous protists and host-specific viruses, which compete for the same bacterial prey while also exhibiting certain synergic effects. It was suggested that protistan grazing that modulates bacterioplankton community composition may specifically stimu-

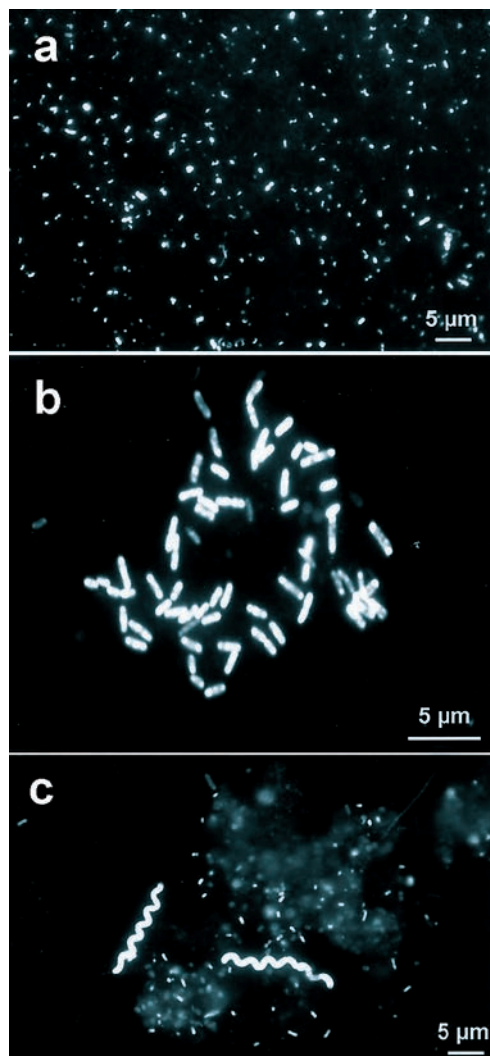


Figure 30: Fluorescence image of DAPI-stained bacterioplankton. When planktonic bacteria (a) are subjected to predation pressure by protists, they start to form large grazing-resistant flocks or filaments (b, c). Photo by Karel Šimek.

late viral activity, since virus infection is prey-density-dependent (Šimek et al. 2001, 2007, Weinbauer et al. 2007) and thus most abundant bacterial taxa (that resisted flagellate grazing effect) become more likely to be infected by host-specific viruses.

The effects of both flagellate grazing and viruses varied among different bacterial groups. For example, filamentous bacteria appeared resistant to both grazing (Šimek et al. 2001, 2006) and viral infection (Šimek et al. 2007).

A quite new experimental design in combination with DNA sequencing approaches has been applied to study the effects of bacterial prey food quality on the community composition of major bacterivores in the Řimov Reservoir, i.e. HNFs (Šimek et al. 2013). Natural flagellate communities were manipulated by additions of different strains isolated from the reservoir and cultivated in the laboratory (Šimek et al. 2013,

Grujčić et al. 2015). The majority of strains from Betaproteobacteria (*Limnohabitans* and *Polynucleobacter* strains) used as food sources yielded significant HNF community growth, while the strain belonging to another bacterial group – Actinobacteria – did not, although it was clearly detected in HNF food vacuoles. Different bacterial prey induced highly significant shifts in HNF community composition detected by DNA sequencing.

Trophic interactions in microbial food webs

Planktonic bacteria are the most important consumers of organic carbon dissolved in water. In the reser-

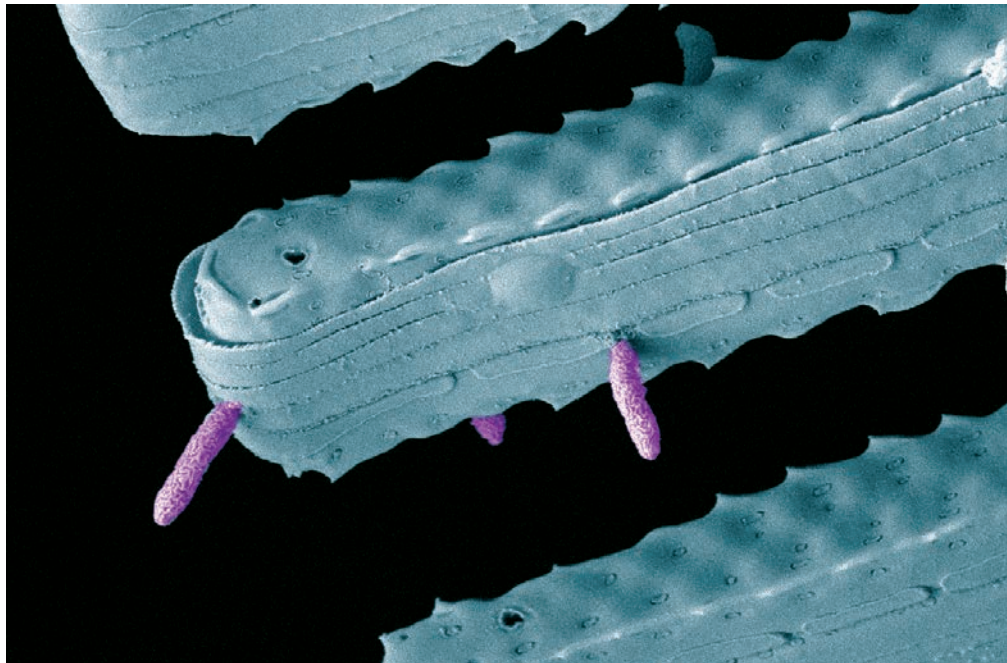


Figure 31: Some bacteria can grow directly on algal cell surface. In this case, bacteria are colonizing a frustule of the diatom. Scanning electron microscopy.

voir, organic compounds can be of allochthonous origin (brought by the river) or autochthonous (produced by primary producers). Although algae and cyanobacteria are primary producers assimilating inorganic carbon, they can both utilize and excrete dissolved organic carbon, which has broad implications for organic carbon fluxes across aquatic food webs (Fig. 31). In the reservoir, phytoplankton utilization of organic carbon is usually low (Znachor & Nedoma 2010), which contrasts with their relatively common and high organic carbon release (Šimek et al. 2008, 2014). Recently, trophic interactions modulated by organic carbon release from phytoplankton to bacteria have been extensively studied. Changes in phytoplankton composition were found to be related to changes in bacterial community composition studied by means of group-specific rRNA-targeted oligonucleotide probes. A trend of increased proportions of certain bacterial groups, mainly of the genus-like R-BT065 subcluster of Betaproteobacteria, was detected for the periods of high carbon excretion, dominated by cryptophytes (Šimek et al. 2008). More than 52% of the seasonal variability in the abundance of the R-BT065 cluster was explained by the changing amount of

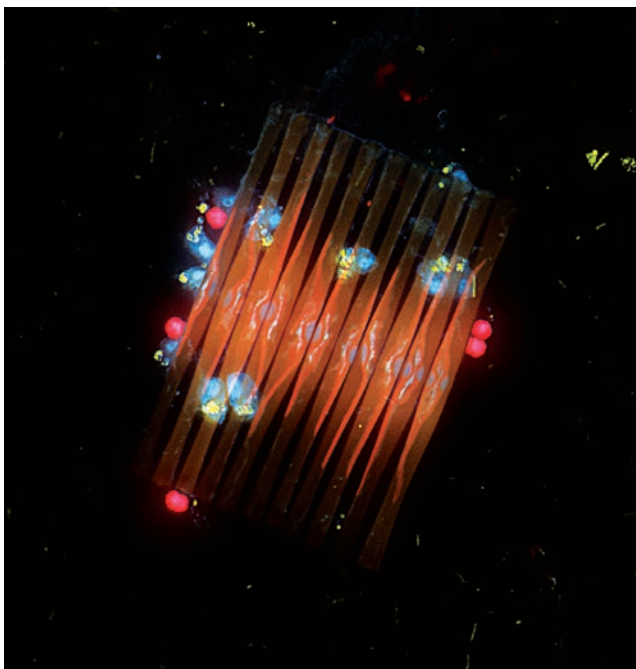


Figure 32: Fluorescence composite image of a colonial diatom *Fragilaria crotonensis* with attached choanoflagellates (blue colour) with ingested bacteria (yellow colour). Red indicates autofluorescence of algal photosynthetic pigments. Photo by Karel Šimek and Jiří Nedoma.

excreted carbon, while experiments indicated a tight taxon-specific algal–bacterial relationship (Šimek et al. 2011).

Since both phytoplankton and bacterial temporal development is highly dynamic, high-frequency sampling is needed to determine the major factors modulating microbial food-web composition and dynamics, especially in spring. Šimek et al. (2014) examined effects of a changing trophic structure of the planktonic community, cascading from the level of zooplankton, through phytoplankton composition and exudation rates, to the level of growth

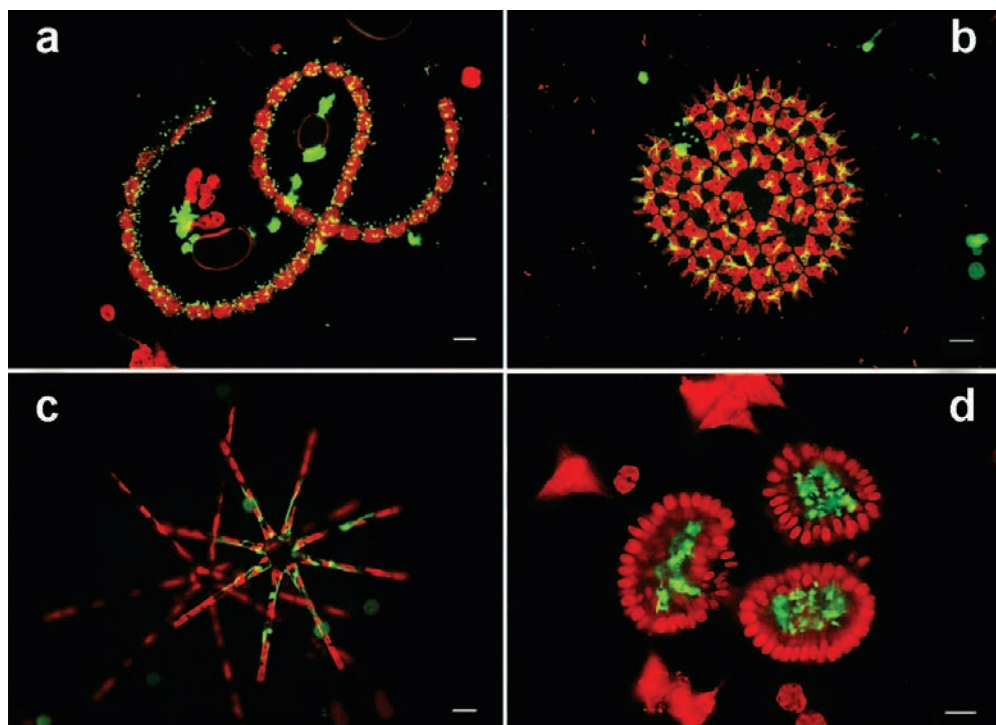


Figure 33: Fluorescence composite image of several phytoplankton taxa labelled with ELF®97 alcohol (green). Cyanobacterium *Dolichospermum* sp. (a), green alga *Pediastrum boryanum* (b), diatom *Asterionella formosa* (c), cyanobacterium *Woronichinia naegeliana* (d). Red indicates autofluorescence of photosynthetic pigments. Scale bars are 10 µm. Photo by Alena Štrojsová.

