School of Doctoral studies in Biology Sciences

University of South Bohemia in České Budějovice

Faculty of Sciences

Biology of predatory fishes in dam reservoirs and lakes

Ph.D. Thesis

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České Budějovice

2018

This Ph.D. Thesis should be cited as:

Vejřík, L. (2018) Biology of predatory fishes in dam reservoirs and lakes. Ph.D. Thesis. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 178 pp.

Annotation

This Ph.D. Thesis is focused mainly on the biology of two typical European predatory fishes, European catfish (*Silurus glanis*) and perch (*Perca fluviatilis*). Catfish is a typical apex predator, whereas perch is a smaller species that plays role of a mesopredator. Although, catfish is the third largest freshwater fish in the world, only few studies dealing with this species have been revealed thus far. The main reason is connected with capturing of the species that is inefficient by standard ichthyologic methods. Studies, that have been revealed recently, focused mainly on expansions of catfish to the West and South Europe. Catfish is unwanted in these localities due to a potential negative impact on native fish community, thus its reduction is desirable. In contrast, catfish occurrence is important in native localities where it plays a key role as a biomanipulative species (I). Catfish is a true generalist, which is a typical feature for large-bodied apex predators connected with high energy consumption of their bodies. The second typical feature is a wide diet plasticity and thus good adaptability to new food sources. It is associated with distribution of various food sources among individuals within the population (II). By contrast, perch is one of the most studied fish in the world and hundreds of studies with IF are revealed every year. However, the more information about biology of perch have been known, the more questions have been arisen. Several phenomena are revealed also in this thesis. For instance, crucial impact of juvenile perch on the entire ecosystem is described. High predation pressure on zooplankton may induce piscivory in primarily zooplanktivorous fish (III). Further, juvenile perch utilize hypoxic pelagic zones as a refuge against predation (IV). The last surprising phenomenon is described in the study dealing with both species, catfish and perch. Their coexistence may lead in strong discrimination of one species caused by special predation that was supposed to be implausible (V).

Declaration [in Czech]

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České Budějovice, 1. června 2018 RNDr. Ing. Lukáš Vejřík

This Ph.D. Thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, supporting doctoral studies in the Zoology.

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Financial support

Ministry of Education, Youth and Sports of the Czech Republic – project No. CZ.1.07/2.3.00/20.0204 (CEKOPOT).

Norwegian Financial Mechanism 2009-2014 under contract number MSMT-28477/2014 – project No. 7F14316.

SoWa Research Infrastructure funded by MEYS CZ grant LM2015075, programme "Projects of Large Infrastructure for Research, Development, and Innovations" and CZ.02.1.01/0.0/0.0/16_013/0001782, operational programme "Research, Development and Education.

ERDF/ESF project Biomanipulation as a tool for improving water quality of dam reservoirs, No. CZ.02.1.01/0.0/0.0/16_025/0007417, funded by MEYS CZ.

Grant Agency of the University of South Bohemia – project No. 04-151/2016/P.

Grant Agency of the University of South Bohemia – project No. 159/2013/P.

Czech Science Foundation – project No. 206/09/P266.

Acknowledgements

First of all, I would like to thank my supervisor, Martin Čech, for introducing me to scientific work. It must have been tough to correct my first writing attempts in my bachelor’s and master´s studies. He spent substantial part of his life by helping me with all of my studies. I would also like to express my gratitude to Jiří Peterka, head of the Fish Ecology Unit, for his willingness and generous support of my research. A big thanks goes to all members of Department of Fish and Zooplankton Ecology for their help with data collecting and for many amazing moments that we spent together in (and out) the field. I thank Zuzana Sajdlová and Luboš Kočvara for overwhelming number of days spent by collecting data for my research in the field. I also thank Petr Blabolil for helping me with statistical and graphical procession of my studies, because my knowledge of statistics comes to the end where his starts.

The warmest thanks belong to my wife and colleague, Ivana Vejříková, for helping me not only with writing of the scientific studies, but also with struggling with obstacles at university, work, and in the whole life. If someone were as lucky as me to meet life partner with the same scope, he would agree that demanding workload is digestible in two. I am very thankful to my family that supported all my minds, wishes and life dreams. My final thanks with all of my heart belong to our son, Matěj, for showing me that world can be even more beautiful place than I have ever imagined.

List of papers and author´s contribution

Vejřík, L., Vejříková, I., Kočvara, L., Blabolil, P., Peterka, J., Sajdlová, Z., Jůza, J., Šmejkal, M., Batroň, D., Kubečka, J., Čech, M. **The pros and cons of the freshwater apex predator, European catfish *Silurus glanis*, and angling as a powerful mechanism for its regulation**. Submitted to: *Ecosystem Services.* Impact factor (2018): 4.4; 5Year IF: 6.

I designed the field sampling, participated in the field sampling, statistically analyzed the data and prepared the manuscript with the help of co-authors.

Vejřík, L., Vejříková, I., Balbolil, P., Eloranta, A.P., Kočvara, L., Peterka, J., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Kiljunen, M., Čech, M. (2017) **European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability.** *Scientific Reports* (7), DOI:10.1038/s41598-017-16169-9. Impact factor (2018): 4.1; 5Year IF: 4.6.

I designed the field sampling, participated in the field sampling, statistically analyzed the data and prepared the manuscript with the help of co-authors.

Vejřík, L., Matějíčková, I., Seďa, J., Blabolil, P., Jůza, T., Vašek, M., Ricard, D., Matěna, J., Frouzová, J., Kubečka, J., Říha, M., Čech, M. (2016) **Who is who: an anomalous predator-prey role exchange between cyprinids and perch.** *PloS ONE* (11), e0156430, DOI:10.1371/journal.pone.0156430. Impact factor (2018): 2.8; 5Year IF: 3.4.

I participated in the field sampling, statistically analyzed the data and prepared the manuscript with the help of co-authors.

Vejřík, L., Matějíčková, I., Jůza, T., Frouzová, J., Seďa, J., Blabolil, P., Ricard, D., Vašek, M., Kubečka, J., Říha, M., Čech, M. (2016) **Small fish use the hypoxic pelagic zone as a refuge from predators.** *Freshwater Biology* (61), 899–913. Impact factor (2018): 3.8; 5Year IF: 3.7.

I participated in the field sampling, statistically analyzed the data and prepared the manuscript with the help of co-authors.

Vejřík, L., Vejříková, I., Kočvara, L., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Peterka, J., Čech, M. (2017) **Thirty-year-old paradigm about unpalatable perch egg strands disclaimed by the freshwater top-predator, the European catfish (*Silurus glanis*)**. *PLoS ONE* (12), DOI:10.1371/journal.pone.0169000 . Impact factor (2018): 2.8; 5Year IF: 3.4.

I designed the field sampling, participated in the field sampling, statistically analyzed the data and prepared the manuscript with the help of co-authors.

Vejřík, L., Vejříková, I., Peterka, J., Sajdlová, Z., Čech, M. (*accepted*) **Area of catfish occurrence and risks connected with introductions to new localities**. In: *Advances in Animal Science and Zoology*, Nova Science Publishers, Inc. NY, USA. ID_53874.

I wrote the chapter with the help of co-authors.

Vejřík, L., Vejříková, I., Peterka, J., Čech, M. (*accepted*) **Methods for capturing catfish and potential regulation of catfish population**. In: *Advances in Animal Science and Zoology*, Nova Science Publishers, Inc. NY, USA. ID_53875.

I wrote the chapter with the help of co-authors.

Vejřík, L., Vejříková, I., Blabolil, P., Peterka, J., Čech, M. (*accepted*) **Catfish as a potential key species for biomanipulation purposes**. In: *Advances in Animal Science and Zoology,* Nova Science Publishers, Inc. NY, USA. ID_53876.

