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The impact of fish and planktonic invertebrate predation on zooplankton in experimental mesocosms

Ph.D. Thesis

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Annotation

This thesis focuses on the effect of fish and invertebrate predation on zooplankton in deep reservoir and shallow lakes. Mesocosms were used to evaluate the separated and combined effect of both type of predation. An appropriate mesocosm approach was modified and used in the Římov reservoir. The last part is dedicated to the effects of predation on zooplankton in contemporary changing environment, mesocosm experiment with different temperature and nutrient levels was conducted.

Declaration [in Czech]

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                                                                                         Michal Šorf

In memory of Prof. Zdeněk Brandl

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. Šorf, M., Brandl, Z., Znachor, P., Vašek, M., 2013. Floating large-volume mesocosms as a simple, low-cost experimental design suitable for the variety of lakes and reservoirs. Fundamental and Applied Limnology, 183(1): 41-48. (IF_{2012} = 1.190)
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II. Šorf, M., Brandl, Z., Znachor, P., Vašek, M. Different effects of planktonic invertebrate predators and fish on the plankton community in experimental mesocosms. Annales de Limnologie – International Journal of Limnology, In Press. (IF_{2012} = 0.736)
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III. Šorf, M., Davidson, T. A., Brucet, S., Menezes, R. F., Søndergaard, M., Lauridsen, T. L., Landkildehus, F., Liboriussen, L., Jeppesen, E. Zooplankton response to climate warming: a mesocosm experiment at contrasting temperatures and eutrophication states. First Draft.
    Michal Šorf was responsible for zooplankton sampling and analysis, statistical processing and participated in the preparation of the manuscript.

Co-authors agreement

The co-authors listed below fully acknowledge that Michal Šorf is the first author of all papers presented. Michal Šorf participated in field sampling and was responsible for processing of the zooplankton samples, data analyses and writing the manuscript (Paper I and II) and the draft of the manuscript (Paper III).

The co-author and consultant Mojmír Vašek, and co-author and tutor of the student stay in Denmark Erik Jeppesen, hereby consent to the publication in the Ph.D. thesis of Michal Šorf.

Mojmír Vašek   Erik Jeppesen

Contents

Introduction

Food webs in lentic ecosystems

Aquatic organisms are linking together into more or less intricate net of mutual relationships resulting in food webs of various complexity (Sabo *et al.*, 2009). Lindeman (1942) introduced the concept of 'more or less discrete trophic levels' where each of such groups depend on a preceding one. All levels depend on a primary production linking solar radiation energy to phytoplankton biomass. Lindeman's fundamental idea present the rough outline of aquatic ecosystem functioning. In most cases, aquatic ecosystems are comprised of four trophic levels: phytoplankton, herbivorous zooplankton, invertebrate and vertebrate zooplanktivors and top predators (Carpenter *et al.*, 1985).

The actual situation in aquatic food webs is not that straightforward and it could vary a lot. For instance, there are components of the food web which fall into more than just one single category (e.g., omnivorous species which may feed on zooplankton as well as on phytoplankton, Šorf & Brandl, 2012). Top predators, piscivorous fish, are known for switching from planktivory to piscivory in their ontogeny (Byström *et al.*, 1998). Some omnivorous fish undergo ontogenetic diet shifts from planktivory in larval fish to omnivory in adults (Stein *et al.*, 1995).

From pool poisoning to size selective predation: a brief history

The late hydrobiologist Jaroslav Hrbáček was among the first modern authors who noticed the structuring role of fish in forming of zooplankton assemblages. In fact, many years ago Frič & Vávra (1898) briefly described how the stocking of brook trout altered zooplankton community. Hrbáček and his colleagues found out that the differences of the zooplankton species composition of various ponds were influenced particularly by the density of fish stock (Hrbáček, 1959; Hrbáček & Hrbáčková-Esslová, 1960; Hrbáček *et al.*, 1961; Hrbáček, 1962; Hrbáček & Novotná-Dvořáková, 1965; Hrbáček, 2010). Small cladocerans *Bosmina longirostris* and *Daphnia cucullata* inhabited ponds with high amount of fish stock, contrary to larger *Daphnia* species, which were more abundant in ponds with either low fish stock or with no fish at all. Grygierek (1962) experimentally bred carp fry in ponds with or without zooplankton and showed that although densities of microcrustaceans increased in treatments with fish fry, their biomass decreased. Moreover, when abundance of carp fry achieved 2500 individuals per hectare or more, large cladoceran *Daphnia magna* disappeared. Higher abundances of carp fry supported the presence of small cladocerans *Bosmina longirostris* and *Ceriodaphnia quadrangula* (Grygierek, 1965). Carp fry also caused an increase in rotifer abundance (*Keratella cochlearis* and *K. quadrata*) in limnetic zone (Hillbricht-Ilkowska, 1964). Hrbáček & Novotná-Dvořáková (1965) and Novotná & Kořínek (1966) studied pools

before and after the elimination of fish by their poisoning. Originally, pools were inhabited by small zooplankton taxa such as *Bosmina*, *Ceriodaphnia*, cyclopoid copepods *Thermocyclops* and *Mesocyclops* and numerous rotifer species. Species composition dramatically changed after poisoning the fish stock. Net plankton was represented mainly by larger *Daphnia* species (and *Cyclops*) and rotifers did not form considerable part of zooplankton assemblage. Another important point was that small-sized zooplankton re-appeared after re-settlement of fish. Furthermore, addition of piscivorous fish set up a similar zooplankton composition as it was after the elimination of planktivorous fish.

Concurrently with the above mentioned authors, Brooks & Dodson (1965) observed similar situation in lakes of New England. Body sizes of planktonic species significantly differed among lakes – some of them were predominated by smaller zooplankton while other by larger species. Lakes seldom contained both large and small zooplankton species together in high abundance. Presence or absence of landlocked populations of alewife (*Alosa pseudoharengus*) represented the main difference among these lakes. Crystal Lake (Connecticut) served as a model: larger species predominated when the lake was sampled in 1942. Re-sampling was done in 1964 when only small zooplankton was observed. The crucial question, what happened in meantime, was connected with the fish stock. Related species of alewife (*A. aestivalis*) was introduced into Crystal Lake between those years. Moreover, mean body size of *Daphnia* was higher in fish stomach than in lake plankton (Galbraith, 1967; Wong & Ward, 1972). Thereafter, Brooks & Dodson (1965) published the paper summarizing the composition and zooplankton size structure before and after the appearance of planktivorous fish and proposed the Size Efficiency Hypothesis (SEH).

Size Efficiency Hypothesis

Many other authors reported size-dependent feeding in fish (e.g., Galbraith, 1967; Brooks, 1968; Gliwicz & Prejs, 1977; McQueen & Post, 1988; Declerck & De Meester, 2003). The SEH proposed that size-dependent predation by fish may be an important determinant of community structure of freshwater zooplankton. There are several reasons why planktivorous fish feed on different size classes of prey differently, size-selectively. First of all, their visual orientation during foraging makes encounter of larger prey item more probable (Li *et al*., 1985). Reactive distance is generally a linear function of prey size (Confer & Blades, 1975; Confer *et al*., 1978) and exponentially increase with fish size (Wanzenböck & Schiemer, 1989). Smaller prey can be relatively easily missed from the visual range. The specific way of swimming behaviour, sinusoidal swimming pattern, helps fish in foraging for zooplankton by highlighting prey with respect to its position in water column (Jarolím *et al.,* 2010). The colouring of prey may also play a significant role in predator-prey relationships. For instance, daphnids with high concentration of haemoglobin are easily detectable by fish (Confer *et al*., 1978). Maier *et al*. (2000) showed higher probability of fish foraging on copepod pairs in copulation or on females with ovisacs than on copepods without eggs. Large

coloured eye of *Polyphemus pediculus* is probably the reason of strong positive selection by both roach and perch in the Římov reservoir (Matěna, 1995).

Limitation in size of gape can be found in fish fry (Guma'a, 1978; Bremigan & Stein, 1994; Mehner *et al.*, 1998b; Gilbert & Hampton, 2001). Young fish preferably feed on food of body size close to their mouth gape size (Wanzenböck, 1995). Lindström (1955) experimentally confirmed that fish fry of *Salmo* sp. consumed food of various sizes and appertaining to different taxa but only when prey moved.

Beyond feeding on particular items, fish use their gill rakers as a plankton sieve. The principle of obtaining the food in this way is very easy – item larger than the distance between gill rakers is caught and consumed (Gal *et al.*, 2006).