responses and losses to grazers of phylogenetically narrow bacterial lineages. Specific FISH probes revealed significant short-lived peaks of genus-like (*Fluviicola* sp. and *Limnohabitans* spp.) or even taxonomically narrower populations of Betaproteobacteria and Flavobacteria. Protozoan grazing on bacterioplankton was studied by using fluorescently labelled bacteria and by direct analyses of FISH-probe-targeted bacterial phylotypes in flagellate food vacuoles (Fig. 32). Evaluations of selective bacterivory, growth responses, and cell biovolumes of various bacterial groups during the

spring bloom indicated that certain bacterial groups such as *Limnohabitans* can contribute to carbon flow to the grazer food chain up to 10-fold more than similarly abundant but small cells of Actinobacteria. During the clear-water phase, filter-feeding cladocerans had dominant effects on bacterioplankton abundance and community dynamics, likely through direct grazing on larger bacteria. Fine-temporal resolution data revealed several environmental scenarios in which the interplay of distinct top-down and bottom-up factors resulted in a competitive advantage for particular bacterial lineages.

The role of extracellular enzymes in carbon and phosphorus cycling

Extracellular enzymes are enzymes produced by microorganisms but acting outside their cells, either attached to their outer membrane or released into the surrounding environment. Their function is to degrade complex molecules into simple ones that can be transported into the cells. Vrba et al. (1992) demonstrated that activity of various extracellular enzymes show a strong seasonal pattern, some of which were correlated with zooplankton biomass, which could be explained by subsequent bacterial hydrolysis of undigested algal or chitinous remains egested by cladocerans and copepods.

Extracellular phosphatases are enzymes that catalyse the liberation of phosphorus from various organic compounds, making it available to microorganisms. Vrba et al. (1993) speculated that phytoplankton responded to phosphorus depletion by enhanced activities of alkaline phosphatases, measured by a fluorimetric assay. This assumption was supported by the later study combining various phosphorus-deficiency indices including measurement of soluble reactive concentration, C:P molar ratio in seston (both plankton and non-living particles in water), extracellular alkaline phosphatase activity, and a direct P limitation bioassay (Vrba et al. 1995). However, phosphatase activity was not related to total

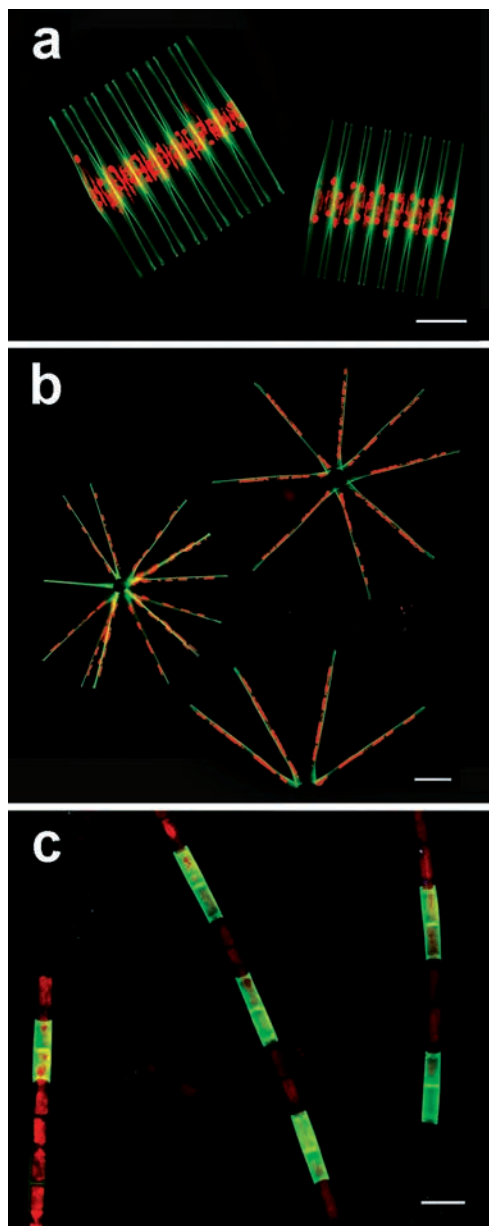


Figure 34: Fluorescence composite image of several diatom species. Using a PDMPO fluorescence probe, green colour indicates newly deposited silica, red autofluorescence of photosynthetic pigments. *Fragilaria crotonensis* (a), *Asterionella formosa* (b), and *Aulacoseira italica* (c). Scale bars are 20 μ m.

biomass or species composition of the phytoplankton.

The approach used provided information on bulk phosphatase activity, but it was not possible to determine which species contributed to the total enzymatic activity. This became possible only after the novel fluorescent substrate, ELF®97 phosphate, became available around the year 2000. This substrate allows for labelling the cells that exhibit phosphatase activity (**Fig. 33**). The method was successfully adopted, and a new protocol based on fluorescence quantification using image cytometry has been established (Nedoma et al. 2003). Using the protocol, Štrojsová et al. (2003) investigated the distri-

bution of phosphatase activity in natural phytoplankton populations in the Řimov Reservoir over three consecutive seasons. Large variability of phosphatase production was found not only among different algal species, but also within the population of one species. Although phosphatase activity was widely detected in the phytoplankton, it was, surprisingly, almost absent in populations of the dominant phytoplankton taxa, while it was rather high in taxa occurring in low numbers. Thus, production of phosphatases does not appear to be necessary for success in phytoplankton competition under P limitation. It is, rather, an additional mechanism of P acquisition and/or is activated during a certain period of the cell cycle.



Figure 35: Non-typical coiled shape of a colony of planktonic diatom *Fragilaria crotonensis*.

Phytoplankton ecophysiology and seasonal dynamics

Recent research into the reservoir phytoplankton has been marked by a combination of classical limnological approaches with application of modern fluorescence techniques (Fig. 34) to depict physiological responses of the phytoplankton to the changing environment. Changes in phytoplankton physiological status may have wide-ranging ecological consequences, making knowledge of factors controlling algal population size of crucial importance. Phytoplankton biomass in the Římov Reservoir forms the most important portion of the annual production in summer (Komárková et al. 2003), and its temporal development usually follows a uni- or bimodal pattern. One intriguing effect of zooplankton predation on colony formation of picocyanobacteria (*Synechocystis*, *Synechococcus*, *Cyanobium*) was revealed and documented during 1998 and 1999. While colonial forms appeared in late spring and summer during strong predation pressure of heterotrophic flagellates and rotifers, unicellular forms survived the winter season (Komárková 2002). The role of flagellate predation in forming the colonies has been also proved experimentally (Jezberová & Komárková 2007).

In earlier years, cyanobacteria, green algae or desmids dominated, but recently diatom has begun to be increasingly abundant. Diatom assemblages tend to be exclusively

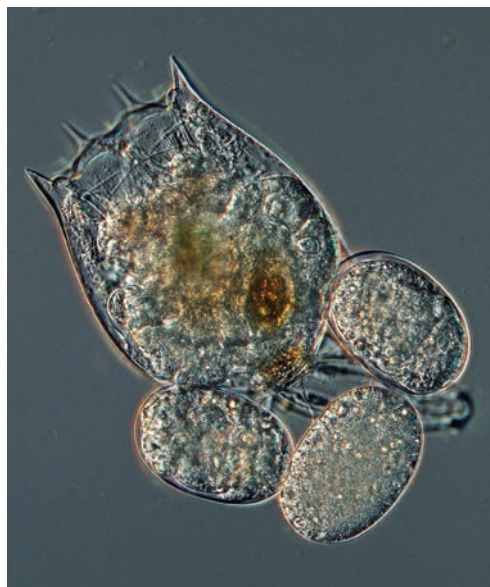


Figure 36: A female of the rotifer *Brachionus* sp. with three eggs.

dominated by a single colonial species, *Fragilaria crotonensis* (Fig. 35). In the beginning of the summer of 2006 diatoms were distributed evenly in the water column, but as soon as stable thermal stratification developed, a vertical profile of diatom biomass exhibited maximum values at the thermocline (Znachor & Nedoma 2008, Znachor et al. 2008). Diatom subsurface maxima were formed by recruitment through passive sinking of *Fragilaria* colonies on a density gradient rather than active growth. Diatom growth at the depth was constrained by low light availability, while at the surface it was limited by phosphorus deficiency. However, factors affecting diatom growth may display high interannual variation, as was shown by Znachor et al (2013). In 2011, when P concentrations were higher

than those previously reported, seasonal variation in diatom growth was driven by daily light exposure, revealing the importance of both seasonal fluctuations of day length and weather conditions.

Seasonal dynamics and spatial distribution of zooplankton

Rotifers, cladocerans and copepods are the most important groups of freshwater zooplankton facilitating carbon flow from microbes, which they graze upon, to fish. In the Římov Reservoir, seasonal dynamics of rotifers usually follow a bimodal pattern with the maximum in spring and a smaller peak in autumn (Devetter 1998). Rotifer

abundance is controlled by ambient environment. Population size also reflects a balance between fecundity and mortality losses. Devetter & Sedá (2003) examined rotifer fecundity (Fig. 36) in relation to the availability of various food sources represented by bacteria, heterotrophic flagellates, and algae. The highest fecundity was observed in the spring and was correlated with all three of the food sources. There were interspecific differences in food preferences, and interestingly, some species could switch their food preferences and adjust their behavior in response to changing environmental conditions during the season. Similarly, the relative importance of rotifer populations is significantly driven



Figure 37: *Daphnia galeata*, the dominant cladoceran species of the Římov Reservoir.



Figure 38: Sampling of pelagic fish by purse seining. Photo by Luboš Piálek.

by their main invertebrate predator, *Cyclops vicinus*. High predation pressure shifts the community to dominance of well-armored but low-natality species (Devetter & Seda 2006).