I wrote the chapter with the help of co-authors.

Declaration of originality

The co-authors fully acknowledge that Lukáš Vejřík is the first author of all papers presented. Most of the data processing as well as most of the statistical analyses were performed by Lukáš Vejřík. He also made a major contribution to writing the manuscripts. All papers contain original results. All co-authors consent to the publication of individual papers in the dissertation of Lukáš Vejřík and four authors listed below hereby support this statement with their signature.

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Content

Prologue

The biology of piscivorous predators has been my main interest since the beginning of my scientific life. My Bachelor thesis, led by my supervisor, Martin Čech, was focused on the impact of predation on a fish community. It dealt particularly with the impact of great cormorant (*Phalacrocorax carbo*), a fish-eating bird with an expanding range and abundances (Čech *et al.*, 2008). I focused on diet preferences and the amount of food utilized by this bird species per day (Čech and Vejřík, 2011). As commonly happens in the scientific world, the more I knew about the impact of predation on fish communities, the more questions arose. Thus, I decided to continue with the topic of biology of predators in my master´s studies. My supervisor was concerned mainly with the reproduction biology of perch (*Perca fluviatilis*; Čech *et al.* 2010; 2011) and that is why I also decided to focus on the same fish species. During my master´s studies, I participated in two studies (Čech *et al.*, 2012a; Čech *et al.*, 2012b) and my rigorous thesis was based on Čech *et al.* (2012a). My major brought me deep into the issue of the reproduction biology of perch. And I knew that I would continue with the biology of predatory fishes in my doctoral degree, but I decided to focus on catfish (*Silurus glanis*). I knew that I could take advantage of my knowledge about perch and I connected it with my findings gained about catfish. Thanks to this combination, a breakthrough study, that disclaimed a thirty-year-old paradigm about unpalatable perch egg strands, was revealed (V). My Dissertation thesis with a very broad concept called ´Biology of predatory fishes in dam reservoirs and lakes´ supported my idea to study both mentioned species. Firstly, I published the results of my two Master´s theses dealing with juvenile perch (III, IV). Secondly, I focused on a predator, that stands at the very top of the food web, its biology is overlooked in the scientific world even though the species has been spreading worldwide (Elvira and Almodóvar, 2001; Copp *et al.*, 2009; Cunico and Vitule, 2014; VI). The main reason is connected with the poor capture efficiency of the species by standard ichthyologic methods (Alp *et al.*, 2003, VII). This obstacle became a challenge for me and it led to the publishing of two studies. We described a method with incredibly high capture efficiency (I, VII) and we revealed new knowledge about the feeding behavior of catfish (II). The latter finding was based on the largest dataset that has been published thus far thanks to the regular monitoring of catfish populations in study sites where catfish was stocked for biomanipulation purposes (I, VIII).

Introduction

Biology of predatory fishes in general

Predators play a key role in both terrestrial (Sinclair *et al.*, 2003) and aquatic ecosystems (Estes *et al.*, 1998). They control abundances of species of lower trophic levels “from the top” and thus they indirectly influence water quality in an aquatic ecosystem (so-called top-down effect; Hrbáček *et al.*, 1961; Brooks and Dodson, 1965). This is the main reason why the presence of predatory fish in high abundances is required in dam reservoirs and man-made lakes (Paine, 1966; Shapiro *et al.*, 1976; Carpenter *et al.*, 1985; Benndorf, 1987).

Although several species of predatory fish in Europe and North America have been deeply studied for decades, such as perch and yellow perch (*Perca flavescens*; Thorpe, 1977; Craig, 2000), we can still find many uncertainties in their biology. In contrast, only a little information is known about some other predatory fish, such as European catfish, although their impact on the aquatic ecosystem is surely significant (Carol *et al.*, 2007). The revealed studies about catfish have mainly a regional character and describe only one feature of catfish, or they focus mainly on diet specifications (Specziár and Rezsu, 2009; Slavík, 2013).

The key role of apex predators in aquatic ecosystems with the example of catfish

European catfish is the largest freshwater predatory fish in Europe and the third largest freshwater fish in the world (Baruš and Oliva, 1995; Copp *et al.*, 2009). East and Central Europe is the main native area. Man-mediated introduction brought catfish to rivers and lakes in South and West Europe, namely Great Britain, France, Italy, Belgium, The Netherlands, Portugal and Spain (Elvira and Almodóvar, 2001; Copp *et al.*, 2009). In Spain, European catfish is listed as an invasive species in the National catalogue of invasive alien species. That is why, holding, transporting, and trading with this species is forbidden. In France and Belgium, fishing of the European catfish is authorized during the whole year and catfish individuals can be taken with no bag limits of size and number of individuals. (Cucherousset *et al.*, 2017). In Italy, release of catfish into aquatic ecosystems is even restricted by law (legge regionale n. 19 del 28 aprile 1998).

European catfish has also spread to non-native localities on three other continents, specifically in Asia (Kazakhstan and China) (Kustareva and Naseka, 2015; Graham *et al.*, 2017), Africa (Morocco) (Boughedir, 2006) and South America (Brazil) (Cunico and Vitule, 2014). Primarily anglers are responsible for the fast spread of catfish throughout the world. Catching such a large-bodied fish brings deep satisfaction and thus angling of catfish is becoming more and more popular (Cucherousset *et al.*, 2017). In addition, the catfish itself contributes to its success of spreading to new localities. Catfish has apparently the ability to cope with an unknown environment that has never been experienced in the species evolutionary history (Kováč, 2016). Although, catfish is an invasive species and significantly influences these localities, only scarce information are known about its impact on aquatic ecosystems (Syväranta *et al.*, 2010). In the Czech Republic, catfish was introduced to lakes created after aquatic restorations of mining pits (North Bohemian brown coal area) to regulate abundances of zooplanktivorous cyprinids as an apex predator (Peterka and Kubečka, 2011; Peterka, 2012). However, practically no reasonable information is known about its impact on the fish community in these aquatic ecosystems. In addition, much of the available information turned out to be wrong. For instance, Slavík (2013) clearly disproved statements pointed out by Carol *et al.* (2007) about the aggressive behavior of catfish to its own species and about strictly night activity. However, features typical for catfish, such as longevity (Bruyenko, 1971), large body sizes (Boulêtreau and Santoul, 2016), fast growth rate (Copp *et al.*, 2009) and large gape size are exceptional in comparison to other European predatory fish (Cucherousset *et al.*, 2017). Thanks to these features, catfish is an ideal fish species for biomanipulation purposes. Nevertheless, Wysujack and Mehner (2005) claimed that catfish is not an efficient biomanipulation species, particularly due to its preferences for relatively small prey. But their study was based on the diet of small catfish individuals (their sizes mostly smaller than 80 cm) and thus the conclusion is distorted.