Zooplankton can be usually found in various size ranges and, for fish, utilization of small number of larger prey is more favourable in terms of energy (optimal foraging – Breck, 1993).

Brooks & Dodson (1965) summarized SEH in five basic assumptions:

- Planktonic herbivores all compete for the fine particulate matter (1 to 15 μm) of the open water.

- Larger zooplankters do so more efficiently and can also take larger particles.

- When predation is of low intensity, the small planktonic herbivores will be competitively eliminated by large forms (dominance of large cladocerans and calanoid copepods).

- When predation is intense, size-dependent predation will eliminate the large forms, allowing the small zooplankters (rotifers, small cladocerans), that escape predation to become the dominants.

- When predation is of moderate intensity, it will, by falling more heavily upon the larger species, keep the populations of these more effective herbivores sufficiently low so that their slightly smaller competitors are not eliminated.

Although the basics of SEH still remains valid, some improvement have been made since the original paper was published. For instance, competition for fine particulate matter is exhibited in case of food limitation (Carpenter *et al.*, 1992) not only in pelagic zone. The interspecific competition exists among producers, their predators and decomposers (Hairston *et al.*, 1960). Planktivorous fish consume preferably large-bodied zooplankton, which is assumed to be a superior competitor for food because of its greater filtering efficiency. Higher efficiency in competition does not have to be exclusively a feature of larger zooplankton. Competitive ability is given not only by body size itself but current physiological state or life history strategies are also influencing such efficiency (Milbrink *et al.*, 2003).

Lower predation intensity on larger zooplankton due to lower fish abundance also means low predation on larger invertebrate predators like predaceous cladoceran *Leptodora kindtii* or *Chaoborus* larvae, which further affects populations of smaller herbivores (Sell *et al.*, 1997). Suppression of small-sized prey by cyclopoid copepods should be also taken in account (Dodson, 1974).

Moderate intensity of predation, the most problematic point of SEH, usually requires knowledge about connection with other features of aquatic ecosystem like lake morphology, behaviour of zooplankton species, type of predation etc. It is well known that changes can be found not only in abundances but also in a body size specific for the certain part of a species life history, e.g. body size of cladocerans reaching maturity (Brooks, 1968; Wells, 1970; Duncan & dos Santos, 1989).

Trophic Cascade Hypothesis

Observations of how fish predation affects freshwater food webs resulted in the concept of cascading trophic interactions, which extended SEH by introducing the Trophic Cascade Hypothesis (TCH). In a nutshell, rising of piscivore biomass causes decreasing of planktivorous fish biomass, which subsequently increases planktonic herbivore biomass, and decreases phytoplankton biomass (Carpenter *et al.*, 1985). Productivity of each trophic level is maximized at an intermediate biomass of its predators (Carpenter *et al.*, 2001). This general scheme is modified by various features – life histories and other interactions (e.g. defence mechanisms) among particular species (Jeffries, 1988; Svensson, 1996; Kolar & Wahl, 1998; Straile & Halbich, 2001). Fish may significantly influence nutrient cycles in lakes (Kairesalo & Seppälä, 1987; Carpenter *et al.* 1992). Schindler *et al.* (2001) proved fish ability of phosphorus translocation throughout the water column. Reduced zooplankton body size also affect nutrient cycles by an increase in phosphorus release per unit biomass (Bartell, 1981). Hence, high fish stock can enhance phytoplankton biomass through direct and indirect nutrient recycling (Mazumder *et al.*, 1989; Vanni & Layne, 1997; Hansson *et al.*, 2004). These findings are widely used during food webs manipulation with ultimate goal of better water quality management (biomanipulation, see below) (Berg *et al.*, 1997; Beklioglu, 1999).

The indirect effect of fish predation on lower food web levels influence not only zooplankton abundance and biomass itselves but also other characteristics like nutrient regeneration or competitive relationships between prey species. The density of protozoans highly increased with increasing fish stock (Yang *et al.*, 2005) or simply with zooplankton removing (Hamilton & Taylor, 1987). Nanoplankton as the main food source used by zooplankton (fraction from 3 to 20 µm) was significantly reduced when fish were not present (Mazumder *et al.*, 1990a). Fish can even induce changes in phytoplankton cells through morphological variation (phenotypical plasticity) like shorten cell length in cryptomonads (Kim *et al.*, 2003).

As a consequence of TCH, some abiotic lake characteristics can be also altered. Low predation pressure on phytoplankton and its increased biomass can contribute to higher temperature of deeper water strata caused by higher light energy absorption (Hambright, 1994). Although the dissolved oxygen concentration relates to many characteristics, it also reflects the structure of the food web (Mazumder *et al.*, 1990b).

Vertebrate and invertebrate predation in lakes

Both fish and invertebrate predators often coexist and hence their impact on zooplankton community is very complex (Chang & Hanazato, 2004). Naturally, there are great differences between separate action of fish or invertebrate predators on final qualitative and quantitative state of zooplankton.

Differences between invertebrate and vertebrate predation are especially given by dissimilarity in body size of such predators and their prey (cf. fish–*Daphnia* and cyclopoid–*Daphnia* body sizes). Invertebrate planktivors like cyclopoid copepods or predaceous rotifers forage their prey by mechanoreceptors (vibrations) and chemoreceptors (Starkweather, 1996) while vertebrate planktivors (fish) are (not exclusively – see a review by Lazzaro, 1987) visually orientated predators (Hairston *et al*., 1982; Aksnes *et al*., 2004). The actual state of zooplankton communities is therefore a result of different way how planktonic invertebrate predators and fish are obtaining their prey and forming the consequent zooplankton species and size structure through size selective feeding. The mutual relationships and interactions between and within predator(s) and prey species contribute to the final structure of zooplankton communities (Johansson, 1995).

Regarding vertebrate predation, the most apparent correlations are found between (large-bodied) cladocerans and fish (e.g., Gophen, 1985; Seďa *et al*., 1989). Although dramatic impact of fish stock was revealed by many studies (e.g., Paper II; Galbraith, 1967; Elser & Carpenter, 1988; Lammens, 1999; Attayde & Hansson, 2001; Chang & Hanazato, 2004), the proportion of total predation caused by invertebrate predators could be higher than influence of fish on lake ecosystems (Lane, 1979; Blumenshine & Hambright, 2003; Liljendahl-Nurminen *et al*., 2003). Decline of densities of larger zooplankton may have another reason than only direct reduction by fish (Hülsmann & Mehner, 1997). Wojtal *et al*. (2004) have found that the role of juvenile fish in daphnid density decline in the pelagic zone of eutrophic reservoir is much smaller than the impact of predatory cladoceran *Leptodora kindtii* which accounted for a reduction up to 50 % of *Daphnia* biomass. This was confirmed in Polish lakes where the share of fish on total predation was relatively high only at the beginning of July (Gliwicz *et al*., 1978). Lane (1979) published results where contribution of invertebrate planktonic predators was much higher compared to fish. Vanni & Findlay (1990) conducted the mesocosm study combining the effect of fish and *Chaoborus* larvae on lower trophic levels. Here the zooplankton biomass decreased under the predation pressure of both types of predators but an increase in phytoplankton biomass was observed only in *Chaoborus* treatment. Selective feeding of *Chaoborus* larvae is affecting mainly large-bodied cladocerans while copepods and rotifers are not influenced (Castilho-Noll & Arcifa, 2007).

Most of the invertebrate predators also feed size selectively, but in contrast to fish, they usually prefer smaller prey even though the probability of encounter with larger prey is higher. Larger prey requires more energy invested into hunting it, and together with losses related to

handling, the effort expended to smaller or moderate-sized prey is more favourable (Brandl, 2005; Chang & Hanazato, 2005). Some predators select not only in terms of body size but also by prey behaviour like its swimming and escape responses.

Planktonic prey can perceive the presence of predator which is releasing traceable substances (Engelmayer, 1995; Lass & Spaak, 2003). Different capture probabilities in various zooplankton are given by different movement patterns (Drenner *et al.*, 1978; Dodson, 1996), and vertebrate/invertebrate predator defence mechanisms, e.g. morphological (Gilbert, 1967; Wong, 1981; Stemberger & Gilbert, 1987; Threlkeld & Choinski, 1987; Williamson, 1987; Barnhisel, 1991; Kolar & Wahl, 1998) or behavioural (Kerfoot, 1977; Dini & Carpenter, 1988; Iyer & Rao, 1995).