Another intriguing aspect of zooplankton ecology is vertical segregation of cladoceran populations in the water column. *Daphnia galeata* (Fig. 37), a dominant species in the Římov Reservoir, was traditionally held to be a non-migratory species that lives in warm epilimnetic waters. However, Seda et al. (2007) found that a small subpopulation lives in the deep cold strata throughout the season and does not migrate. Using allozyme electrophoresis, the subpopulation from the depth was found to be clearly genetically different from that in the epilimnion.

The genetic differentiation is likely the result of both the different depth preferences of various *D. galeata* clones and distinct selective pressures at both layers.

Fish ecology

Fish are the top predators in the aquatic food chain and exert a “top-down” effect that shapes the composition of plankton communities. As such, fish behaviour, reproduction, migration and trophic interaction have been extensively studied in the Římov Reservoir since the mid-1980s. The reservoir also served as the development area for designing the methods for sampling the fish communities in other lakes and reservoirs (Fig. 38). Traditional sampling of inshore habitats was extended to regular monitoring

of pelagic habitats in 1999 and led to a general model of spatial distribution of different age groups in summer (Jůza et al. 2014, Říha et al. 2015). In the pelagic region, Čech & Kubečka (2002) discovered intriguing behavior of adult fish performing peculiar sinusoidal cycling movements instead of normal swimming. After sunrise, fishes started to swim up-and-down and continued doing so during daytime (Jarolím et al. 2010). Before sunset, the sinusoidal movement was replaced by direct movement. Up-and-down fish swimming is likely to be an efficient way of visually inspecting a larger volume of the epilimnion for prey, mainly large zooplankton (*Daphnia*, *Leptodora*), whose epilimnetic density in the reservoir is low and patchy in summer.

Many fish were shown to migrate upstream to the reservoir's main

tributary (Hladík & Kubečka 2003, Říha et al. 2013). The fish species living in the reservoir can be divided into three groups: (i) the obligatory tributary spawners (asp, bleak, chub, and white bream), (ii) generalists – fish spawning at suitable places both in the tributary and the reservoir (bream, roach, perch, pike, and ruffe), and (iii) fish spawning in the reservoir or elsewhere (carp, pikeperch, eel, and catfish; **Fig. 39**). Downstream migration from the river (salmonids) appears to be less important. Not only do fish migrate up- and downstream, but they also show the diel horizontal migration between the littoral and pelagic zones of the reservoir (Muška et al. 2013). The pelagic zone represents a risky place for small fish during daylight, since piscivorous fish (pikeperch, asp, and large perch) are abundant in this habitat. Most juvenile and small-sized fish therefore avoid the pelagic zone with



Figure 39: Wels catfish (*Silurus glanis*). Photo by Jiří Peterka.



Figure 40: Pikeperch (*Sander lucioperca*). Photo by Jiří Peterka.

a higher occurrence of predatory fish until dusk and move back to the littoral at dawn. This strategy allows them to utilize the abundant zooplankton in the offshore zone during twilight, when they are still able to visually detect their prey, and yet can still minimize the chance of encountering a predator.

Utilizing an 11-year time series of data, Jůza et al (2014) classified age-0 fish according their behaviour and habitat use during the diel cycle: (i) pelagic species (pikeperch, small perch, bream, at night; **Fig. 40**); (ii) littoral species (large perch, asp, dace); (iii) migratory species likely performing diel horizontal migrations (bleak); (iv) species abundant in the littoral habitat both during day and night and also in the pelagic habitat at night (roach); and (v) species detected in both littoral and pelagic habitats exclusively

at night (ruffe). Two attempts were made to use long-term data for predicting the abundance (recruitment) of age-0 fish (Jůza et al. 2009, Blabolil et al. 2016). Recruitment of asp fry was affected by zooplankton abundance, predator density and temperature, while that of pikeperch fry reflected the number of predators, temperature and water-level fluctuations.

Exploring the spatial heterogeneity of the reservoir

Similar to other temperate canyon-shaped reservoirs, the Římov Reservoir is characterized by pronounced longitudinal gradients in various physical, chemical and biological parameters. According to the reservoir zonation concept, three distinct zones can be recognized along the reservoir's longitudinal axis (**Fig. 8**). The shallow riverine zone

close to the river inflow is characterized by high flow, turbidity and nutrient concentrations. Due to a short water residence time, phytoplankton is mostly of allochthonous origin and thermal stratification is virtually absent. Downstream of the plunge point – where the river water enters the reservoir and mixes with the epilimnion – the transition zone of the reservoir starts (**Fig. 41**). Phytoplankton biomass and production increases due to decreasing flow velocity, increased water residence time and light penetration. The lacustrine ("lake-like") zone is situated downstream near the dam and has the longest residence time, lowest nutrient concentrations, highest transparency and deepest light penetration. The reservoir is strati-

fied downstream of the plunge point from spring to autumn (summer stratification).

Aquatic biota responds sensitively to the aforementioned abiotic gradients, yielding remarkable spatial heterogeneity in their distribution and composition. Composition of both bacterial and phytoplankton assemblages differs markedly between the riverine zone and the rest of the reservoir (Mašín et al. 2003, Ryčtecký & Znachor 2011). At the river inflow, different sources of organic carbon and of bacterial mortality control bacterioplankton dynamics and community composition than at the lacustrine zone near the dam. Bacteria mostly utilize allochthonous organic substrates brought by the



Figure 41: Aerial view of the transition zone of the Římov Reservoir downstream of the plunge point.

river, while in the reservoir they rely on the organic carbon excreted by phytoplankton. Protists grazing on bacteria were shown to remove only a small portion of bacterial production in the river, but in the reservoir they accounted for 50–75% (Jezbera et al. 2003, Šimek et al. 2008). Bacterial production and abundance were highest shortly after the plunge point (Mašín et al. 2003). Due to continuous nutrient supply, the transition zone is the most productive region of the reservoir, often experiencing cyanobacterial or algal blooms in summer (**Fig. 41**, Rychtecký & Znachor 2011, Znachor et al. 2013). While a dense cyanobacterial bloom occurs in the transition zone, desmids (Rychtecký & Znachor 2011) or diatoms (Znachor et al. 2013) have been recently

reported to dominate at the dam. This illustrates that species succession along the reservoir is driven by complex interactions between phytoplankton and their environment.

Actual phytoplankton biomass reflects growth and loss processes that run at different rates along the longitudinal profile of a reservoir (Znachor et al. 2013, Rychtecký et al. 2014). For instance, predation pressure of zooplankton on algae is higher at the transition zone than at the dam due to high zooplankton abundance. In 1996, rotifers (**Fig. 42**) were dominant by numbers and formed on average 60–95% of the total zooplankton numbers (Seda & Devetter 2000). There was a consistent pattern of increasing relative abundance of



Figure 42: Predatory rotifer of the genus *Asplanchna*.



Figure 43: Perch (*Perca fluviatilis*). Photo by Jiří Peterka.

rotifers in the transition zone compared with the lacustrine part of the reservoir. Large rotifer populations could develop at the upstream part of the reservoir, often coinciding with high inflow episodes, but also with reduced abundance of crustaceans and increased turbidity. The timing of the seasonal succession of zooplankton species showed a coherent pattern along the whole longitudinal profile.

Vašek et al. (2003) studied the diet of three cyprinid species (roach, bream and bleak) along the reservoir. The diets of all the cyprinids were made up almost exclusively of crustacean zooplankton, namely *Daphnia* and *Leptodora*. A decreasing trend in the mean size of *Daphnia galeata* was observed from the dam to the river inflow, indicating stronger fish predation pressure in the upstream part of the reservoir.

There is also an obvious decreasing trend towards the dam in fish abundance and biomass (Vašek et al. 2004). From 1999–2007, Prchalová et al. (2009) explored spatial distribution of the fish and effects of depth, distance from the dam to the river inflow, and habitat type (benthic and pelagic) on fish community structure. Redundancy analysis revealed that the effects of the three environmental variables were significant and that most variability was explained first by depth, then by distance from the dam, and then by habitat type. The total number of species and abundance and biomass of all species except perch (Fig. 43) increased upstream and peaked near the river inflow. Responses of juvenile fish to the distance from the dam partly differed from that of adult fish (see also Jůza et al. 2009). Furthermore, the structure of fish community differed in benthic and pelagic habitats,

with species preferring to occupy epipelagic (bleak, asp, rudd, juvenile bleak, roach, and bream), mesopelagic (pikeperch and perch), or littoral waters (perch, pikeperch, ruffe, roach, bream, and juvenile percids). Fish distribution in the reservoir followed a distinct pattern, which was probably shaped by a combination of physiological constraints plus a trade-off between food resources and competition.

Effects of high inflow episodes on reservoir ecosystem

River inflows represent one of the major forcings of ecosystem function in canyon-shaped reservoirs. High inflow episodes (Fig. 44) following heavy rainfalls act as disturbances, which can be recognized by their effects of delaying, arresting or diverting seasonal succession

from its expected pattern. These events can permit the development of earlier successional assemblages by producing conditions similar to those usually established earlier in the season – so-called reversions. In summer, high inflow episodes are associated with nutrient pulses, hydraulic disruptions of the water column, and breakdowns of the thermal stratification. In August 2002, after record-breaking rainfall in the catchment, the reservoir experienced an extreme flood wave corresponding to a return period of 1000 years. Although water in the reservoir was replaced within a few days, plankton communities quickly recovered (within 14 days). In the fish stock, two groups of species brought with the flood were detected: (i) fish brought in from the river above the reservoir (brown and rainbow trout, gudgeon, dace) and (ii) fish flushed from



Figure 44: Water withdrawal over the spillway of the Římov Reservoir during the high inflow episode in June 2013.

aquaculture ponds in the catchment (common and gibel carp, tench). In the next year after the flood, both groups showed increased proportion but declined before a summer survey in 2003 (Kubečka et al. 2004, Vašek et al. 2004). In conclusion, the climax cyprinid-dominated fish stock proved to be very resistant to the extreme flood.

In summer 2006, two extreme rainfalls substantially altered nutrient chemistry, mixing regimes and phytoplankton dynamics, resulting in marked population growth of diatoms at the dam (Znachor et al. 2008). These high inflow episodes brought nutrients that fuelled algal growth and produced turbulences that allowed diatoms to remain entrained in the upper illuminated surface layers. Considering phytoplankton seasonal succession, the first storm virtually initiated the development of summer phytoplankton assemblage while the later one was substantial enough to reverse phytoplankton succession to the earlier

diatom-dominated stage (Fig. 45). In late summer 2007, phytoplankton response to a flood event followed another scenario and was revealed using fine-scale temporal measurement of the whole reservoir. Cyanobacteria, originally accumulated in the transition zone, expanded and dominated across the whole reservoir within a week of the flood. During the flood, excessive water withdrawal over the spillway supposedly resulted in preferential displacement of the epilimnion, which facilitated cyanobacterial transport to the dam area where they replaced desmid-dominated phytoplankton. This clearly emphasizes the importance of having an intensive phytoplankton monitoring program, which would allow for detecting consequences of sudden flood events on phytoplankton spatial and temporal heterogeneity, which significantly affect water quality at the dam area used for drinking-water purposes.