The main reason for the absence of studies is due to difficulties connected with efficient capturing of the species by standard ichthyologic methods (Carol *et al.*, 2007). The scarce studies revealed lately were based on catches from anglers using rods, or from divers using spear guns (Syväranta *et al.*, 2010; Cucherousset *et al.*, 2012). Electrofishing is another ichthyologic method that can be used for capturing catfish in shallow waters (Slavík and Horký, 2012). Other common ichthyologic methods, such as gillnets, large seine nets and purse seine nets, are either inefficient or non-selective and can be fatal for captured fish (Doğan Bora and Gül, 2004; Wysujack and Mehner, 2005; Carol *et al.*, 2007)

Catfish is not a diet specialist utilizing only fish, such as Northern pike (*Esox lucius*). Its diet consists of a wide spectrum of vertebrates but also invertebrates (Baruš and Oliva, 1995; Wysujack and Mehner, 2005). Copp *et al*. (2009) indicated that the diet of European catfish may consist of 50 species of fish, several species of frogs, birds and invertebrates such as insects, crayfish, clams and worms. Further, Cucherousset *et al.* (2012) described an unusual and impressive technique of catching pigeons (*Columbia livia*). The catfish's technique of catching pigeons on the shore is similar to the beaching behavior of a killer whale (*Orcinus orca*) that catches seals on beaches. This study demonstrates that the topic of catfish diet has high publication potential, particularly when modern diet analyses are used, such as stable isotope analysis (SIA). This analysis was used by Syväranta *et al.* (2010) and revealed the wide diet niche of the species and its large potential to adapt to different types of food sources. The latest study by Boulêtreau *et al.* (2018) focused on the impact of catfish on migrating Atlantic salmon (*Salmo salar*) and its targeted hunting in the upper part of fish ladders. It supports findings about the unusual learning abilities of apex predators presented in this Ph.D. Thesis. In addition, the study of Boulêtreau *et al.* (2018) clearly demonstrated the threat of catfish as an invasive apex predator on native fish species. The situation in this case is even more serious considering that catfish choose the fish ladder as a hunting place. Because it is the only way for anadromous fish species (Croze *et al.*, 2008) but also for rheofil fish species to avoid man-made barriers that occur in rivers (Musil *et al.*, 2012; Radinger *et al.*, 2017).

The role of predatory fish at a lower trophic level with the example of perch

The biology of several predators such as perch has been intensively studied by many scientists and even large groups of researchers. Basic information is well summarized for instance in Craig (2000), or Thorpe (1977). The genus Perca is commonly studied because it is easily captured by standard ichthyologic methods and its area of occurrence (Holarctic) is large. It is the focus of many scientists mainly due to the high impact of the genus Perca on fish communities and on the entire aquatic ecosystem (Craig, 2000). Perch is widely spread in many rivers, dam reservoirs and lakes, where it belongs to a dominant fish genus (Tonn *et al.*, 1990). In addition, it is one of the most popular fish genera in terms of industrial and also recreational fishing (Knuston and Peterka, 1969; Thorpe, 1977; Schaefer, 1977).

A commonly known feature of perch is so-called “cycling”. It means that their abundance in a water ecosystem repeatedly fluctuates over several years and thus the abundances of predators from the upper trophic levels fluctuates, too. Pike are most often food-dependent on perch (Menshutkin and Zhakov, 1964; Mills and Hurley, 1990; Pivnička, 1991).

The other typical features of the genus Perca are three food specializations that a fish goes through during its life. They initially utilize zooplankton, then switch to zoobenthos and eventually utilize fish (Rask, 1986; Terlecki, 1987; Persson *et al.*, 2000). This fact implies that perch start to be real predators during the adult period of life (Craig, 2000; Haakana *et al.*, 2007). A very common feature connected with perch is cannibalism (Craig, 1978; Persson *et al.*, 2000). A perch population can survive even in monoculture fish stock, and then the young-of-the-year fish (YOY fish) are the main food source for adult individuals (Thorpe, 1977; Craig, 1978). In these monoculture fish populations, not only high predation takes place, but also strong competition within each age group (Alm, 1946; 1952, Persson *et al.*, 1996). When intra-specific competition is too strong, a stunted fish population can appear due to an insufficient number of food sources. A stunted fish population is extremely numerous and cannibalism is limited or appears only on the smallest and youngest individuals. These populations are typical for small water bodies (Alm, 1946, 1952; Sumari, 1971).

Recently, great attention has been focused on the juvenile stages of perch and their life in the pelagic zone (Jůza *et al.*, 2009). Formerly, YOY fish of perch were assumed to be present in the warm upper water zone called epilimnion (Whiteside *et al.*, 1985; Post and McQueen, 1988; Treasurer, 1988; Wang and Eckmann, 1994; Matěna, 1995). However, the highest abundances were observed rather in the deeper zone called metalimnion where both temperature and oxygen concentration decrease (Kahl and Radke, 2006; Jůza *et al.*, 2009) or in the even deeper hypolimnion with even colder water (Perrone *et al.*, 1983; Čech *et al.*, 2005; Čech and Kubečka, 2006; Čech *et al.*, 2007a). Many scientists pointed out that juvenile stages of perch perform longer or shorter vertical migrations between particular water zones during the day depending on the light intensity (Ward and Robinson, 1974; Eckmann and Imbrock, 1996; Goldspink, 1990; Čech *et al.*, 2005). Migration to deeper water zones can be driven by several things, such as hiding from potential predators that are mostly absent in the hypolimnion (Levy, 1990; Čech and Kubečka, 2006). Another reason is the high presence of their potential food sources, specifically zooplankton (Lass *et al.*, 2000). Further, Holčík (1998) claimed that colonization of bathypelagic zones by perch is caused by their marine origin. Sajdlová *et al.* (2018) contributed to the topic of juvenile stages of perch with a unique in situ experiment that revealed daily vertical migrations of early juvenile European perch under direct control of light intensity. The early juveniles utilize deep and dark zones of the lake as a refuge against predators during the daytime. The findings are supported by a sophisticated experiment and also field sampling conducted using hydroacoustic and sampling with several types of nets. Thanks to this study, we can finally state that light plays a key role in these migrations and it calibrates biological clocks synchronized to daily rhythms of environmental conditions (Jackson *et al.*, 2001; Čech *et al.*, 2012). A very interesting finding was revealed by Roberts *et al.* (2009; 2011; 2012) who observed yellow perch (*Perca flavescens*) in high abundances in the pelagic zone with hypoxic conditions (< 2 mg L^{-1}). The reason was the utilization of zooplankton.

Sufficient food availability is important for predators. Then the growth rate increases whereas mortality decreases. In contrast, lack of food induced by intra- or interspecific competition leads to starvation and in extreme situations to death (Begon *et al.*, 1996). In aquatic ecosystems, the depletion of zooplankton, the main food source for many fish species, is often induced by numerous juvenile fish that highly utilize zooplankton at the beginning of the vegetative season (Vašek *et al.*, 2006). It is caused mainly by the high fecundity of fish and high survival rate of their juveniles in the first months in some years (Jůza *et al.*, 2014). In the case of perch, the high abundances of YOY fish are probably caused by their evolutionary strategy of laying egg strands, i. e., the eggs are assembled together at one place (Newsome and Tompkins, 1985) The strands contain a chemical defense in the form of potentially noxious components, including piperideine and the galactose-specific lectin, nattectin (Almeida *et al.*, 2017). Thanks to this strategy, perch are able to produce abundant populations of YOY fish. These abundant cohorts (perch in particular; Sajdlová *et al.*, 2017) cause the consumption of zooplankton, the food base that is not only utilized by juvenile fish, but also by adult zooplanktivorous fish (Vašek and Kubečka, 2004). This is followed by a rapid decrease in the guilty juveniles and by calming down of the initial chaos in the entire aquatic ecosystem (Jůza *et al.*, 2014).

Summary of results, general conclusions and perspectives

This Ph.D. Thesis contributes crucial findings to the general knowledge of two key predatory fish in Europe, European catfish and perch. Both species have a fundamental impact on forming fish communities in many aquatic ecosystems. In the case of catfish, adult individuals have the essential impact of apex predators. They drive all lower trophic levels in the aquatic ecosystems with their generalism (II). Although, most individuals within the population are generalists, some of them are short-term specialists or specialists on one type of diet. There is still space for future studies that should try to understand more deeply the individual specialization of apex predators. In our study, we pointed out two typical features of catfish, specifically enormous generalism and adaptability to new prey. Similar behavior was also observed in other large-bodied apex predators (Sinclair *et al.*, 2003; Estes *et al.*, 1998).