Generally, cyclopoid copepods feed on rotifers, larval stages of copepods and even cladocerans of an appropriate size (Brandl & Fernando, 1974; Williamson, 1983; Brandl & Pražáková, 2002; Brandl, 2005). High abundance of *Cyclops vicinus* was accompanied by lower share of daphnid juveniles as a result of their selectiveness (Brandl, 1998). Blumenshine & Hambright (2003) found higher predation pressure of cyclopoid copepods over fish which impacted zooplankton community of subtropical Lake Kinneret. Size-selective predation provided by cyclopoid copepods in experimental polyethylene tanks revealed the strong effect on relationships between two sympatric species of *Bosmina*. *Bosmina fatalis* was negatively affected by cyclopoids while there was no significant effect on *Bosmina longirostris*. Suppression of *B. fatalis* enhanced rotifer densities, probably through releasing them from competition (Chang & Hanazato, 2005).

Hansson & Tranvik (1996) have concluded that invertebrate predators have only marginal effect in the comparison with vertebrate predation pressure on zooplankton. An extensive meta-analysis by France *et al.* (1995) revealed that the majority of reviewed data sets fitted well with the top-down effect of invertebrate predators. Nevertheless the correlations were weak in most cases and other variables should be important.

From these examples, it is clear that questions about biomanipulation and trophic cascade are still incompletely answered and that the statement of Carpenter & Kitchell (1992) that 'a rigorous re-examination of accumulated results is beneficial' is relevant even after 15 years.

Fish-zooplankton relations in practice: biomanipulation

Shapiro *et al.* (1975) introduced a term 'biomanipulation' as a type of biological engineering where reduction of algae is used by virtue of biotic components' manipulation in aquatic ecosystems. Initially, the idea of successful biomanipulation was partly based on SEH and TCH: the reduction of planktivorous fish (by introduction of piscivorous fish and/or by controlled fisheries management) enhances the larger cladocerans which increased densities are able to inhibit phytoplankton biomass. The fact that the fish impact could be altered when their density decrease is well known for years (e.g., Warshaw, 1972; Shapiro & Wright, 1984; Elser & Carpenter, 1988). Although the reduction of phytoplankton biomass was observed

during grazing by larger zooplankton (Benndorf *et al.*, 1989; Kasprzak *et al.*, 1993; Reynolds, 1994), this state was often time-constrained and accompanied by shifting in phytoplankton populations (cyanobacterial blooms) and recycling in microbial loops (Wetzel, 2000). The early phase of biomanipulation may increase biomass of invertebrate predators such as *Chaoborus* or *Leptodora kindtii* (Benndorf *et al.*, 1989; Sell *et al.*, 1997). Now, we know that biomanipulation should not be applied without additional processes such as submerged macrophytes establishment, nutrient loading reduction or prevention of sediment particle re-suspension (Tüzün & Mason, 1996; Hansson *et al.*, 1998). An effort to eliminate eutrophication by biomanipulation have only short-term effect without removing or displacement of nutrient reserves from ecosystems (Benndorf, 1987; Wetzel, 2000). As reviewed by Hansson *et al.* (1998), fish reduction often leads to high recruitment of young-of-the-year fish, which feed intensively on zooplankton. Hence, the suppression of YOY recruitment is also important during successful biomanipulation. With these premises, the biomanipulation should be a reasonable method for restoration even in large deep eutrophic lakes.

Predator-prey interactions in changing environment

There are solid evidences that the climate is undergoing significant changes no matter who or what is causing it (IPCC, 2007). Plankton organisms may serve as a good model because of their short turn-over. Hence, there is a good chance that some of the important issues regarding climate change such as the impact of extremes in weather conditions or intensification of eutrophication could be answered thanks to the plankton ecology (Lürling & de Senerport Domis, 2013). Zooplankton can be affected directly by the rising temperature depending on their ontogeny and physiology (Huntley & Lopez, 1992), but also indirectly by altered size and nutrient quality of phytoplankton, being their main food source. Warming may also modify the zooplankton communities by strenghtening of the top-down regulation (Gyllström *et al.*, 2005; Shurin *et al.*, 2012) or by altering competition (Fey & Cottingham, 2012). Higher temperature of water tend to house smaller *Daphnia* species and larger abundance of smaller fish alongside with increased phytoplankton (also cyanobacterial) biomass (Moss *et al.*, 2011). Warming is altering the period of predation on daphnids by both fish and invertebrate predator, *Leptodora kindtii* (Wagner *et al.*, 2013).

There are still significant gaps in zooplankton ecology. Namely, poor knowledge what is causing increases or declines of zooplankton communities prevent us from explanation of the past events and predicting the future ones. For instance, we often do not know all reasons of zooplankton seasonal changes, where predator-prey relationships play an important role (e.g., Wagner *et al.*, 2004).

Aims of the Study

The general goal of this thesis was the evaluation of the effect of fish and planktonic invertebrate predators (cyclopoid copepods) on zooplankton communities under the different conditions in various freshwater ecosystems. We investigated deep man-made reservoir (the Římov reservoir, Czech Republic) and shallow lakes (Lemming, Denmark) using mesocosm approach. Such different ecosystems were studied in order to generalize the results.

The original premises of Brooks & Dodson (1965) and the current state of knowledge lead to the proposing of ideas behind the doctoral thesis:

    I.   To evaluate the influence of separated predation by fish and planktonic invertebrate predators on plankton communities in experimental mesocosms.

        (a) To what extent are cyclopoid copepods affecting rotifer and cladoceran populations?

        (b) How does fish predation affect probable competition between prey population of rotifers and cladocerans?

    II. To determine and describe the effect of fish predation on zooplankton communities in different temperature regimes and nutrient loading.

As a mean to test our hypotheses, we had to modify the mesocosm approach to be used in the pelagic zone of the Římov reservoir (and other deeper lakes and reservoirs).

Methods

There is a wide range in experimental volumes used for testing of hypotheses in the field of limnology from smaller volumes enabling to resolve questions about planktonic invertebrates (e.g., Chang & Hanazato, 2004) to the whole lake experiments which can comprehend the complexity of food web including fish component (e.g., Elser & Carpenter, 1988; Byström *et al.*, 1998). Mesocosm experiments, defined by Lampert & Sommer (2007) as sections of the natural environment that are isolated by means of artificial barriers such as transparent plastic sheets, allow us to set up natural-like conditions in terms of physico-chemical gradients and densities of organisms. The term 'mesocosm' is generally used for the range of volumes from 1 to 1000 m^3 (Bloesch, 1988). Not only volume of mesocosm itself, but other dimensions like depth and diameter which determines separated space of enclosure from lake water, have to be set up according to studied problem. Mesocosm studies (also known as enclosures or 'bag studies') were used to determine zooplankton-phytoplankton relationships (Cottingham *et al.*, 1997) as well as linking between zooplankton and fish component of lakes (e.g., Kurmayer & Wanzenböck, 1996; Paper I and II).

Despite known limitations which can result in wrong interpretation of measured data, mesocosm approach is a reasonable possibility how to address some important issues in aquatic sciences (Carpenter, 1996; Riebesell *et al.*, 2010). The following limitations are mainly: volumes and dimension, sedimentation and pertinent differences in nutrient cycles compared with surrounding lake, periphyton growth on mesocosm walls and durability of plastic material. In our case, volume and dimension were set up with the intention of stocking fish. Floating construction carrying experimental mesocosms made of polyethylene was found to be a suitable device for a deep lake such as the Římov reservoir (Fig. 1; Paper I and II). Since our goal was to introduce fish into deep mesocosms, we decided for volume of 16 m^3 and depth of 9.5 m, which roughly corresponded to offshore catches of perch (*Perca fluviatilis*) reported for the Římov reservoir by Vašek *et al.* (2006). The polyethylene bags were closed at the bottom and entirely open above water level with no mesh on the top (cf. Mumm & Snell, 1995 who used mesh both at the top and on the bottom). The common problem of the mesocosm studies – the periphyton growth on mesocosm walls – cannot be easily avoided. One need to be sure that periphyton would not increase its biomass to the levels higher than other component of food webs (Rees, 1979). I believe that no special treatment like wall cleaning is a reasonable way. I decided for simply stopping the experiment after an appropriate time when I expected the sufficient response of the zooplankton community to the manipulation and also not a prominent biofilm growth at the same time (Fig. 1; Paper I and II).