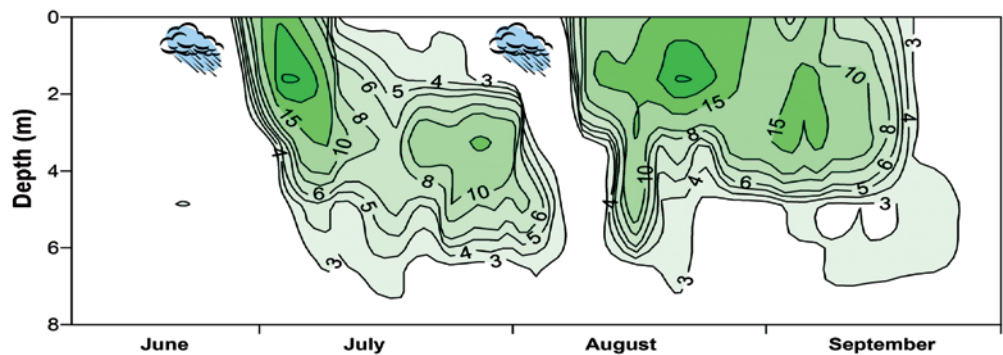


Figure 45: Seasonal succession of phytoplankton in the upper 8-m layer of the water column at the dam of the Řimov Reservoir in 2006. The cloud pictograms indicate high inflow episodes. Isopleths with numbers designate diatom chlorophyll *a*.

Slapy Reservoir

| | |
|--------------------------|---|
| Ecosystem type | Manmade freshwater reservoir |
| Site coordinator/contact | Michal Šorf /michal.sorf@centrum.cz |
| Institution | Institute of Hydrobiology, Biology Centre CAS |
| Address | Na Sádkách 7, České Budějovice, CZ-37005, Czech Republic, more details on www.hbu.cas.cz |

Site characteristics

| | |
|---|---|
| Surface area / volume | 11.6 km ² / 269 × 10 ⁶ m ³ |
| Maximum / average depth | 58 / 23 m |
| Latitude / longitude / water level maximum altitude | 49°45'58"N / 14°24'50"E / 271 m a.s.l. |
| Mean air temperature / annual precipitation | 9.5°C / 681 mm |
| Long-term mean retention time | 36 days |

The Slapy Reservoir is a 44 km long canyon-shaped reservoir with steep banks (Figs. 46, 47). The dam (70 m high and 260 m long) was constructed at the 91.7 km point of the Vltava River (~30 km upstream to Prague) from 1949–1955 and the reservoir was impounded in 1955. The mean annual discharge is 85.2 m³ s⁻¹ and the catchment area is 13 thousand km² (Kopáček et al. 2014a,b). The Slapy Reservoir is a part of the Vltava Cascade, a system of eight reservoirs of varying age, retaining altogether 1.4 billion m³ of water. The most upstream member of the cascade, the Lipno Reservoir, was built from 1952–1959. The largest reservoir in the cascade (Orlík) was built upstream of the Slapy Reservoir in 1963. Downstream of the Slapy Reservoir (directly below the dam) starts the small, regulating Štěchovice Reservoir, built from 1938–1944.

The major purpose of the Slapy Reservoir is hydropower generation. The hydropower station is operated

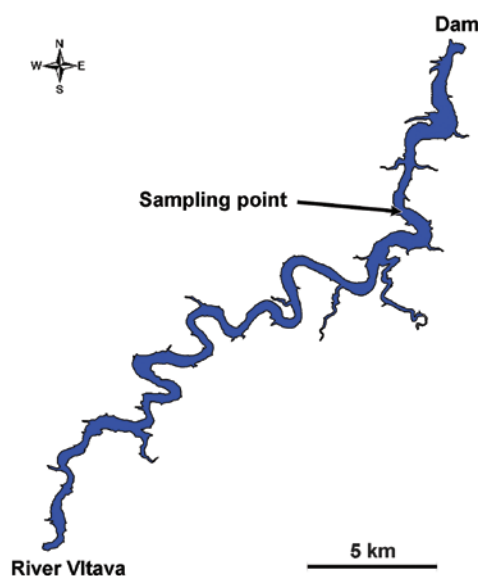


Figure 46: A map of the Slapy Reservoir.

in a peak regime (morning and evening), causing periodic seiches and pronounced water-level fluctuations. This management practice together with steep morphology of shores largely prevents the development of a littoral zone with aquatic plants. Besides hydropower

production, the reservoir is also used for recreation activities and locally as a drinking-water source. The seasonal thermal regime of the Slapy Reservoir resembles a warm monomictic lake, as it receives water from low outlets of the upstream Orlik Reservoir. Consequently, the temperature of the inflow is relatively stable, relatively cold in summer and warm in winter, which maintains long autumn–winter overturn and prevents ice cover formation. In contrast, it supports stable thermal stratification of the water column in summer.

Brief history of the long-term ecological research into the Slapy Reservoir

Czech reservoirs began to be studied in the late 1950s and the research into them is tightly associated with the former Hydrobiological Laboratory of the Czechoslovak Academy of Sciences in Prague (HBL), which operated a field station at the Slapy Reservoir (**Fig. 47**). The HBL team, led by Jaroslav Hrbáček, set up the regular monitoring of the reservoir, including of water chemistry and plankton, at three-week intervals starting in 1959. In 1990 the monitoring program was taken over by the newly



Figure 47: Aerial view of the central part of the Slapy Reservoir, nine kilometres upstream of the dam. The IHB field station is on the right bank, near the bridge that crosses the reservoir.

founded Institute of Hydrobiology in České Budějovice. The Slapy Reservoir was enlisted in the LTER network in 1996. Regular measurement takes in major physical and chemical characteristics and pelagic biota (bacteria, protists, phytoplankton and zooplankton, [Table 2](#)). The sampling point is 8.8 km upstream of the dam in the lacustrine zone of the reservoir ([Figs. 46, 47](#)). Long-term research

into the reservoir has yielded valuable findings on long-term effects of anthropogenic processes and land-use changes in the catchment, such as the construction of the upstream reservoir, agricultural practices (e.g. drainage, changes in arable land area, fertilization rates), wastewater treatment, road de-icing etc., on the water chemistry and biology of the reservoir.

Table 2. Major long-term data available for the Slapy Reservoir since 1959.

| Measured variables | |
|----------------------|---|
| Physical environment | transparency, vertical profiles of temperature and dissolved oxygen concentration |
| Hydrochemistry | alkalinity, conductivity, major ions, nutrients (various forms of C, N, P) |
| Hydrobiology | chlorophyll <i>a</i> , phytoplankton abundance and biovolume; crustacean abundance and biomass; rotifer abundance (since 2011); bacterial abundance (and biomass since 1996); HNF abundance (since 1994); ciliate species composition, abundance and biomass (since 1994) |

Long-term changes in temperature and water chemistry in the Vltava River basin

The catchment of the Slapy Reservoir reflects the development typical for central and eastern European countries, which witnessed socio-economic shifts from the market to the planned economy in the 1950s and then back to the market economy since the early 1990s, connected with the changes in the land use and agricultural practice (Kopáček et al. 2013a, 2014b).

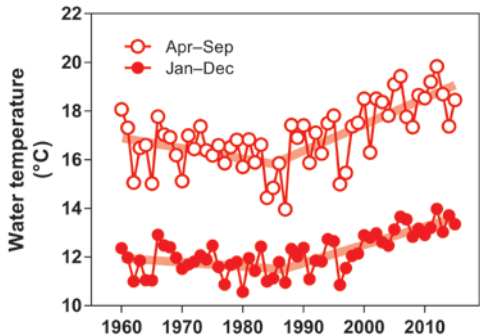


Fig. 48: Long-term trends in water temperature. Open circles indicate period of thermal stratification (April-September), full circles are annual averages.

The ongoing research into the Slapy Reservoir has produced long-term data on stratification, chemistry, and plankton (**Table 2**). We observed a significant increasing trend in surface water temperature, which has been especially apparent over the last two decades (**Fig. 48**). A similar yet more pronounced increasing trend in water temperature was determined for the April–September period of stable thermal stratification.

The long-term trend in water conductivity (integrating major ion concentrations, **Fig. 49a**) basically reflects application rates of synthetic fertilizers in the catchment and atmospheric pollution, both peaking in the late 1980s (Kopáček et al. 2013b). The most pronounced changes occurred in concentrations of sulphate and nitrate (**Fig. 49b,c**). The dominant factor controlling the nitrate export from agricultural land was (beside fertilizers) the extensive building of drainage systems in farmland during the 1970s–1980s (Kopáček et al. 2013b). Annual mean concentrations of sulphate and chloride continuously increased till the 1980s–1990s. Sulphate inputs to the catchment through atmospheric deposition and in fertilizers (mostly superphosphate) thereafter markedly decreased (Kopáček et al. 2014b, **Fig. 49b**). The decrease in concentrations of chloride was associated with reduced application of potassium fertilizers (mostly KCl), while their growth after 2000 resulted from increasing use of NaCl for

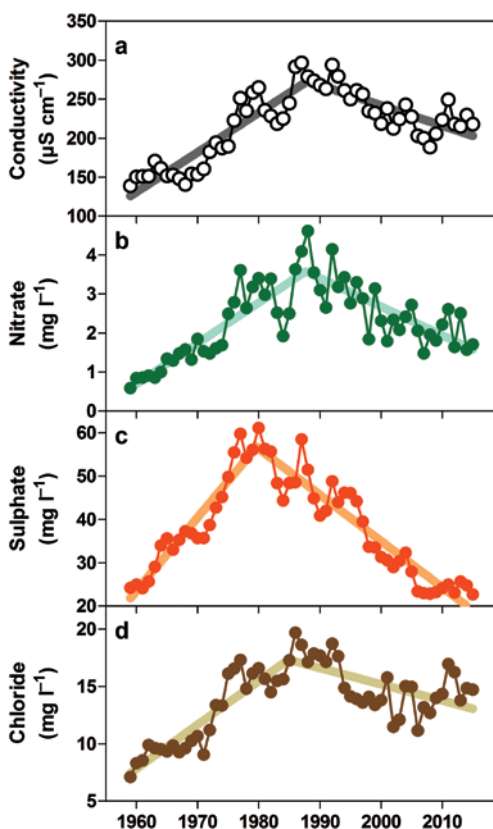


Figure 49: Long-term changes in conductivity (a), nitrate (b), sulphate (c), and chloride (d). A remarkable temporary drop in nitrate concentrations was due to reduced runoff in the relatively dry early 1980s.

road de-icing (Kopáček et al. 2014a, **Fig. 49d**).