As mentioned above, catfish influence the entire food web, however, the impact is not equal. Species with nocturnal activity dominated in the diet (II). The reasons are in particular the nocturnal activity of catfish itself (I, II) and also detection using hydrodynamic traces (Pohlmann, 2004; Cucherousset *et al.*, 2012). Thus, the presence of other predators ideally with daylight activity is advisable. When more than one species of predatory fish is present, the multiple predator effect provides high stability and well-balanced biodiversity in the ecosystem (Wasserman *et al.*, 2016). Catfish with the impact of an apex predator is beneficial in native localities and contributes to proper stability of the ecosystem. In contrast in non-native localities, catfish behaves as an invasive species and causes many problems (I; VI). Catfish is a serious threat in fish communities with species that have not had to resist such predation during evolution (Kennedy *et al.*, 2002; Copp *et al.*, 2009). Particularly, endemic species may not withstand extinction. Thus, catfish is unwanted in these localities and its reduction to a harmless level should be provided (I; VII). However, it is not easy to capture catfish by standard ichthyologic methods. The very efficient method of long-lines has recently been applied in the latest catfish studies (I; VII). It can be used as an efficient method of capturing catfish not only for scientific purposes, but also for reduction in localities where catfish is unwanted (I; VII). In terms of its invasive behavior, the occurrence of catfish in tropical areas would deserve more attention. Tropical areas in Asia and South America represent megadiverse regions of the world but are still overlooked (IV).

In contrast to catfish, perch has an essential impact on the juvenile stage of life (III). Juvenile perch have a high survival rate during the first months of life thanks to efficient utilization of refuges (IV). Juveniles utilize unusual habitats as a refuge against predation, such as the cold and dark bathypelagic zone (Čech *et al*., 2005; Čech and Kubečka, 2006; Jůza *et al*., 2010), or even hypoxic pelagic zones (IV). These hypoxic zones are caused by cultural eutrophication (Carpenter *et al.,* 1998) and they are becoming frequent not only in marine (Diaz and Rosenberg, 2008) but also in freshwater ecosystems (Ludsin *et al*., 2001; Klumb *et al*., 2004) throughout the world. Survival in this habitat poor in oxygen is enabled thanks to small body sizes (Robb and Abrahams, 2003). Requirements for oxygen increase with body size and thus hypoxic zones represent an inhospitable habitat for potential predators whereas smaller prey are able to survive (Vanderploeg *et al*., 2009; Larsson and Lampert, 2011). Thus hypoxic zones are often used as a refuge from predation by zooplankton (Vanderploeg *et al*., 2009) and similarly by small fish individuals (Robb and Abrahams, 2002; Yamanaka *et al.* 2006). However, studies dealing with hypoxic zones as a refuge have mainly been conducted in laboratory conditions (Robb and Abrahams, 2002; 2003) or they were focused on shallow littoral habitats (Suthers and Gee, 1986; Chapman *et al*., 1996 a, b). Therefore, the study by Vejřík *et al*. (2016; Paper IV) is unique because it has proved the use of the hypoxic pelagic zone as a refuge from predation by small fish in a large reservoir system. Hypoxic zones are more and more common in aquatic ecosystems, and thus it is a good opportunity to provide useful research revealing the unique behavior of some species, such as juvenile perch (IV).

An absence of zooplankton may occur in the first months of life of juvenile perch that are highly abundant thanks to survival in refuges (III). Consequently, it induces conflict with cyprinid fish, because their diet also consists particularly of zooplankton (Vašek *et al*., 2006; Kratochvíl *et al*., 2010). This is connected with the development of a new searching and hunting model (Tinbergen, 1960). Newly preferred prey in this hungry system may even be the juvenile perch that caused the tense situation. Consequently, a natural phenomenon occurs, the population of a predator is controlled by the population of potential prey (anomalous role exchange, Paper III). Thanks to the piscivory of cyprinids, the abundant population of juvenile perch is regulated and the stability of the aquatic ecosystem is established again. A similar “role exchange” phenomenon is also discussed by Šmejkal et al. (2017). This study describes in detail predation pressure on asp eggs (*Leuciscus aspius*) induced by bleak (*Alburnus alburnus*). Thus we may assume that the phenomenon of “role exchange” is much more common in aquatic ecosystems than we expected and it only escaped our scientific attention.

A very unique reduction of a perch population may happen even before hatching. We found that perch egg strands are utilized by catfish as a seasonal food source during spring (V). Laying eggs in compact egg strands is evolutionarily advantageous supposing that egg strands are unpalatable thanks to chemical defense. Otherwise, the reproductive material is lost when a predator easily swallows the entire strand (Newsome and Tompkins, 1985; Diamond and Wakefield, 1986). Recent studies proved that a gelatinous egg matrix complicates swallowing of eggs by small predators. Larger predators should be discouraged by a variety of potentially noxious components (Almeida *et al.*, 2017). Nevertheless, the chemical and physical defenses of perch egg strands apparently do not present an obstacle for catfish, such an extremely generalist predatory fish. Our study is the first one that described frequent utilizing of perch egg strands as an advantageous food source for catfish during spring (V). It would be advisable to reveal, whether perch egg strands are commonly utilized by catfish in most aquatic ecosystems. It is probable, that no cases have been recorded before our finding due to the insufficient number of studies focused on catfish diet (Copp *et al.*, 2009)., in particular on the diet during the cold early spring when perch reproduction occurs (Gillet and Dubois, 1995; 2003). On the other hand, we cannot exclude the option that our observations (even though the perch egg strands were found repeatedly) are unique in the study lakes, Milada and Most. Both lakes have low trophy and catfish individuals may be forced to utilize an uncommon food source poor in nutrients due to starvation. Thus, research focused on catfish diet during the whole year, not only in summer, is very necessary to deeply understand the feeding patterns of catfish. It is obvious that the topic of diet behavior of catfish is full of interesting phenomena that deserve scientific attention.

Many of the topics and ideas outlined in this Ph.D. Thesis will be solved in the new, large biomanipulation project awarded to the Institute of Hydrobiology, Biology Centre CAS

for the years 2018–2022 by the Ministry of Education, Youth and Sport (ERDF/ESF project Biomanipulation as a tool for improving water quality of dam reservoirs, under contract number CZ.02.1.01/0.0/0.0/16_025/0007417).

Image attachments from the field sampling

Figure 1. The canyon-shaped Vír Reservoir (224 ha, 56 ×10^6 m^3, max. depth 64 m) is the main locality for presented study:

Vejřík *et al.* 2016: Small fish use the hypoxic pelagic zone as a refuge from predators.