Essentially, mesocosm studies performed in shallow lakes carry the similar advantages and disadvantages as discussed above for deep lakes. The experimental arrangement provided in shallow lakes could be slightly different. We usually do not need to perform the experiments

in so large volumes as in deep lakes. Therefore, the basic difference lies in the possibility of using a solid material for mesocosm construction. I took part in two shallow lake mesocosm experiment where a solid tank was used to separate manipulated treatments from outside environment (Paper III). The methodology was extensively described by Liboriussen *et al.* (2005).
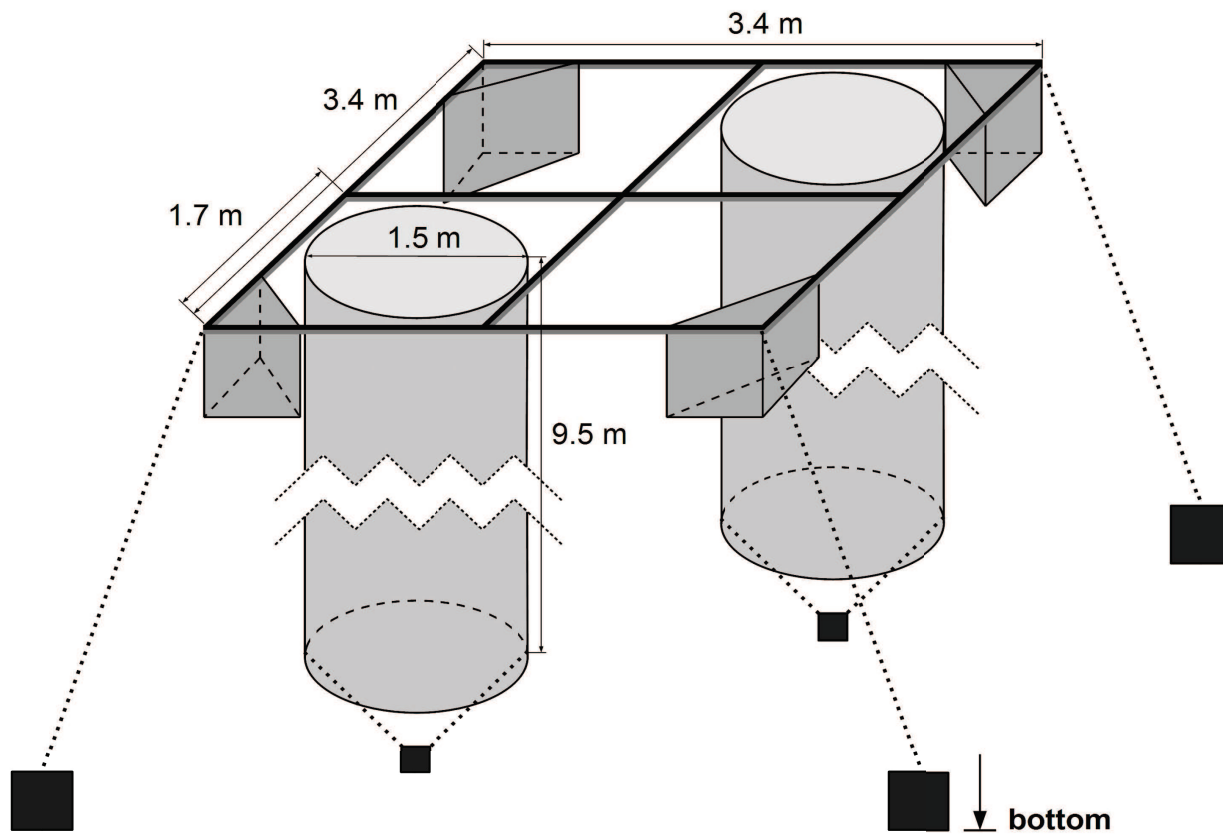

Figure 1. A general scheme of the mesocosm design used in the Římov reservoir. The supporting metal framework is capable of carrying four polyethylene bags (two were omitted to simplify the illustration) (Paper I).

Results and Discussion

Mesocosm experiments as a tool for food web studies

Manipulative experiments, varying according to the type of locality, involved organisms or differing in used technical design, provided an insight into functioning of aquatic food webs. The principal method behind all results of this thesis is based on a mesocosm approach. When dealing with mesocosms – including both their positives and negatives – one need to consider the aim of the experiment. We succeeded in developing of the relatively inexpensive design suitable for deep lakes and/or reservoirs (Table 1 in Paper I). The main advantages of the suggested floating mesocosm construction are (i) carrying four mesocosms instead of maintaining individual treatments separately, (ii) dimensions enabling us to use fish as a top predator, and (iii) keeping light conditions similar to the adjacent water mass. Paper I summarizes all the negatives derived from introducing of an artificial barrier into the open water zone of the lake. Possible solutions of some mesocosm limitations are suggested.

Besides the Řimov reservoir (Paper I and II), shallow lakes were studied using different mesocosm approach with stable tanks (Liboriussen *et al.*, 2005; Paper III). Participating on such highly sophisticated mesocosm design allowed the evaluation of zooplankton response to the combination of biotic and abiotic factors. The emphasis behind all presented papers was aimed at zooplankton and its response to the variety of both biotic and abiotic factors like vertebrate/invertebrate predation and coupling between water temperature and nutrient loading.

Řimov reservoir: vertebrate over invertebrate predation

Short-term mesocosm experiment simulating the pelagic zone of the Řimov reservoir clearly revealed the dramatic impact of fish over invertebrate predation on zooplankton (Paper I). Large-bodied cladocerans were suppressed by introducing the yearling roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) into the mesocosms (Fig. 4 in Paper II). An alteration of the cladoceran assemblage from a dominance of *Daphnia* spp. at the beginning of the experiment to the prevalence of the smaller *Bosmina longirostris* occurred (Fig. 5 in Paper II). In accordance to the TCH, chlorophyll-a concentration (and rotifer abundances) increased when daphnids were eliminated by fish (Fig. 2). The decline of daphnids was reported many times as shown in Table 1. The elimination of large-bodied cladocerans by fish is widely recognised as a general pattern (Wells, 1970; Post & McQueen, 1987; Ramcharan *et al.*, 1996; Mehner & Thiel, 1999; Nicolle *et al.*, 2011).

Despite the extensive biomanipulation effort which decreased fish biomass in the Řimov reservoir from 650 kg.ha^{-1} in the 1980s to 100 kg.ha^{-1} in the 1990s, its effect on phytoplankton remained poor (Seďa & Kubečka, 1997). Post & McQueen (1987) also reported a weak effect

of planktivorous fish on phytoplankton biomass through the trophic cascade. McQueen (1990) stated the difference between shallow and deep lake in biomanipulation effort. The effectiveness of biomanipulation in deep lakes is dependent on an alteration in phytoplankton composition – the development of non-grazable taxa suppress the effect of fish manipulation. Generally, there are many reasons why the response of phytoplankton differ from the theoretical foundations of TCH like the stoichiometric state of the lake or simply different responses and/or demands at lower taxonomic levels (Kitchell & Carpenter, 1993; Reynolds, 1994; Gulati & DeMott, 1997; Hansson *et al.*, 2004). For instance, McQueen *et al.* (1992) reported no response in zooplankton biomass and size structure in fish biomass up to 142 kg.ha^{-1}.

Roach and perch account for ca. 40% of the total fish assemblage in the Římov reservoir which is now considered to be in its cyprinid phase (Vašek *et al.*, 2008; Říha *et al.*, 2009). Both juvenile roach and perch are known to feed mainly on microcrustaceans (Hammer, 1985; Macháček & Matěna, 1997; Peterka & Matěna, 2009). Vašek & Kubečka (2004) showed that roach fed almost exclusively on daphnids in the pelagic zone of the Římov reservoir. *Daphnia* was highly positively selected over other zooplankton taxa such as *Bosmina* sp. (Vašek *et al.*, 2008). Besides on cladocerans, perch fed also on copepods in the Římov reservoir (Macháček & Matěna, 1997; Vašek *et al.*, 2006). Laboratory experiments with perch fry revealed that calanoid copepod *Eudiaptomus gracilis* was preferred to *Daphnia galeata* in case of longer experimental duration (minutes) (Furnass 1979). Calanoid copepods were the common prey of perch in Římov as well (Macháček & Matěna, 1997). In accordance to our results, Witeska (1995) found an increase in cyclopoid biomass in the presence of fish.