Long-term trends in concentrations of total phosphorus and nitrate illustrate gradual eutrophication of the reservoir, which peaked in the early 1990s (**Figs. 49c, 50c**). Surprisingly, neither phytoplankton (**Fig. 50b**) nor zooplankton (data not shown) appeared to follow the increase in nutrients in any straightforward pattern. There are two pos-

sible explanations for the absence of any significant correlation. First, the annual means of both phosphorus and nitrogen are biased by high values in winter, when these nutrients cannot be used for plankton growth due to low temperatures and/or light availability (Procházková et al. 1973). Plankton is thus nutrient-limited only during the period of thermal stratification, whereas high nutrient concentrations in winter pass through the reservoir. Second, both phytoplankton and zooplankton assemblages were able to respond to the varying nutrient supply by shifting in species composition.

Pelagic food webs

Despite time series of chemical parameters in the Slapy Reservoir having been recently evaluated (Kopáček et al. 2013a, b, 2014a, b), biological data as yet unpublished provide other opportunities for a thorough analysis. Evaluations of partial time series have brought many important findings about the functioning of the aquatic ecosystem since the start of monitoring in 1959. In the first decade of monitoring the difference between aquatic ecosystems of headwater reservoirs and those located in the cascade was clarified after the filling of the upstream Orlik Reservoir (1961–1963), which substantially changed the hydrodynamics of the Slapy Reservoir, modified its seasonal patterns of temperature and oxygen stratification, and reduced inputs of sediment and nutrients (Straškraba et al. 1973).

These changes had many consequences, mainly decreased nutrient (phosphorus and nitrogen) concentrations (Procházková et al. 1973), reduced occurrence of cyanobacterial blooms, modified seasonality of phytoplankton species (Javornický & Komárková 1973), and impacts on benthos (Hruška 1973). Later studies focused on analysing regulation mechanisms in plankton communities and showed, among other things, that phytoplankton are strongly influenced by seasonal development of climatic and flow conditions (Desortová 1989, Komárková

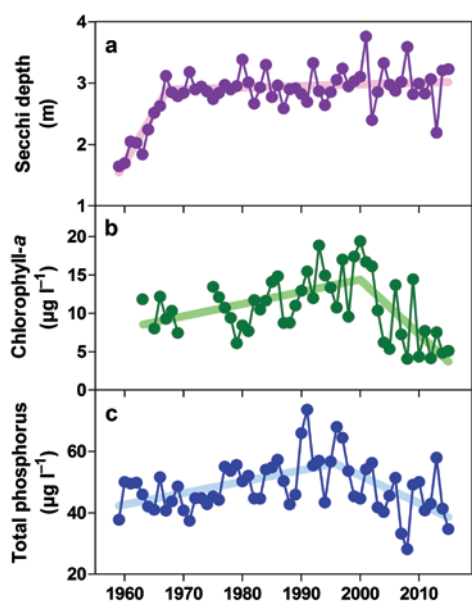


Figure 50: Long-term changes in transparency (a), chlorophyll-a (b), and total phosphorus (c). Lower transparency until the mid-1960s was caused by both high turbidity after the filling of the Slapy Reservoir and direct nutrient input before the filling of the upstream Orlik Reservoir.

& Vyhnálek 1998). The spring phytoplankton peak of biomass is usually formed by small, fast-growing taxa of centric diatoms (**Fig. 51**), cryptophytes or green algae, while larger species of diatoms, dinoflagellates, desmids and cyanobacteria tend to dominate in summer. Seasonal development of zooplankton is controlled by both food resources (Straškraba & Hrbáček 1966) and predation by fish and/or carnivorous zooplankton species (e.g. *Leptodora kindtii*; Pichlová & Brandl 2003, Devetter 2011). Straškraba & Hrbáček (1966) described a switch in the character of zooplankton during the first two years of their development in the Slapy Reservoir from riverine to lacustrine.

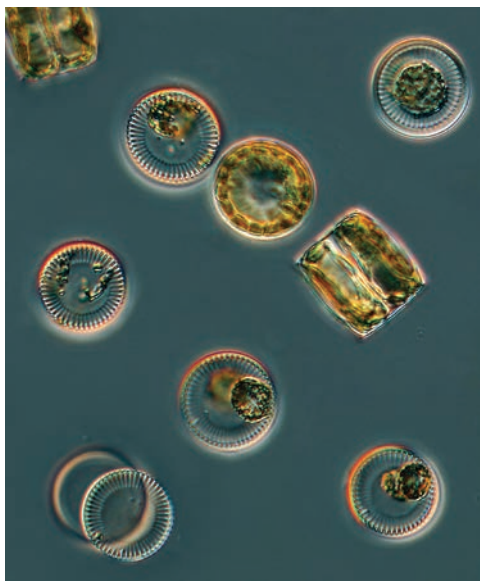


Figure 51: Fast growing small centric diatoms dominate the spring phytoplankton.



Figure 52: Bream (*Abramis brama*). Photo by Jiří Peterka.

Fish communities

The Slapy Reservoir was too large to study as a whole. The sole attempts to evaluate fish communities in the reservoir were hydroacoustic, along with fry studies done in 2004 (Drašík et al. 2006, 2008, Jůza et al. 2006, Jůza & Kubečka 2007) within a project surveying four reservoirs of the Vltava Cascade. At the time, fish composition was still influenced by the ingress of fish from the catchment during the great flood in 2002 (Boukal et al. 2012) and by water-level fluctuations caused by subsequent dam repair, which explains why even the fry communities were dominated by cyprinid species like bream, roach and bleak.

Most of the long-term data on fish communities in the Slapy Reservoir come from analyses of annual angling statistics (Hanel & Čihař 1983, Hrbáček 1984, Drašík et al. 2004). These records clearly show that, after the construction of the upstream Orlík Reservoir, cyprinid fish, especially bream (Fig. 52), became gradually less important because of spawning limitation (combination of colder water intrusion and water-level fluctuation due to peaking hydropower production). The low success of cyprinids opened a new niche for perch, which occurs in unusually high densities (Drašík et al. 2004). Both percid and cyprinid fish strongly dominate the diet of local avian predators like great cormorant *Phalacrocorax carbo* (Čech et al. 2008) and kingfisher *Alcedo atthis* (Fig. 53, Čech & Čech 2015).

Using acoustic data and complementary net catches, Čech et al. (2005) have described unique sympatric occurrence of epipelagic and bathypelagic perch fry communities. Epipelagic perch fry stayed all day in the relatively warm and zooplankton-rich epilimnion, while bathypelagic perch fry conducted regular diurnal vertical migrations with an amplitude exceeding 10 m and controlled by the light intensity. During the daylight, the bathypelagic perch fry stayed in cold, dark and zooplankton-poor water, (Kraatochvíl et al. 2008) which is classical predator-avoidance behaviour (Čech et al. 2016). In late May and June the hydroacoustic scattering layer of bathypelagic perch fry containing >10 million individuals could be observed along the whole longitudinal and transversal profile of the reservoir (Čech et al. 2005, 2007). Recently, the phenomenon of diel migration of bathypelagic perch fry has also been described for other Czech reservoirs such as Orlík and Římov (Čech et al. 2016).



Figure 53: Common kingfisher (*Alcedo atthis*) and its prey – gudgeon (*Gobio gobio*). Photo by Pavel Čech.

Conclusions and future research perspectives

Two manmade reservoir sites involved in the Czech LTER network and managed by the Institute of Hydrobiology BC CAS serve as suitable models for monitoring biogeochemical, climatic and management changes affecting entire catchments. To our knowledge, there are very few reservoirs where systematic long-term multidisciplinary research of the whole ecosystem is being conducted. Our complex and detailed studies concentrate on basic understanding of the reservoir ecosystem functioning and give detailed insights into the immediate state and into emerging changes. The model reservoirs also help develop appropriate survey methods and serve as reference sites to which many other recent and future results can be related.

Recent evaluation of long-term trends in environmental variables brings evidence that the almost sixty years of monitoring records from the Slapy Reservoir represent a unique chronicle of socio-economic development in the entire South Bohemian region, possibly representing characteristic trends for the whole area of central Europe, and also reflect ongoing changes in climatic conditions. At the same time, the so far under-explored biological time series suggest diverse responses to these environmental drivers. The Slapy Reservoir, which is an intensively used system in the reservoir cas-

cade, and the headwater Římov Reservoir, which is not affected by upstream reservoirs, can serve as two most common examples of reservoir operations. The two long-term time series could solicit possible mechanisms driving both short- and long-term changes in the reservoir ecosystems.

Hence, the unique combination of biological and environmental data forms a favourable framework for testing general ecological hypotheses, addressing for instance factors affecting the growth and species composition of plankton and fish species, trophic interactions across aquatic food webs, reservoir ageing, and changes to climatic and hydraulic conditions and nutrients levels. The Institute of Hydrobiology welcomes cooperation with other research organizations that would like to use its extensive datasets to track basic waterbody understanding and compare effects of global processes on other waterbodies studied over the long term.



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Figure 54: The Římov Reservoir – construction of the dam, 1974–1975. Photo from the Archive of Vltava River Authorities.



Figure 55: The Římov Reservoir – construction of the dam, 1974–1975. Photo by the Archive of Vltava River Authorities.



Figure 56: The Římov Reservoir – construction of the dam 1974–1975. Photo from the Archive of Vltava River Authorities.



Figure 57: The Římov Reservoir – construction of the dam 1977. Photo from the Archive of Vltava River Authorities.



Figure 58: The Římov Reservoir – construction of the dam 1977. Photo from the Archive of Vltava River Authorities.



Figure 59: The Římov Reservoir – present view of then reservoir from the dam.



Figure 60: Aerial view of the Římov Reservoir. In the background lies the city of České Budějovice (population ~94 000), 20 km north of the reservoir.



Figure 61: Aerial view of the Římov Reservoir. In the foreground (centre) is a wastewater treatment plant of nearby Velešín town (population ~4 000). Wastewaters are pumped outside the catchment of the reservoir.



Figure 62: Aerial view of the Římov Reservoir. On the left is a nearby Velešín town (population ~4 000). The bridge crossing the reservoir was built from 1975–1979.



Figure 63: Aerial view of the dam area of the Římov Reservoir. On the left bank of the River Malše downstream the dam, the Římov municipality is situated (population ~800).



Figure 64: Aerial view of the central part of the Slapy Reservoir. In the front there is side tributary of the Mastník Stream.



Figure 65: Aerial view of the dam area of the Slapy Reservoir. Downstream of the dam are the steep slopes of the original River Vltava canyon, nowadays an impoundment of the Štěchovice Reservoir.