Vejřík *et al.* 2016: Who is who: an anomalous predator-prey role exchange between Cyprinids and perch

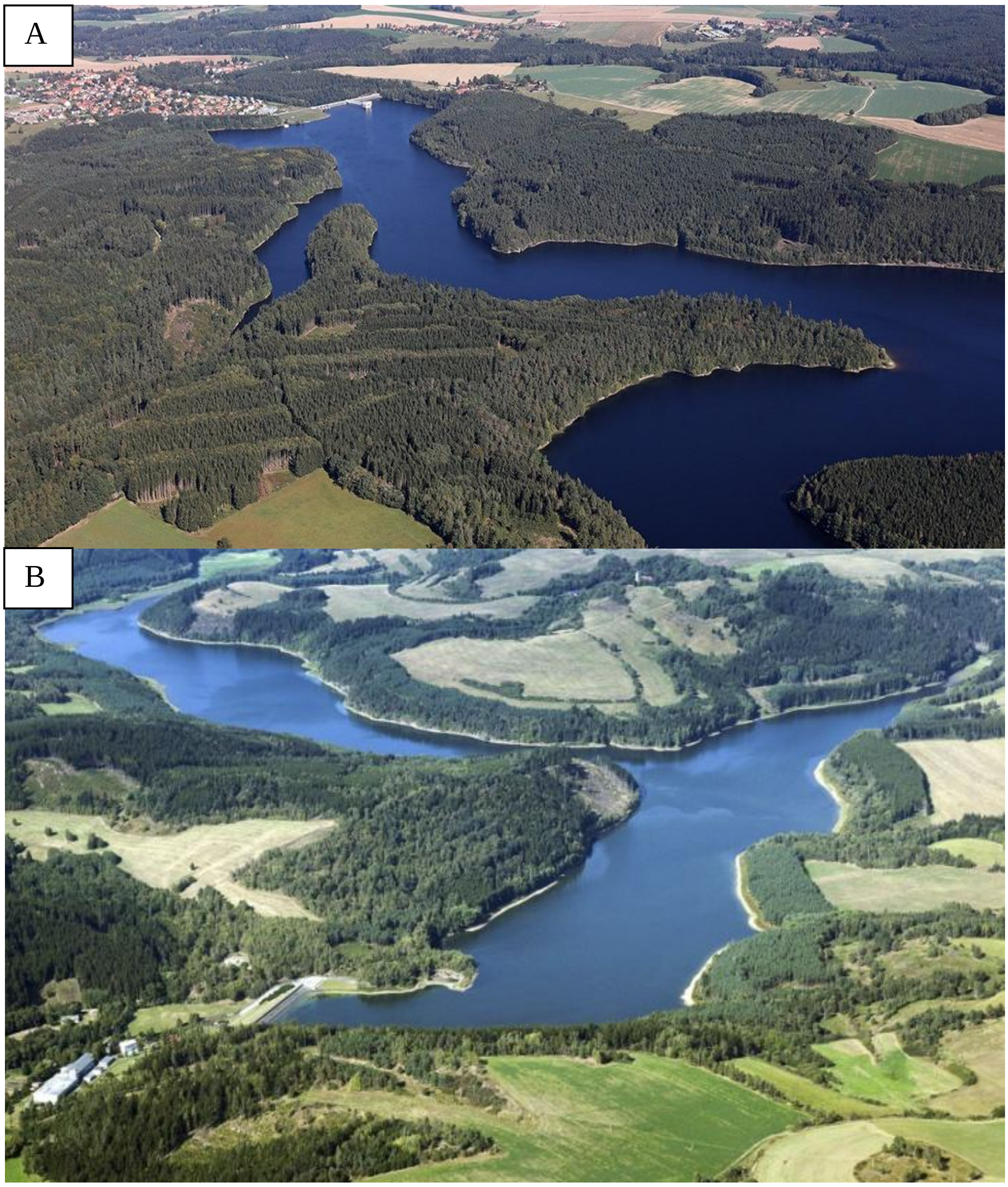

Figure 2. A) Římov Reservoir (210 ha, 34×10^6 m^3, max. depth 45 m) B) Žlutice Reservoir (161 ha, 16×10^6 m^3, max. depth 23 m). Římov and Žlutice Dam Reservoirs were used as comparative water bodies in the following studies:

Vejřík *et al.* 2016: Who is who: an anomalous predator-prey role exchange between Cyprinids and perch.

Vejřík *et al.* submitted: The pros and cons of the freshwater apex predator European catfish and fisheries as a powerful mechanism for regulation of their populations.

The further studies dealing with biology of catfish will take place in the Římov and Žlutice Dam Reservoirs, too.

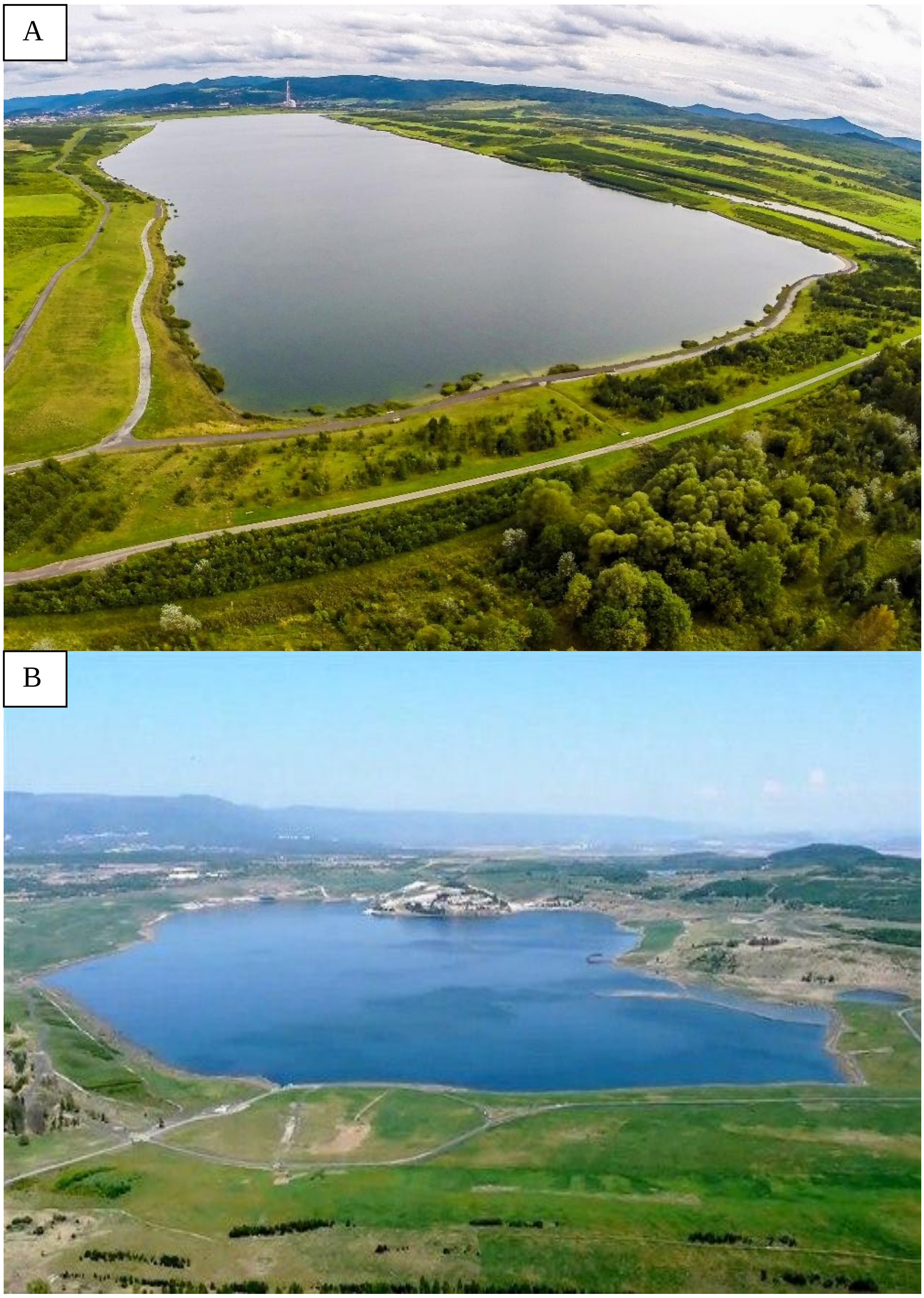

Figure 3. A) The oligo- to mesotrophic Milada Lake (250 ha, 36×10^6 m^3, max. depth 25 m). B) The oligotrophic Most Lake (311 ha, 70×10^6 m^3, max. depth 75 m).