Cyclopoid copepods were relatively very abundant in fish treatment probably because of (i) the different fish selectivity of roach and perch, and (ii) the presence of high biomass of suitable food (Paper II). There were no other invertebrate predators like *Leptodora kindtii* in fish treatment. Roach is very efficient in feeding on *Leptodora* (Vašek *et al.*, 2003). Moreover, *Leptodora* occurence fall to the summer period (Liljendahl-Nurminen *et al.*, 2008).

When fish predation pressure was high, zooplankton decreased no matter how much food was available (Nicolle *et al.*, 2011). In our study, the proportion of large cladocerans clearly showed the effect of successful manipulation (Fig. 5 in Paper II). Hrbáček & Hrbáčková-Esslová (1960) recorded that *Daphnia* species (and clones) exhibited similar growth pattern reflecting the fish stock: higher abundance of fish decreased increments of cladocerans. On the contrary, the highest increments were found in ponds with lower fish stock. A decrease of average body size and the size of primiparae was also reported (Wells, 1970; Manca *et al.*, 2008). Fish can even induce the formation of resting eggs and elicit summer diapause (Pijanowska & Stolpe, 1996). Moreover, the number of eggs per clutch is generally higher in cladocerans suffering of dense fish stock (Culver *et al.*, 1984). The combination of all described effects determines the coexistence of *Daphnia* species (Johnson & Kitchell, 1996; Declerck & De Meester, 2003).

There were also (rarer) cases where the decline of daphnid populations was not due to fish predation (Table 1). Fish consumption may not be so high to cause the declines in zooplankton (Boersma *et al.*, 1996; Mehner *et al.*, 1998a). Ecological stoichiometry together with the knowledge about a particular lake can help us with interpreting of such 'surprising' results. Table 1 also shows an inconsistency in the effect of fish on *Bosmina*. Ślusarczyk (1997) observed no significant differences in densities of *Bosmina* between fish and fish-free mesocosms, but larger individuals of *Bosmina* were reduced in the presence of fish. No higher reproduction of *Bosmina* in fish-free treatments was found. Hence the prediction of species response to predation is still not simply inferable.

Table 1
Summary of the selected experimental studies using roach or perch as the top predator of the zooplankton community. The selection of published papers was based mainly on the amount of available variables which can be compared. The impact on phytoplankton, rotifers, *Daphnia* and *Bosmina*, and water transparency is marked with "+" for increase in abundances or "-" for a decreasing trend.

fish class	abund. ind.m^3	phytopl.	Rotifera	*Daphnia*	*Bosmina*	Secchi	volume m^3	duration weeks	reference
perch and roach									
1+	0.3	+	+	-	+	-	13	5	present study
perch									
0+	0.3	+		-	+	-	750	16	Post & McQueen, 1987
0+	0.8	+		-	+	-	750	16	Post & McQueen, 1987
0+	1.9	+	+	-	-	-	9.5	6.7	Bertolo *et al.*, 2000
0+	2	+		-		-	40	10.9	Kurmayer & Wanzenböck, 1996
>1+	0.1			-	-	+	9.5	6.7	Bertolo *et al.*, 2000
roach									
0+	2	+		+		-	40	10.9	Kurmayer & Wanzenböck, 1996
0+	12.5-105	+		-	-		0.4	6	Nicolle *et al.*, 2011
1+	3-4	+	+	-	+		ca 1	5.6	Hansson *et al.*, 2004
1+	10	+	+				0.3	1.6	Ślusarczyk, 1997
1+	13-21	+	+	-	-		ca 1	5.6	Hansson *et al.*, 2004
2+	0.4-0.5		+	-	-		7	4	Hessen, 1985

Cyclopoid predation on zooplankton was found as less prominent contrary to the impact of fish (Paper I and II). We established the initial abundance of cyclopoids to 2 ind.l⁻¹ to keep it close to the real reservoir condition (Paper II). Brandl & Pražáková (2002) reported regular feeding on rotifers, copepod developmental stages and cladocerans (*Daphnia galeata*, *Diaphonosoma brachyurum* and *Bosmina longirostris*) in cyclopoid abundances between 1 and 10 ind.l⁻¹. Therefore, the initial cyclopoid abundance was appropriate to the experiment. The effect can be more prominent when fish biomass would be lower.

Cyclopoid copepods generally prefer smaller individuals of prey species (e.g., Brandl & Fernando, 1974). The majority of cyclopoids are probably omnivorous species (Brandl, 2005; Šorf & Brandl, 2012). Contrary to daphnids, cyclopoids feed on larger phytoplankton taxa (Sommer *et al.*, 2001). Phytoplankton in fish treatments was hence determined by the combined action of fish eliminating daphnids, cyclopoids feeding on larger phytoplankton and abundant rotifers escaping the competition with large-bodied cladocerans (Paper II).
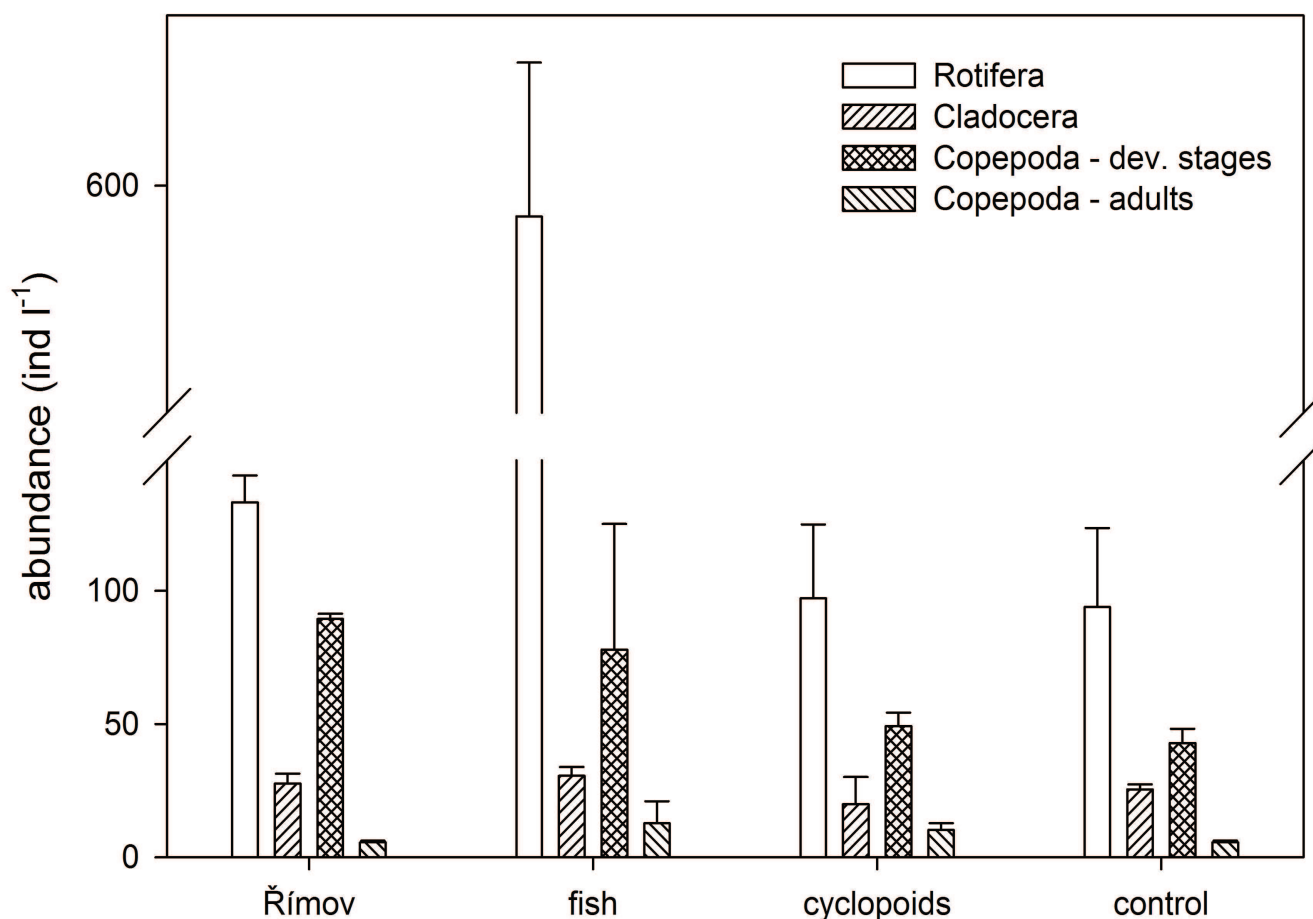

Figure 2. Time-weighted averages of zooplankton abundance (mean ± SD) in different treatments and the reservoir (Paper I).