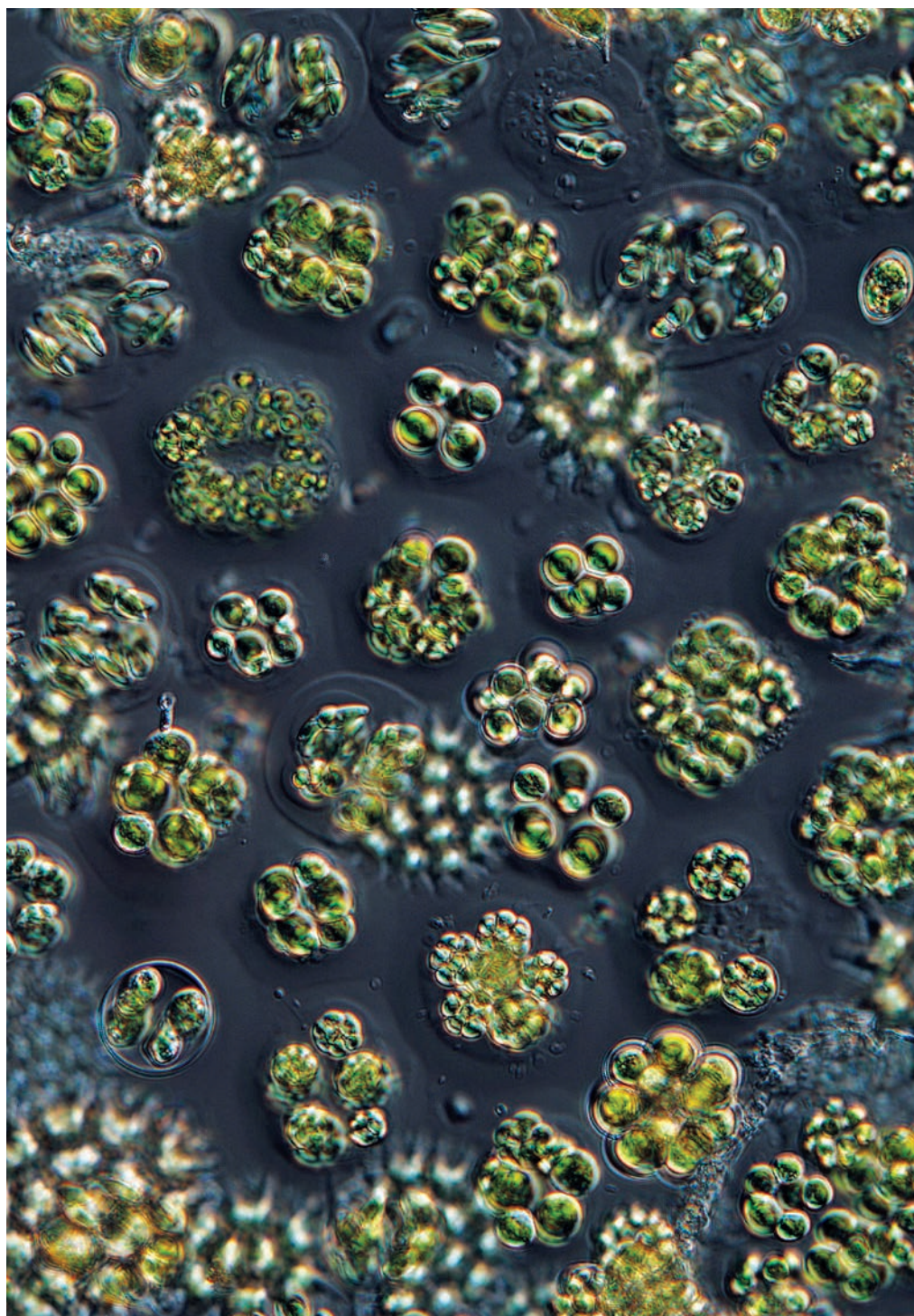


Figure 66: Various chlorococcal algae dominating the phytoplankton of the Římov Reservoir in early years.

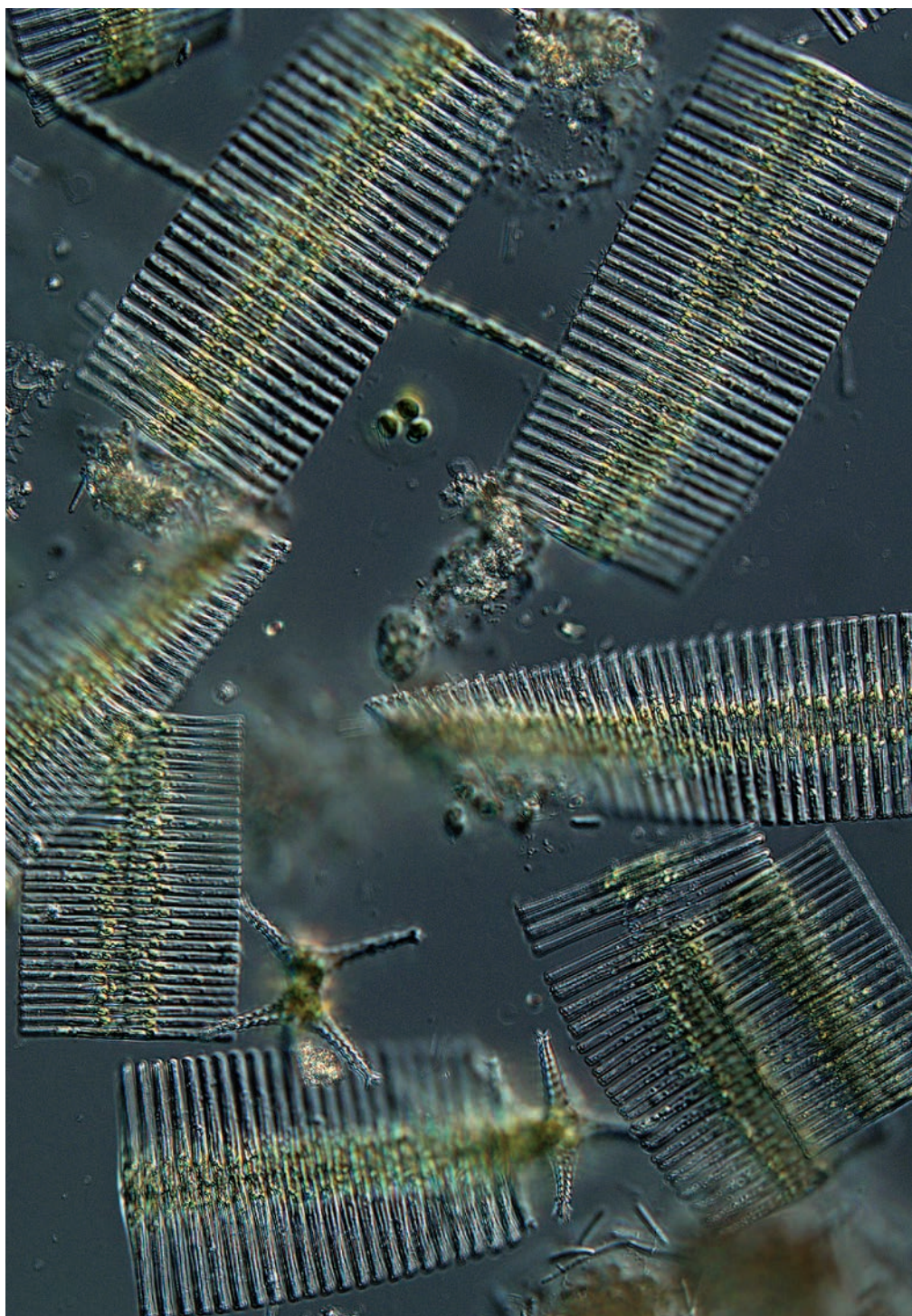


Figure 67: Colonies of a common planktonic diatom *Fragilaria crotonensis* dominate recently the summer phytoplankton of the Římov Reservoir.



Figure 68: Filamentous bloom-forming cyanobacterium *Dolichospermum lemmermannii*.

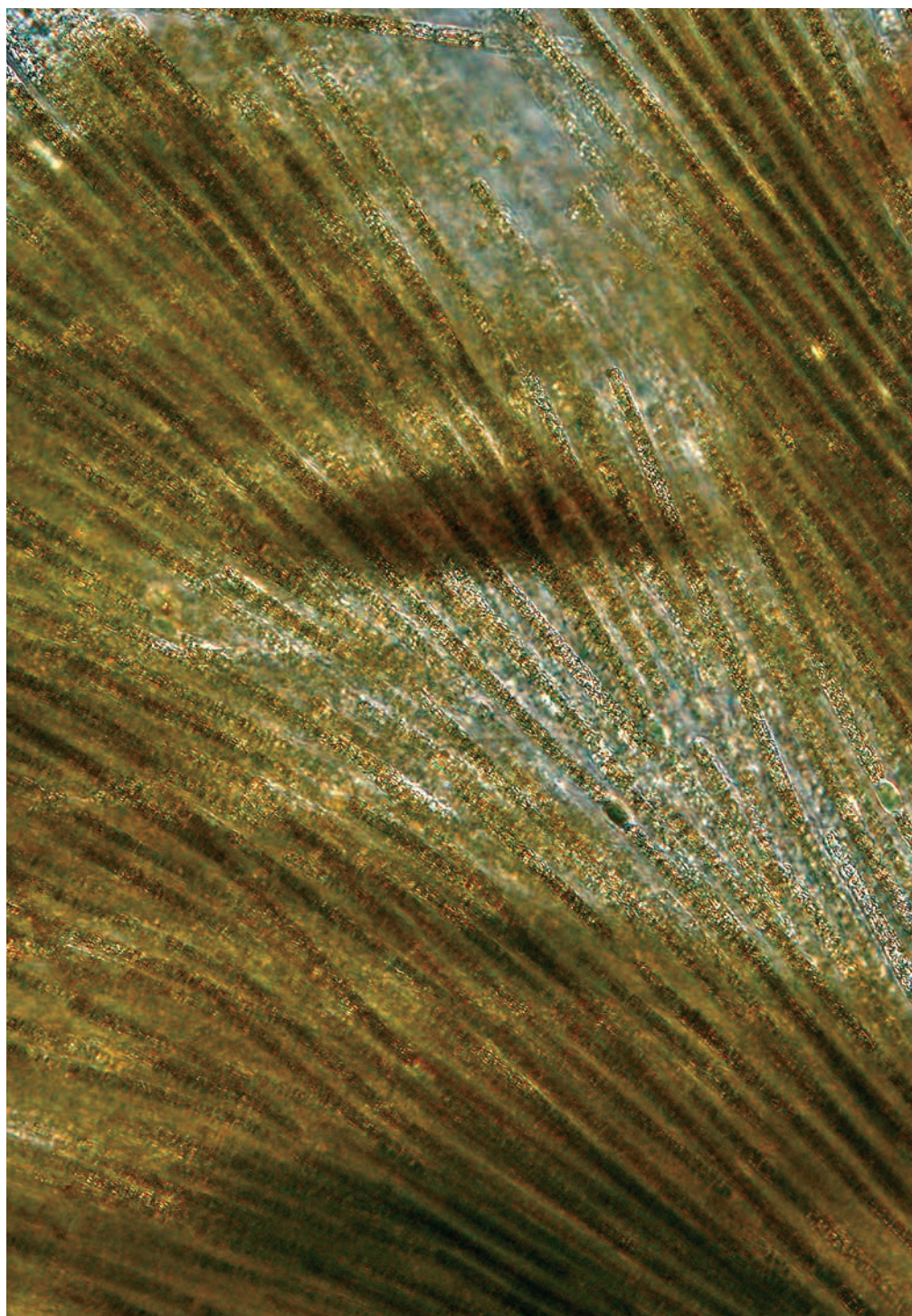


Figure 69: Detailed view of the colonial filamentous bloom-forming cyanobacterium *Aphanizomenon flos-aquae*.