Milada and Most Lakes in Figures 4 and 5 are the most studied post-mining lakes in terms of ichthyologic research. Many important knowledge regarding perch and European catfish were obtained from these localities. Both lakes are the key sites in these studies:

Vejřík *et al.* submitted: The pros and cons of the freshwater apex predator European catfish and fisheries as a powerful mechanism for reduction of their populations.

Vejřík *et al.* 2017: Thirty-year-old paradigm about unpalatable perch egg strands disclaimed by the freshwater top-predator, the European catfish (*Silurus glanis*).

Vejřík *et al.* 2017: European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability.

Vejřík *et al.* accepted: Methods for capturing catfish and potential regulation of catfish population.

Vejřík *et al.* accepted: Catfish as a potential key species for biomanipulation purposes

Figure 4. Electrofishing using electrical generator provides basic knowledge of potential fish prey that is available for predators in the lakes. In addition, bait fishes used for long-lines are captured by electrofishing. It took place in the tributary zone of Žlutice Reservoir.

Figure 5. Although electrofishing is used to capture bait fish, even European catfish can be often captured.

Figure 6. Evening checking of long-lines in Žlutice Reservoir.

Figure 7. European catfish, the first key species for the PhD. Thesis. This individual origins from Most Lake where catfish commonly use branches for rest during the day when hunting activity is low.

Figure 8. Perch (YOY individual), the second key species for the PhD. Thesis. This individual origins from Milada Lake and is hidden in the macrophyte cover. Different behavior can be observed in deep canyon reservoirs, where YOY perch occur mainly in the wide pelagic zone.

Figure 9. Physiological and behavioral constraints hinder albino individuals. Albino animals are rare in the wild because they are easily detected by predators. Albinism-related ostracism results in a solitary existence, usually followed by enhanced predation risk (Slavík *et al.* 2015). Despite this fact, absence or partly absence of pigmentation is common in catfish. The individuals can survive probably due to nocturnal activity, using of refuges in juvenile stage and fast growth that ensures larger size than the sizes of potential predators. A) Albino catfish in Most Lake, B) Albino catfish from Žlutice Reservoir that was recaptured for three times.

Figure 10. A method how to obtain catfish diet and not to harm the individual. Using a bare hand, you can enter the catfish stomach that is directly connected with the gullet and mouth. This sampling was carried out during reproduction of roach (*Rutilus rutilus*) that composed a dominant part of catfish diet during that short period. Other time of the year, roach is disregarded probably due to its passive sleep during night (Vejřík *et al*. 2017; II).

Figure 11. Many captured individuals have empty stomach. However, sometimes one individuals with mass of 8 kg has 2 kg of diet in its stomach (mass of rudd: 0.9 kg, mass of great crested grebe: 1.3 kg). The individual is able to live from such energy income for very long time. It probably does not have to utilize any other diet for several months (Vejřík *et al.* 2017 II).

Figure 12. European catfish captured by long-lines on chicken wing that was used as a bait to test preferences of catfish for fish or bird prey (results have not been published yet).

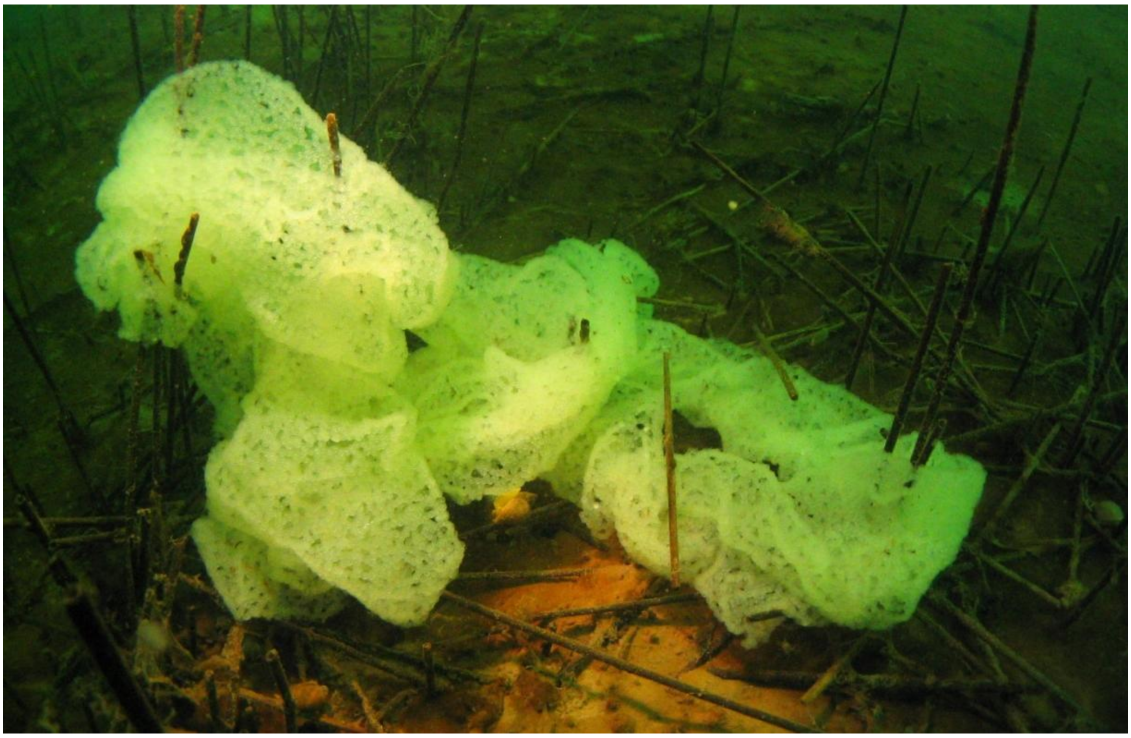

Figure 13. Perch egg strands were considered to be unpalatable for decades (Newsome and Tompkins, 1985; Diamond and Wakefield, 1986). Recently, repellent compounds were described in this reproduction material that should discourage predators (Almeida *et al.*, 2017). However, European catfish is able to utilize perch egg strands as the food source. We found many strands in the stomachs of catfish during spring season (Vejřík *et al.* 2017 V). Photo by Jiří Peterka.

References

Alm, G.L. (1946) Reasons for the occurrence of studied fish populations. *Rep. Inst. Freshwat. Res. Drotting* 25, 1–146.

Alm, G.L. (1952) Year class fluctuations and span of life of perch. *Rep. Inst. Freshwat. Res. Drotting* 40, 17–38.

Almeida, L.Z., Guffey, S.C., Krieg, T.A., Hook, T.O. (2017) Predators Reject Yellow Perch Egg Skeins. *Transactions of the American Fisheries Society* 146, 173–180.

Alp, A., Kara, C., Buyukcapar, H.M. (2003) Reproductive biology in a native European catfish, *Silurus glanis* L., 1758, population in Menzelet Reservoir. *Turkish Journal of Veterinary and Animal Sciences* 28, 613–622.

Baruš, V., Oliva. O. (1995) Mihulovci *Petromyzontes* a ryby *Osteichthyes*. Fauna ČR a SR. *Academia, Praha.*

Begon, M., Harper, J.L., Townsed, C.R. (1996) Ecology: Individuals, Populations & Communities. 3rd ed. Blackwell Science, Oxford, UK.

Benndorf, J. (1987) Food web manipulation without nutrient control - a useful strategy in lake restoration. *Swiss Journal of Hydrology* 49, 237–248.

Boughedir, W. (2006) Etude de lécobiologie du Silure (*Silurus glanis*, L. 1978) dans la retenue du barrage de Sidi Dalem. Tunis, Institut National Agronomique de Tunisie, 81 p.