Contrary to our results, cyclopoid copepods were sometimes found to be more important predators than fish (e.g., Lane, 1979; Brabrand *et al.*, 1986). In some cases, top-down control by predatory rotifers and copepods determines rotifer populations (Yoshida *et al.*, 2000; Green & Shiel, 2001). The mutual effect of competition with daphnids and predation by cyclopoid copepods probably formed the rotifer assemblage in fishless treatments of our experimen.

To conclude, the addition of fish can dramatically lower daphnid biomass and caused an increase in small-bodied cladocerans and rotifers (Fig. 5 in Paper II; Hessen, 1985; Ramcharan *et al.*, 1996). The phytoplankton response may depend on other more or less related factors like species composition (of both phyto- and zooplankton), life history parameters or nutrient state of the lake.

Fish predation in changing environment

The combined effect of temperature and nutrient level (as simulated in the heated mesocosms with nutrient addition) is generally stronger than that of heating or nutrient enrichment alone (Özen *et al.*, 2013). The total phosphorus concentration is the most important variable affecting zooplankton community structure (Gyllström *et al.*, 2005). Comparisons of different nutrient levels clearly confirmed the widely accepted theory that the character of shallow lakes can vary from a clear water to a turbid state (Scheffer *et al.*, 1993; Scheffer & van Ness, 2007). Trophic cascade is weakened in nutrient-poor lakes where the bottom effect is probably more important (Jeppesen *et al.*, 1997, 2000).

Generally, rotifers were associated with high nutrient mesocosms and high fish abundance, while copepods, represented mainly by *Macrocyclops albidus*, tended to occur within macrophytes in clear water mesocosms (Fig. 6 in Paper III). Bērzinš and Pejler (1989a, b) reviewed the relationship of rotifers with temperature and trophy, but they were unable to draw generalisations due to the overall wide tolerance of rotifers to abiotic factors. Based on our results, *Synchaeta* sp. clearly preferred ambient temperature over heated treatments.

A switch from the rotifer to cladoceran dominance occurred in nutrient enriched (and turbid) mesocosms with reference temperature (Fig. 3 in Paper III). The dramatic decrease in rotifers may be attributed to the occurrence of YOY (cf. Fig. 1 and 3 in Paper III). Nutrient effect and fish predation could partially cover each other due to the experimental design where low nutrient treatments were inhabited by 1 stickleback while high nutrient treatments were inhabited by an incoherent number usually higher than 5 (Fig. 1 in Paper III). Nutrient recycling by fish is probably one of the most important factors maintaining turbid mesocosms in a turbid state (Scheffer & Van Ness, 2007).

Higher zooplankton biomass in enriched mesocosms was accompanied by lower size diversity (Fig. 5 in Paper III). The presence of the most abundant cladocerans depended on body size: small *Bosmina longirostris* and *Alona rectangula* were positively correlated with turbidity and occur mainly in nutrient enriched mesocosms. On the other hand, large-bodied *Simocephalus vetulus* and medium-sized *Chydorus sphaericus* were correlated with PVI, occurring mainly in low nutrient mesocosms.

Metabolic rates increase exponentially with temperature (Brown *et al.*, 2004). Thus, the food demand of sticklebacks would expectedly be higher in the heated mesocosms. Higher abundance of sticklebacks in the reference temperature mesocosms was accompanied by a very low copepod biomass. Besides predation and competition relationships, individual

growth (and development) of copepods occurs more rapidly at higher temperature than in colder water (Forster *et al.*, 2011).

The lowest relative densities of adult fish along with the highest recruitment of YOY sticklebacks were observed at ambient temperature. YOY stickleback densities were generally lower in the heated mesocosms. The lowest density of YOY fish occurred in the higher temperature despite high abundance of adult fish. Moran *et al.* (2010) have experimentally proved the negative effect of warming on three-spined stickleback survival and reproduction. A 60% reduction in stickleback biomass occurred at temperature increase by 4°C. The combined effect of heating and enhanced nutrient loading lead to sticklebacks population breakdown. The explanation is an indirect effect of warming and low concentrations of dissolved oxygen concentration (Moran *et al.*, 2010). In some turbid mesocosms we also observed aggregation of fish near the surface, which suggest an effect on sticklebacks of low dissolved oxygen levels.

In general, the effect of fish predation would mean a decrease in *Daphnia* fecundity, proportion of adults and maximum body size while the effect of invertebrate predation decreases abundances and proportion of juveniles (Manca *et al.*, 2008).

Conclusions

Zooplankton, being in the middle position between primary producers and top predators in aquatic food webs, need to cope with factors influencing it from both the bottom and the top of the food web. The detailed understanding of how zooplankton deals with factors influencing its species composition, biomass and/or size structure is crucial for comprehension of freshwater ecosystems. Although predation is one of the most common food web interaction, determination and prediction of its outcome is difficult due to the complexity of direct and indirect effects of predation.

The suitable methodological approach should be necessarily used when such a complex model food web including all levels from phytoplankton to fish is the goal of our study. Here we modified and successfully tested large-volume mesocosms easy to use in deeper lakes and reservoirs.

Our results showed the strong effect of fish over cyclopoid predation in the forming of zooplankton assemblages and in turn impacting phytoplankton biomass. The effect of cyclopoid predation on rotifer and cladoceran populations was less clearer than that of fish. An intermediate level of abundance proportion of large-bodied cladocerans between fish and the control revealed predation of cyclopoids on cladocerans. Since fish and invertebrate predation greatly differ by nature, we can expect the different effect on cladoceran size structure and proportion of juveniles.

In terms of abundance, rotifers benefited from fish predation on cladocerans even in lower trophic state as in the Římov reservoir. Their lower efficiency in reducing phytoplankton was shown. Elimination of larger *Daphnia* spp. allowed for dominance of smaller *Bosmina longirostris* when fish were presented. This is generally in accordance with the traditional concept of biomanipulation.

We also studied the effect of predation in conditions simulating contemporary changing environment. In the last study, we showed that fish responded to various temperature level by different survival and reproduction rate. Higher temperature suppressed abundance of YOY fish with consequences to zooplankton assemblages. YOY sticklebacks caused a switch in dominance from rotifer to cladoceran biomass and eliminated all developmental stages of copepods. On the other hand, relatively low fish biomass in the warmest treatment was accompanied by high copepod biomass (mainly nauplii) and moderate biomass of rotifers and cladocerans. Comparing ambient temperature, low fish abundance allowed development of copepods. The combination of predation by copepods and competition with cladocerans and nauplii probably caused decrease in rotifer abundance in condition of low nutrient availability.

Future Perspectives

The coupling of fish predation and food limitation

Derived not only from mesocosm experiments, there are many evidences that fish could control large-bodied zooplankton (Paper I and II; Hessen, 2008). The persisting question should be addressed: how is zooplankton limited by the quality and quantity of food under different conditions? For instance, there is no direct effect of herbivorous zooplankton on inedible phytoplankton (in terms of body sizes), especially colonial cyanobacteria (Burns, 1987). To what extent is zooplankton regulated by the coupling of fish predation and food limitation in conditions of temperate lakes and reservoirs? The synergy of the top-down and bottom-up constraints (cf. Rothhaupt, 2000; Gliwicz, 2002) need to undergo further investigation. Nutrient enrichment, another example of common application of mesocosms, did not depress grazing efficiency of larger cladocerans (Cottingham *et al.*, 1997). Via elemental food quality, ecological stoichiometry provided the new potential mechanism linking resource supply to grazers (Hall *et al.*, 2004). Unfortunately, a sufficient number of experimental studies concerning such design is still absent.

The indirect effect of predation on prey populations

The direct effects of both vertebrate and invertebrate predation could be more or less easily studied by observing the results of particular experimental treatments. There are other – indirect – effects behind changes in abundance, biomass and size diversity. Cladoceran populations differentiated genetically and selective predation could prefer various clones (Hembre & Megard, 2006). How can predator(s) affect prey species populations? How can contemporary changing environment affect predator-prey interactions?

The impact of climate change on planktonic food webs

The broad discussion how European freshwater ecosystems will be affected by the climate change have not reached a satisfying conclusion enabling us to predict the near future development and/or changes in food web structure. Both direct and indirect effects of rising temperature should be taken into account. Experimental tests of various scenarios covering manipulation with different temperature and nutrient levels and fish stocks differed in species composition would help with interpreting of climate change impact.