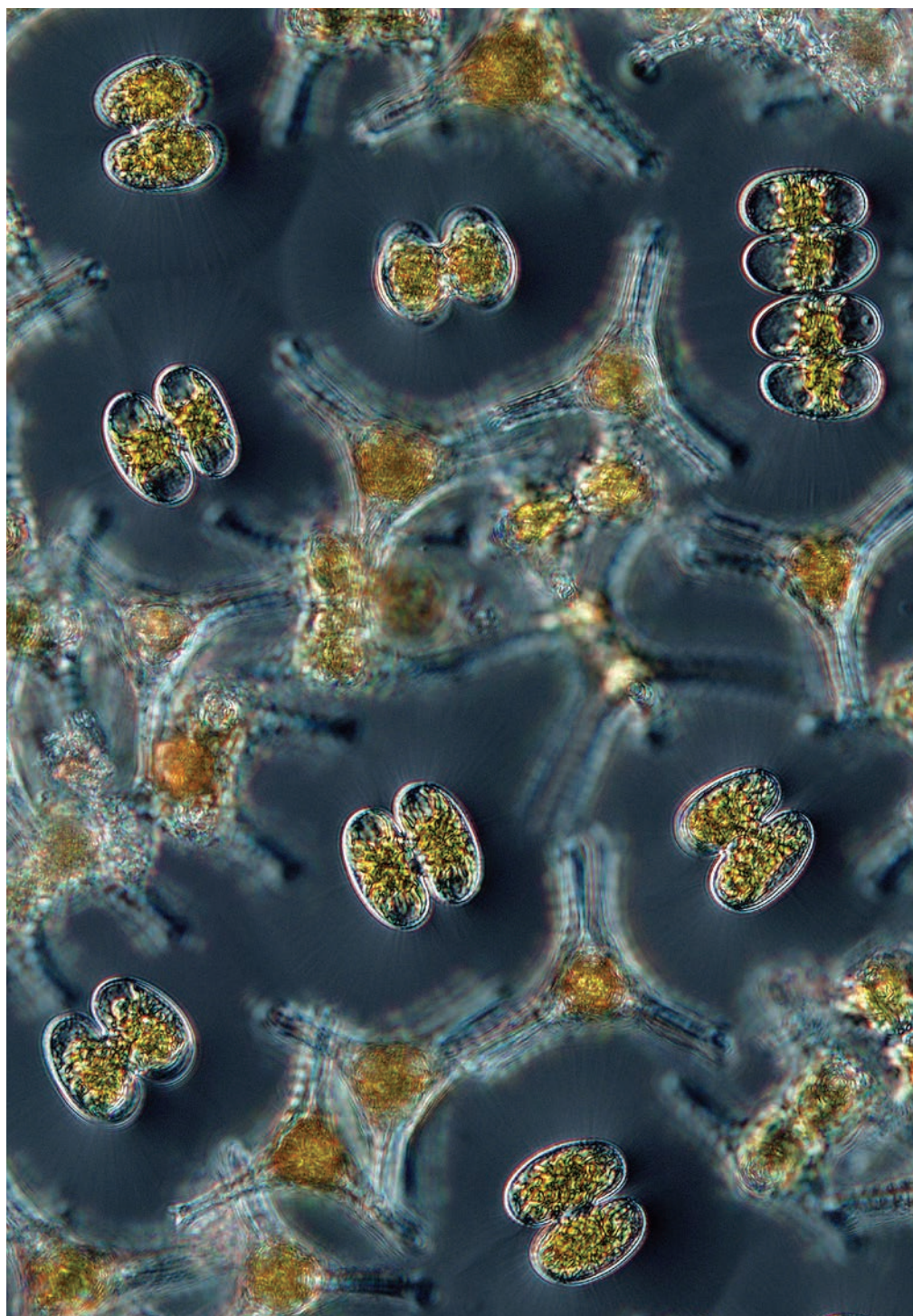


Figure 70: Planktonic desmids from the genus *Cosmarium* which dominated the summer phytoplankton of the Římov Reservoir in the dry year 2015.

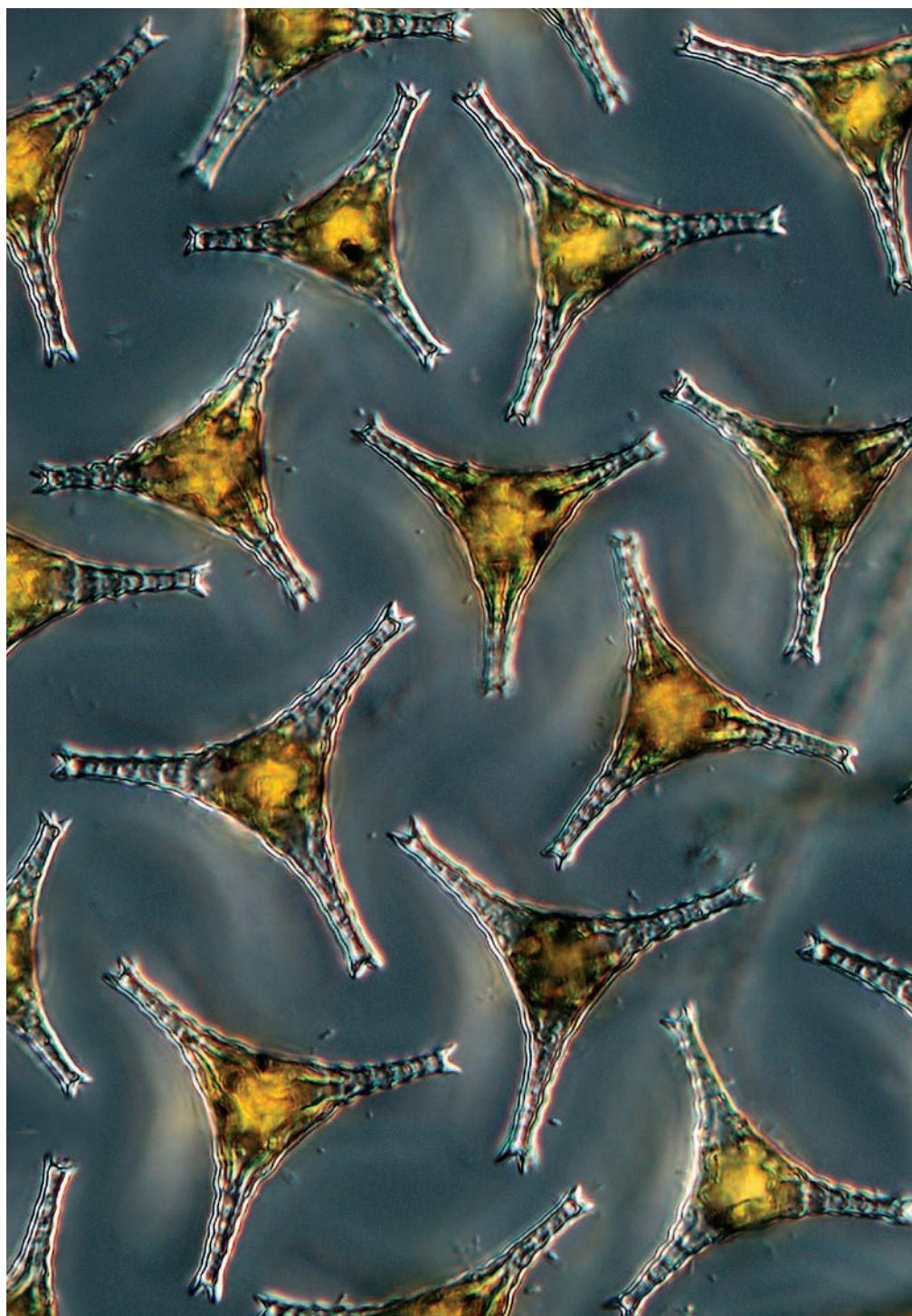


Figure 71: Planktonic desmids *Staurastrum planctonicum* which was extremely abundant in the Římov Reservoir in the years 1993, 1994, 2000 and 2001.