Boulêtreau, S., Santoul, F. (2016) The end of the mythical giant catfish. *Ecosphere* 7, e01606.

Boulêtreau, S., Gaillagot A., Carry, L., Tétard, S., De Oliveira, E., Santoul, F. (2018) Adult Atlantic salmonhave have a new freshwater predator. *Plos One* 13, e0196046.https:// doi.org/10.1371/journal.pone.0196046.

Brooks, J.L., Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science* 150, 28–35.

Bruyenko, V.P. (1971) Age and seasonal variation in the feeding of *Silurus glanis* in the lower reaches of the Danube. *Zoologicheskij zhurnal* 50, 1214–1219 [In Russian].

Carol, J., Zamora, L., García-Berthou, E. (2007) Preliminary telemetry data on the movement patterns and habitat use of European catfish (*Silurus glanis*) in a reservoir of the River Ebro, Spain. *Ecology of Freshwater Fish* 16, 450–456.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R. (1985) Cascading trophic interactions and lake productivity. Fish predation and herbivory can regulate lake ecosystems. *BioScience* 33, 634–639.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., Smith, V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8, 559–568.

Čech, M., Kratochvíl, M., Kubečka, J., Draštík, V., Matěna, J. (2005) Diel vertical migrations of bathypelagic perch fry. *Journal of Fish Biology* 66, 685–702.

Čech, M., Kubečka, J. (2006) Ontogenetic changes in the bathypelagic distribution of European perch fry *Perca fluviatilis* monitored by hydroacoustic methods. *Biológia Bratislava* 2, 211–219.

Čech, M., Kubečka, J., Frouzová, J., Draštík, V., Kratochvíl, M., Jarošík, J. (2007) Impact of flood on distribution of bathypelagic perch fry layer along the longitudinal profile of large canyon-shaped reservoir. *Journal of Fish Biology* 70, 1109–1119.

Čech, M., Čech, P., Kubečka, J., Prchalová, M., Draštík, V. (2008) Size selectivity in summer and winter diets of great cormorant (*Phalacrocorax carbo*): Does it reflect season-dependent difference in foraging efficiency? *Waterbirds* 31, 438–447.

Čech, M., Peterka, J., Říha, M., Draštík, V., Kratochvíl, M., Kubečka, J. (2010) Deep spawning of perch (*Perca fluviatilis*, L.) in the newly created Chabařovice Lake, Czech Republic. *Hydrobiologia* 649, 375–378.

Čech, M., Peterka, J., Říha, M., Muška, M., Hejzlar, J., Kubečka, J. (2011) Location and timing of the deposition of egg strands by perch (*Perca fluviatilis* L.): the roles of lake hydrology, spawning substrate and female size. *Knowledge and Management of Aquatic Ecosystems* 403, 1–12.

Čech, M., Vejřík, L. (2011) Winter diet of great cormorant (*Phalacrocorax carbo*) on the River Vltava: estimate of size and species composition and potential for fish stock losses. *Folia Zoologica* 60, 129–142.

Čech, M., Peterka, J., Říha, M., Vejřík, L., Jůza, T., Kratochvíl, M., Draštík, V., Muška, M., Znachor, P., Kubečka, J. (2012a) Extremely shallow spawning of perch (*Perca fluviatilis* L.): the roles of sheltered bays, dense semi-terrestrial vegetation and low visibility in deeper water. *Knowledge and Management of Aquatic Ecosystems* 406, 09p1–09p12.

Čech, M., Vejřík, L., Peterka, J., Říha, M., Muška M., Jůza, T., Draštík, V., Kratochvíl, M., Kubečka, J. (2012b) The use of artificial spawning substrates in order to understand the factors influencing the spawning site selection, depth of egg strands deposition and hatching time of perch (*Perca fluviatilis* L.). *Journal of Limnology* 71, 170–179.

Chapman, L.J., Chapman, C.A., Chandler, M. (1996a) Wetland ecotones as refugia for endangered fishes. *Biological Conservation* 78, 263–270.

Chapman, L.J., Chapman, C.A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L.S., Keiter, A. E. (1996b) Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conservation Biology* 10, 554–561.

Copp, H.G., Britton, J.R., Cucherousset, J., García-Berthou, E., Kirk, R., Peeler, E., Stakėnas, S. (2009) Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries* 10, 252–282.

Craig, J.F. (1978) A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshwater Biology* 8, 59–68.

Craig, J.F. (2000) Percid Fishes - Systematics, Ecology and Exploitation. *Blackwell Science, Dunscore, Scotland*, 352 pp.

Croze, O., Bau, F., Delmouly, L. (2008). Efficiency of a fish lift for returning Atlantic salmon at a largescale hydroelectric complex in France. *Fisheries Management and Ecology* 15, 467–476.

Cunico, A.M, Vitule, J.R.S. (2014) First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). *BioInvasions Records* 3, 117–122.

Cucherousset, J., Bouletreau, S., Azemar, F., Compin, A., Guillaume, M., Santoul, F. (2012) ‘‘Freshwater Killer Whales’’: Beaching Behavior of an Alien Fish to Hunt Land Birds. *Plos One* 7, e50840.

Cucherousset, J., Horký, P., Slavík, O., Ovidio, M., Arlinghaus, R., Boulêtreau, S., Britton, R., García-Berthou, E., Santoul, F. (2017) Ecology, behaviour and management of the European Catfish. *Reviews in Fish Biology and Fisheries*, https://doi.org/10.1007/s11160017-9507-9.

Diamond, M., Wakefield, P.M. (1986) The consumption of eggs of the perch, *Perca fluviatilis* L., by macroinvertebrates in the field. *Freshwater Biology* 16, 373–376.

Diaz, R.J., Rosenberg, R. (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929.

Doğan Bora, N., Gül, A. (2004) Feeding Biology of *Silurus glanis* (L., 1758) Living in Hirfanli Dam Lake. *Turkish Journal of Veteriary and Animal Science* 28, 471–479.

Elvira, B., Almodóvar, A. (2001) Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st centrury. *Journal of Fish Biology* 59, 323–331.

Estes, J.A., Tinker, M.T., Williams, T.M., Doak, D.F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282, 473–476.

Gillet, C., Dubois, J.P. (1995) A survey of the spawning of perch (*Perca fluviatilis*), pike (*Esox lucius*), and roach (*Rutilus rutilus*), using artificial spawning substrate in lakes. *Hydrobiologia* 300–301, 409–414.

Gillet, C., Dubois, J.P. (2007) Effect of water temperature and size of females on the timing of spawning of perch *Perca fluviatilis* L. in Lake Geneva from 1984 to 2003. *Journal of Fish Biology* 70, 1001–1014.

Graham, N.A., Pueppke, G.S., Uderbayev, T. (2017) The Current Status and Future of Central Asia’s Fish and Fisheries: Confronting a Wicked Problem. *Water* 9, 701; doi:10.3390/w9090701

Haakana, H., Huuskonen, H., Karjalainen, J. (2007) Predation of perch on vendace larvae: diet composition in an oligotrophic lake and digestion time of the larvae. *Journal of Fish Biology* 70, 1171–1184.

Hrbáček, J., Dvořáková, M., Kořínek, V., Procházková, L. (1961) Demonstration of the effect of the fish stock on the species compo composition of zooplankton and the intensity of metabolism of the whole plankton assemblage. *The Proceedings of the International Association of Theoretical and Applied Limnology* 14, 192–195.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D. (2001) What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 157–170.

Jůza, T., Vašek, M., Kubečka, J., Seďa, J., Matěna, J., Prchalová, M., Peterka, J., Říha, M., Jarolím, O., Tušer, M., Kratochvíl, M., Čech, M., Draštík, V., Frouzová, J., Hohausová, E., Žaloudík, J. (2009) Pelagic underling communities in a canyon-shaped reservoir in late summer. *Journal of Limnology* 68, 304–314.