Recently, Lürling & de Senerport Domis (2013) summarized research gaps related to plankton and climate change dynamics. Predator-prey interactions should be studied with regard to the role of winter, possible alteration in ecological stoichiometry (e.g. increase in

nutrient loading and promoted eutrophication – Moss *et al.,* 2011) and other anthropogenic pressures.

Management of lakes and reservoirs

The eutrophication along with subsequent problems of lakes and reservoirs could not be solved by community alteration only (especially in deep systems, e.g. Scharf, 2008). The complexity of interactions within planktonic food webs may cause shifts in zoo- or phytoplankton dominance which could be the reason of the failure of biomanipulation. The effort should aimed at both community manipulation (mainly with the fish stock) and overall nutrient reduction. The nutrient loading will be probably higher due to the climate change. Fish population structure, individual ontogeny and seasonal dynamics will alter due to rising temperature. Apart from existing and currently developing strategies how to manage freshwaters, more experimental studies are needed to address the fish (and/or invertebrate) predation under different climate conditions. To which extent will fish stock affect (large-bodied) zooplankton in warmer lakes?

The unique pond ecosystems developed especially in Central Europe. Ponds represent man-made shallow water bodies with regulated water inflow and outflow. Ponds were constructed with the purpose of fish breeding and integrated naturally into our landscape. Nowadays ponds suffer from all negative effects like eutrophication etc. which can be altered by proper management. In order to apply mechanisms mitigating the current state of ponds we need to go back and get more information about their ecosystems.

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Research papers

Paper I

Šorf, M., Brandl, Z., Znachor, P., Vašek, M.

Floating large-volume mesocosms as a simple, low-cost experimental design suitable for the variety of lakes and reservoirs.

Floating large-volume mesocosms as a simple, low-cost experimental design suitable for the variety of lakes and reservoirs

Michal Šorf[1, *], Zdeněk Brandl[1], Petr Znachor[1, 2] and Mojmír Vašek[2]

With 5 figures and 2 tables

Abstract: Mesocosms represent a helpful tool enabling *in situ* experiments within the pelagic zone of lakes and reservoirs. Experimental studies using mesocosms are widely used in shallow lakes. Here, we describe an improved method suitable for deep freshwater ecosystems. We use a metal supporting framework carrying four polyethylene bags (circular cross-section, diameter 1.5 m, length 9.5 m). The mesocosm dimensions allow us to test hypotheses covering whole pelagic assemblages including the entire food chain up to fish as the top consumers. The floating construction is light, reusable and inexpensive. The suggested mesocosm design maintains conditions close to those occurring in the adjacent lake water and thus effectively simulates the pelagic environment for various experimental studies.

Key words: mesocosms, enclosures, methods, lakes, reservoirs.

Introduction

Our understanding of complex interactions within freshwater ecosystems is often constrained by the methodological approach used. The greater the ecological complexity, the more coherent the experimental setup that should be applied. Here, whole-lake manipulation appears to be a reasonable approach since our findings can be effortlessly transferred to natural systems (Carpenter et al. 2001). The insufficient number of replicates (often caused by the extent of financial support) and the uniqueness of every single lake represent serious limitations of such an approach. Although whole-lake manipulation provides valuable results especially for comparative studies, its routine experimental use is rather problematic. Mesocosm experiments can be used as an eligible alternative at a

scale enabling resolution of relatively detailed interactions within a strictly defined ecosystem simulation.

There is a wide range of experimental volumes used for testing of various hypotheses. In spite of laboratory experiments which are mostly conducted for detailed studies regarding often not more than a few species, topics involving community structure and function or ecosystem processes demand a field experiment or a large indoor mesocosm facility. Mesocosms, defined by Lampert & Sommer (2007) as sections of the natural environment isolated by means of artificial barriers, allow us to set up natural-like conditions. The technical design of mesocosms can markedly affect some abiotic factors, such as thermal characteristics, light conditions or mixing potential of the enclosed water column. To obtain "natural-like" conditions in mesocosms means keeping the differences in abiotic

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Paper II

Šorf, M., Brandl, Z., Znachor, P., Vašek, M.

Different effects of planktonic invertebrate predators and fish on the plankton community in experimental mesocosms.

Different effects of planktonic invertebrate predators and fish on the plankton community in experimental mesocosms

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Abstract

The impact of fish and cyclopoid copepod predation on zooplankton communities was evaluated using large-volume mesocosms (depth 9.5 m; volume 13 m^3) in the Římov reservoir (Czech Republic). Two yearling roach and perch individuals introduced into mesocosms represented the fish treatment, which was compared to cyclopoid copepods (initial abundance of 2 ind.L^{-1}) and a control with no initial addition of predators. Our results clearly support the hypothesis that planktivorous fish feeding leads to the suppression of large-bodied cladocerans. In the presence of fish, the cladoceran community changed from a dominance of large-bodied *Daphnia* spp. at the beginning to dominance by the smaller *Bosmina longirostris* at the end of the experiment. Chlorophyll-a concentration and rotifer abundances increased in the absence of daphnids. In the absence of fish, the presence of large-bodied cladocerans resulted in decreasing chlorophyll-a concentration. Although no significant differences were observed between cyclopoid abundances in treatments stocked with cyclopoids and the control, the proportion of large cladocerans clearly showed the effect of the manipulation. The similar trends in both these treatments did not confirm the importance of cyclopoid

predation in our experiment. The overall strong effect of fish over cyclopoid predation suggests the main role of fish predation in the forming of zooplankton communities and in turn impacting phytoplankton biomass in mesocosms.

Key words: predation, zooplankton, perch, roach, mesocosms

Paper III

Šorf, M., Davidson, T. A., Brucet, S., Menezes, R. F., Søndergaard, M., Lauridsen, T. L., Landkildehus, F., Liboriussen, L., Jeppesen, E.

Zooplankton response to climate warming as derived from a mesocosm experiment ran at contrasting temperatures and eutrophication states.

First Draft

First Draft

Zooplankton response to climate warming: a mesocosm experiment at contrasting temperatures and eutrophication states

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Abstract

Zooplankton community response to the effects of nutrients+fish (hereafter nutrients), temperature and their interaction was studied in the longest running shallow lake mesocosm experiment in the world during May to August 2010 after seven previous years of continued experiment. We found a positive effect of nutrients on zooplankton biomass, chlorophyll-a concentration and turbidity, but a decrease in zooplankton species and size diversity, as well as in submerged macrophyte PVI. The community composition of zooplankton in the high nutrient mesocosms was determined by the chlorophyll-a concentration and the level of turbidity, while composition in low nutrient mesocosms were well correlated with macrophyte cover.

Temperature affected sticklebacks CPUE. The lowest adult stickleback CPUE along with the highest recruitment of YOY observed in unheated mesocosms implies a negative relation between high temperature and stickleback breeding.

No direct effect of temperature on the zooplankton was found, but multivariate dispersion as a measure of variability between treatments revealed a clear temperature effect on zooplankton community structure. High nutrient treatments had similar dispersions at the various temperature levels, while the low nutrient treatments differed markedly. The higher the temperature in these mesocosms, the higher was the multivariate dispersion and heterogeneity in zooplankton communities. Nevertheless, compared to nutrient and fish effects the temperature effects on the zooplankton community were modest.

Key words: zooplankton, mesocosms, nutrients, climate change

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Curriculum vitae

Michal Šorf

Date and place of birth:
11 June 1982, Příbram, Czechoslovakia

Address:
Department of Ecosystem Biology
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Czech Republic

Education:
2001-2004 BSc. study at University of South Bohemia, Faculty of Biological Sciences, České Budějovice
2004-2007 MSc. study at University of South Bohemia, Faculty of Biological Sciences, České Budějovice
since 2007 PhD. study at University of South Bohemia, Faculty of Science, České Budějovice, PhD. Thesis: The impact of vertebrate and invertebrate predation on zooplankton assemblage in a canyon-shaped reservoir (supervisors: prof. RNDr. Zdeněk Brandl, CSc., prof. RNDr. Jaroslav Vrba, CSc. & Mgr. Mojmír Vašek, Ph.D.)

Professional qualification:
2004 - BSc. in Biology, Thesis: Seasonal changes of zooplankton in the Kačležský rybník (Supervisors: RNDr. Miloslav Devetter, Ph.D. & RNDr. Jaromír Seďa, CSc.)
2007 - MSc. in Ecology, Thesis: Animal component in a diet of two *Eudiaptomus* species (Copepoda: Calanoida) (Supervisor: prof. RNDr. Zdeněk Brandl, CSc.)