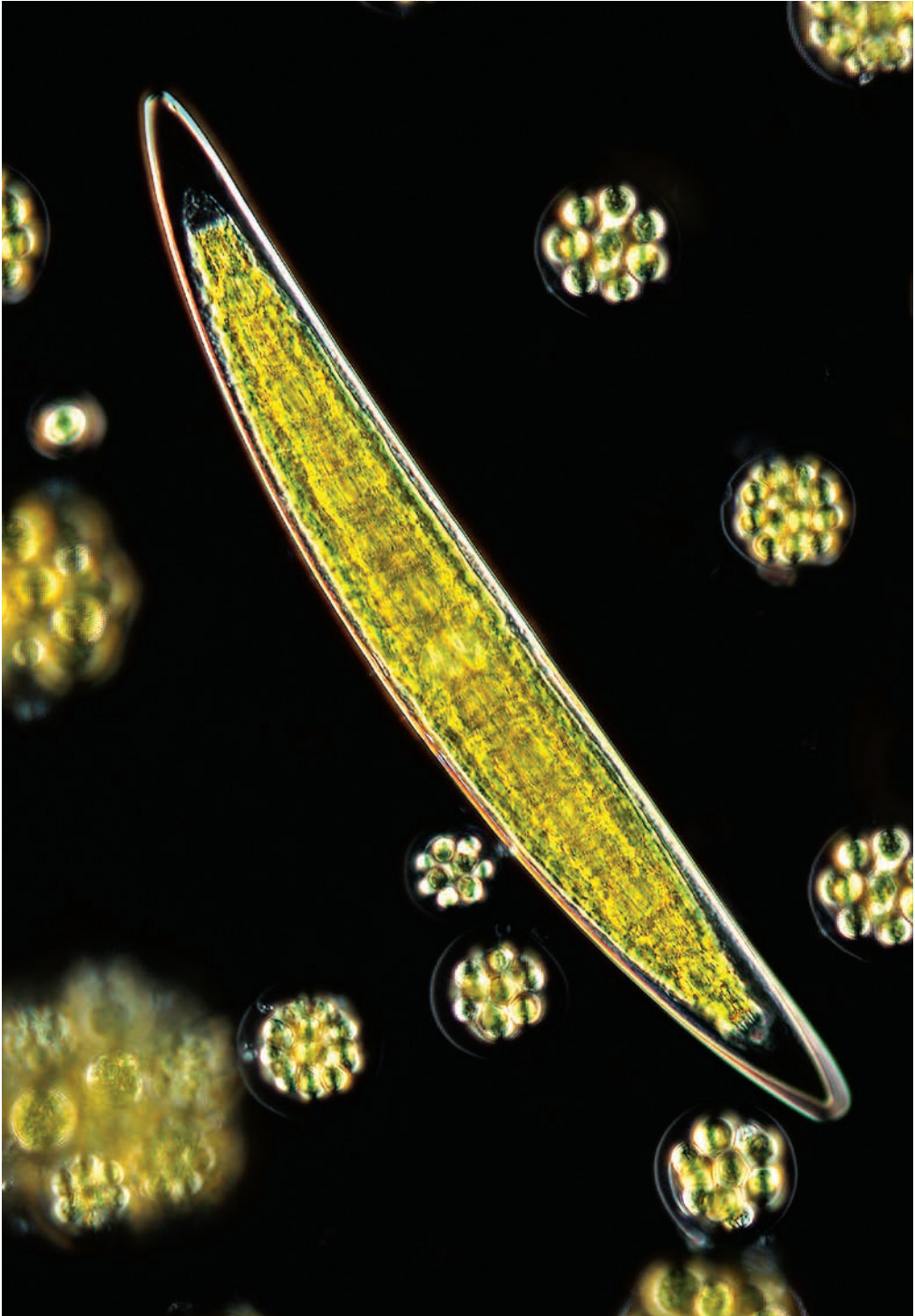


Figure 72: Large planktonic desmid from the genus *Closterium* (~ 200 μm).

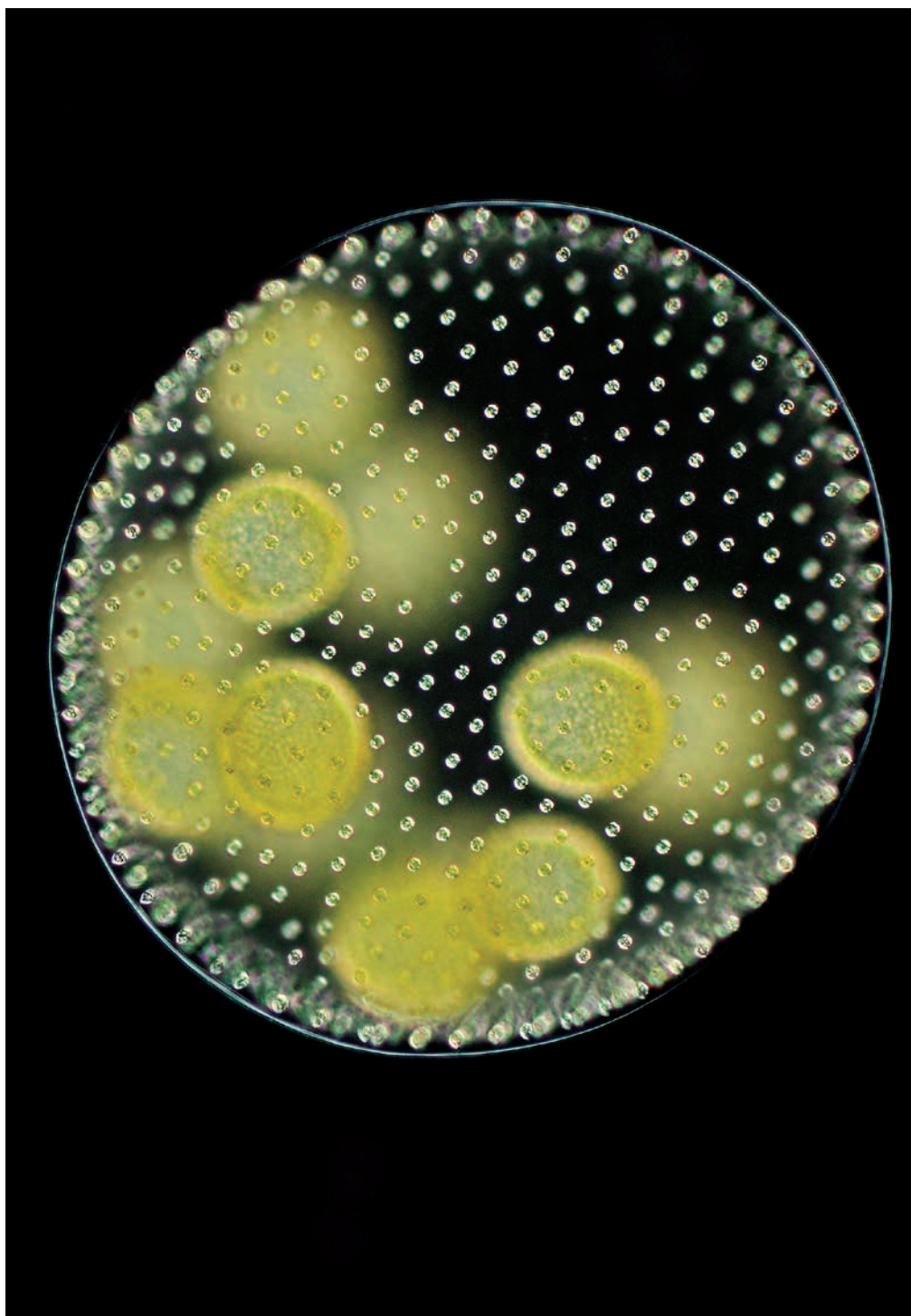


Figure 73: Cenobial green alga *Volvox aureus* occasionally occurring in the transition zone the Římov Reservoir.

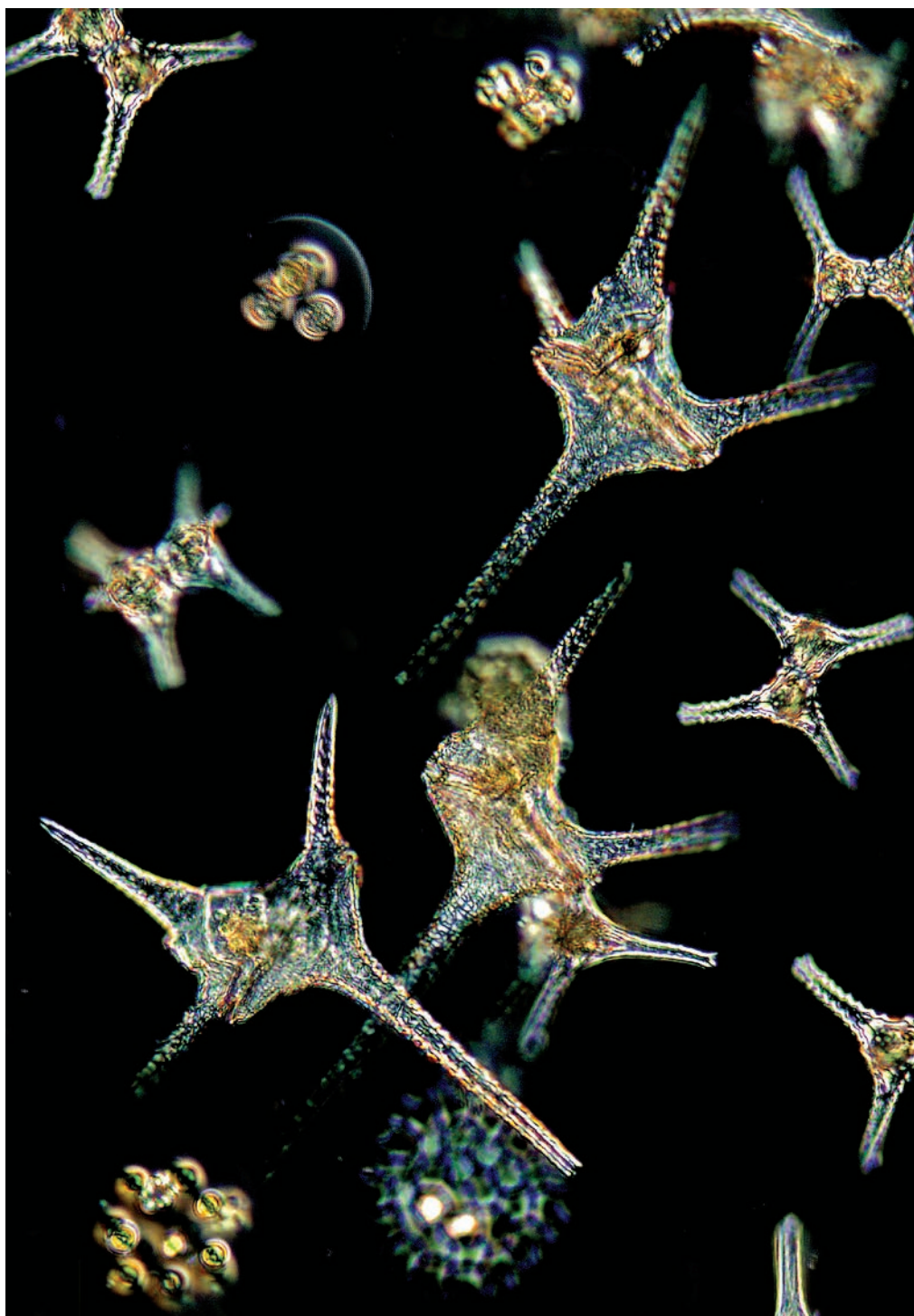


Figure 74: Large cells ($\sim 150\ \mu\text{m}$) of a common dinoflagellate *Ceratium hirundinella* accompanied by desmids and colonial algae and cyanobacteria.



Figure 75: *Daphnia galeata*, the dominant cladoceran species of the Římov Reservoir.



Figure 76: *Polyphemus pediculus*, a typically littoral predatory cladoceran.



Figure 77: Planktonic copepod from the genus *Thermocyclops*.



Figure 78: Common planktonic rotifer *Keratella quadrata*.



Figure 79: Colonial planktonic rotifer from the genus *Conochilus*.



Figure 80: Sunset over a reservoir. Photo by Milan Říha.

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Pike (*Esox lucius*). Photo by Jiří Peterka.



Capturing European catfish using a booming boat. Photo by Lukáš Vejřík.



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