Practise:
since 2008 Faculty of Science, University of South Bohemia
2010-2013 Institute of Hydrobiology, Biology Centre of the Academy of Sciences of the Czech Republic (part-time job within the project EU FP-7 Theme 6 project REFRESH (Adaptive strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems)
    REFRESH Project Meetings: Aberdeen, United Kingdom (3.-8.4.2011); Sitges, Spain (19.-23.3.2012) and Antalya, Turkey (22.-26.2013)

Scientific and professional experience:

Research interests include taxonomy (Rotifera, Cladocera, Cyclopoida, Calanoida), seasonal dynamics of zooplankton and predator-prey interactions among zooplankton species.

Projects:

2009 - Clonal structure of *Daphnia galeata* (Cladocera, Anomopoda) under vertebrate and invertebrate predation in a mesocosm experiment in the Římov reservoir
(Studentská grantová agentura PřF; co-investigator)

2008 - How can multiple predation influence competition among planktonic invertebrates?
(University Development Fund 19/2008; principal investigator)

2008 - The impact of combined action of vertebrate and invertebrate predators on zooplankton assemblage in a canyon-shaped reservoir
(Internal grant of the University of South Bohemia 24/2007/P-PrF; principal investigator)

2008 - The occurence of bentho-littoral cladocerans (Macrothricidae and Ilyocryptidae) in South Bohemia: Are there really so rare?
(Mattoni Awards; principal investigator)

International cooperation:

April – September 2010 - student stay: National Environmental Research Institute, Århus University, Silkeborg, Denmark (supervisor Erik Jeppesen)

7.-11.7.2008 - workshop: Systematics, Morphology, and Techniques for Identification of Copepods and Their Larval Stages (Khon Kaen, Thailand)

Membership in scientific societies:

since 2006 - Czech Limnological Society

Reviewing:

I reviewed 1 paper in Annales de Limnologie - International Journal of Limnology.

I also reviewed two BSc. theses: Daniela Hlávková (2011) - Clearance rate and food selectivity of bdelloid rotifers (Rotifera) in soil and Pavla Šalandová (2011) - The effect of experience on the frequency-dependent food selectivity of predatory aquatic insects.

Student training:

I have helped to train several students in the field of zooplankton ecology.

Kateřina Zadinová - BSc. thesis, University of South Bohemia, Faculty of Science (co-supervisor; succesfully defended 2011): The biomanipulation as a possible tool for water reservoir restoration, the example of Orlík reservoir. The limitation of biomanipulation in the deep reservoir with high nutrient input from tributaries.

Kateřina Zadinová - MSc. thesis, University of South Bohemia, Faculty of Science (co-supervisor; since 2011): Species composition and size structure of the zooplankton community in experimental mesocosms of different depths and nutrient levels.

Jana Zemanová - BSc. thesis, University of South Bohemia, Faculty of Science (co-supervisor; succesfully defended 2013): The importance of aquatic plants for food web of shallow lakes.

Jana Zemanová - MSc. thesis, University of South Bohemia, Faculty of Science (co-supervisor; since 2013): The mutual effect of littoral habitat structure and fish predation on zooplankton assemblages in shallow lakes.

Veronika Kreidlová - BSc. thesis, University of West Bohemia, Faculty of Education (supervisor; succesfully defended 2013): The seasonal dynamics of zooplankton in the shallow pond Vydymáček near Plzeň.

Veronika Kreidlová - MSc. thesis, University of West Bohemia, Faculty of Education (co-supervisor; since 2013): Rotifers of the Jizera Mountains reservoirs in the period of acidification and recovery.

Nikola Vajdiaková - BSc. thesis, University of South Bohemia, Faculty of Science (supervisor; since 2013): Morphological changes in rotifers under the predation pressure by cyclopoid copepod.

Jan Jiran - BSc. thesis, University of South Bohemia, Faculty of Science (supervisor; since 2013): Reproductive characteristics and possible inter-species crossbreeding in cyclopoid copepod *Acanthocyclops*.

Publications

Papers with impact factor:

Šorf, M., Davidson, T. A., Brucet, S., Menezes, R. F., Søndergaard, M., Lauridsen, T. L., Landkildehus, F., Liboriussen, L., Jeppesen, E. Zooplankton response to climate warming: a mesocosm experiment at contrasting temperatures and eutrophication states. First Draft.

Šorf, M., Brandl, Z., Znachor, P. & M. Vašek. Different effects of planktonic invertebrate predators and fish on the plankton community in experimental mesocosms. Annales de Limnologie - International Journal of Limnology, In Press. IF = 0.736

Šorf, M., Brandl, Z., Znachor, P. & M. Vašek, 2013. Floating large-volume mesocosms as a simple, low-cost experimental design suitable for the variety of lakes and reservoirs. Fundamental and Applied Limnology 183(1): 41-48. IF = 1.190
DOI: 10.1127/1863-9135/2013/0364

Özen, A., **Šorf, M.**, Trochine, C., Liboriussen, L., Beklioglu, M., Søndergaard, M., Lauridsen, T., Johansson, L. & E. Jeppesen, 2013. Long term effects of warming and nutrients on microbes and other plankton in mesocosms. Freshwater Biology 58: 483-493. IF = 3.082
DOI:10.1111/j.1365-2427.2012.02824.x

Šorf, M. & Z. Brandl, 2012. The rotifer contribution to the diet of *Eudiaptomus gracilis* (G.O. Sars, 1863) (Copepoda: Calanoida). Crustaceana 85(12-13): 1421-1429. IF = 0.649
DOI:10.1163/15685403-00003133

Šorf, M. & M. Devetter, 2011. Coupling of seasonal variations in the zooplankton community within the limnetic and littoral zones of a shallow pond. Annales de Limnologie - International Journal of Limnology 47: 259-268. IF = 0.930
DOI:10.1051/limn/2011006

Papers in English without impact factor:

Šorf, M. & Z. Brandl, 2011. Subterranean populations of cyclopoid copepods (Copepoda: Cyclopoida) collected at a historical mining area in Central Bohemia (Czech Republic). Acta Societatis Zoologicae Bohemicae 75: 307-310.

Mikeš, V., **Šorf, M.** & T. Ploc, 2006. Noteworthy feeding behaviour of the Hooded Crow (*Corvus corone cornix*). Studia Universitatis Babeş – Bolyai, Biologia 51(2): 19-20.

Conference proceedings:

Šorf, M., Jeppesen, E. & R. F. Menezes, 2012. Zooplankton in shallow mesocosms: the impact of temperature, nutrient level and fish stock. XVI. konferencia Slovenskej limnologickej spoločnosti a České limnologické společnosti - Zborník príspevkov, 25.-29. jún 2012, Jasná, p. 163. (oral presentation in Czech)

Zadinová, K., **Šorf, M.** & J. Hejzlar, 2012. Species composition and size structure of the zooplankton community in experimental mesocosms of different depths and nutrient levels. XVI. konferencia Slovenskej limnologickej spoločnosti a České limnologické společnosti - Zborník príspevkov, 25.-29. jún 2012, Jasná, p. 226. (poster in Czech)

Šorf, M. & Z. Brandl, 2009. *Eudiaptomus gracilis*: herbivor i lovec vířníků. [*Eudiaptomus gracilis*: herbivore and predator of rotifers.] XV. Conference of The Czech Limnological Society, p. 251. (poster in Czech)

Šorf, M. & Z. Brandl, 2008. Rotifer compound in a diet of calanoid copepods: the effect of omnivorous feeding on survival and reproduction of *Eudiaptomus gracilis* (Copepoda: Calanoida). 10th International Conference on Copepoda. Abstract Book, p. 93. (oral presentation in English)

Šorf, M., Brandl, Z. & M. Vašek, 2008. The different response of nauplii, copepodites and adult copepods to the presence and absence of underyearling perch (*Perca fluviatilis*) in experimental mesocosms. 10th International Conference on Copepoda. Abstract Book, p. 207. (poster in English)

Papers in Czech language:

Šorf, M. & M. Devetter, 2005. Druhové složení zooplanktonu Kačležského rybníka u Jindřichova Hradce. Sborník Jihočeského muzea v Českých Budějovicích, Přírodní vědy 45: 103-111.

The impact of fish and planktonic invertebrate predation on zooplankton in experimental mesocosms

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