Jůza, T., Čech, M., Kubečka, J., Vašek, M., Peterka, J., Matěna, J. (2010) The influence of the trawl mouth opening size and net colour on catch efficiency during sampling of early fish stages. *Fisheries Research* 105, 125–133.

Jůza, T., Vašek, M., Kratochvíl, M., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Muška, M., Peterka, J., Prchalová, M., Říha, M., Tušer, M., Kubečka, J. (2014) Chaos and stability of age-0 fish assemblages in a temperate deep reservoir: unpredictable success and stable habitat use. *Hydrobiologia* 724, 217–234.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D., Reich, P. (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417, 636–638.

Klumb, R.A., Bunch, K.L., Mills, E.L., Rudstam, L.G., Brown, G., Knauf, C., Burton, R., Arrhenius, F. (2004) Establishment of a metalimnetic oxygen refuge for zooplankton in a productive Lake Ontario embayment. *Ecological Applications* 14, 113–131.

Knuston, K.M., Peterka, J.J. (1969) Age and growth of yellow perch in Lake Ashtabula. *Reprinted from the proceedings of the North Dakota Academy of Science* 23, 14–24.

Kováč, V. (2016) The fish itself, not only environment, should be considered in studying invasion. *Ecology of Freshwater Fish* 25, 674–677.

Kratochvíl, M., Čech, M., Vašek, M., Kubečka, J., Hejzlar, J., Matěna, J., Peterka, J., Macháček, J., Seďa, J. (2010) Diel vertical migrations of age 0+ percids in shallow, well-mixed reservoir. *Journal of Limnology* 69, 305–310.

Kustareva, L.A., Naseka, A.M. (2015) Fish diversity in Kyrgyzstan: Species composition, fisheries and management problems. *Aquatic Ecosystem Health and Management* 18, 149–159.

Larsson, P., Lampert, W. (2011) Experimental evidence of a low-oxygen refuge for large zooplankton. *Limnology and Oceanography* 56, 1682–1688.

Lass, S., Boersma, M., Spaak, P. (2000) How do migrating daphnids cope with fish predation risk in the epilimnion under anoxic conditions in the hypolimnion? *Journal of Plankton Research* 22, 1411–1418.

Lawton, J.H., Beddington, J.R., Bonser, R. (1974) Switching in invertebrate predators. In: *Ecological stability* (eds: Usher, M.B. & Williamson, M. H.), pp. 141–58. *Chapman & Hall, London, UK.*

Levy, D.A. (1990) Sensory mechanism and selective advantage for diel vertical migration in juvenilie sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 47, 1796–1802.

Ludsin, S.A., Kershner, M.W., Blocksom, K.A., Knight, R.L., Stein R.A. (2001) Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecological Applications* 11, 731–746.

Matěna, J. (1995) Ichthyoplankton and 0+ pelagic fish in the Římov reservoir (Southern Bohemia). *Folia Zoologica* 44, 31–43.

Menshutkin, V.V., Zhakov, L.A. (1964) Opyt matematicheskogo opredeleniya kharakteria dinamiki chislennosti okunya v zadannykh ekologicheskikh usloviyakh. Ozera karelskou Peresheika, 140–155, In: Craig, J.F. (1987): The biology of perch and related fish. Timber Press 184, 333pp.

Mills, C.A., Hurley, M.A. (1990) Long-term studies on the Windermere populations of perch (*Perca fluviatilis*), pike (*Esox lucius*) and Arctic charr (*Salvelinus alpinus*). *Freshwater Biology* 23, 119–136.

Musil, J., Horký, P., Slavík O., Zbořil, A., Horká, P. (2012) The response of the young of the year fish to river obstacles: Functional and numerical linkages between dams, weirs, fish habitat guilds and biotic integrity across large spatial scale. *Ecological Indicators* 23, 634–640.

Newsome, G.E., Tompkins, J. (1985) Yellow perch egg masses deter predators. *Canadian Journal of Zoology* 63, 2882–2884.

Ostracism of an Albino Individual by a Group of Pigmented Catfish. Available from: https://www.researchgate.net/publication/277327648_Ostracism_of_an_Albino_Individual_by_a_Group_of_Pigmented_Catfish [accessed May 19, 2018].

Paine, R.T. (1966) Food web complexity and species diversity. *The American Naturalist* 110, 65–75.

Persson, L., Byström, P., Wahlström, E. (2000) Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivory. *Ecology* 81, 1058–1071.

Peterka, J., Kubečka, J. (2011) Komplexní průzkum rybí obsádky jezera Most v roce 2011. *Biologické centrum AV ČR, Hydrobiologický ústav*, 14 pp (in Czech only).

Peterka, J. (2012) Komplexní průzkum rybí obsádky jezera Most v roce 2011. *Biologické centrum AV ČR, Hydrobiologický ústav,* 16 pp (in Czech only).

Pivnička, K. (1991) Long-term study of the growth of four fish species in the Klíčava Reservoir with respect to the changes of abundance and temperature. *Acta Universitatis Carolinae* 5, 91–106.

Pohlmann, K., Atema, J.W., Breithaupt, T. (2004) The importance of the lateral line in nocturnal predation of piscivorous catfish. *Journal of Experimental Biology* 207, 2971–2978.

Post, J.R., McQueen, D.J (1988) Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predator? *Canadian Journal of Fisheries and Aquatic Sciences* 45, 1820–1826.

Radinger, J., Essl, F., Holker, F., Horký, P., Slavík, O., Wolter, C. (2017) The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Global change biology* 23, 4970–4986.

Rask, M. (1986) The diet and feeding activity of perch, *Perca fluviatilis* L., in a small lake in southern Finland. *Annales Zoologici Fennici* 23, 49–56.

Robb, T.L., Abrahams, M.V. (2002) The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. *Behavioural Ecology and Sociobiology* 52, 25–30.

Robb, T., Abrahams, M.V. (2003) Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small. *Journal of Fish Biology* 62, 1067–1081.

Roberts, J.J., Hook, T.J., Ludsin, S.A., Pothoven, S.A., Vanderploeg, H.A., Brandt, S.B. (2009) Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology* 381, 132–142.

Roberts, J.J., Brandt, S.B., Fanslow, D., Ludsin, S.A., Pothoven, S.A., Savia, D. Hook, T.O. (2011) Effects of hypoxia on consumption, growth, and RNA:DNA ratios of young yellow perch. *Transactions of the American Fisheries Society* 14, 1574–1586.

Roberts, J.J., Grecay, P.A., Ludsin, S.A., Pothoven, S.A., Vanderploeg, H.A., Hook, T.O. (2012) Evidence of hypoxic foraging forays by yellow perch (*Perca flavescens*) and potential consequences for prey consumption. *Freshwater Biology* 57, 922–937.

Sajdlová, Z., Jůza, T., Frouzová, J., Seďa, J., Čech, M. (2017) Bathypelagic percid fry, the strongly predominated fry community in the deep European reservoir. *Hydrobiologia* 787, 341–352.

Sajdlová, Z., Frouzová, J., Draštík, V., Jůza, T., Peterka, J., Prchalová, M., Říha, M., Vašek, M., Kubečka, J., Čech, M. (2018) Are diel vertical migrations of European perch

(*Perca fluviatilis* L.) early juveniles under direct control of light intensity? Evidence from a large field experiment. *Freshwater Biology* 63, 473–482.

Schaefer, W.F. (1977) Growth patterns, food habits and seasonal depth distribution of yellow perch in southwestern lake Michigan. *Wisconsin Academy of Sciences, Arts and Letters* 64, 204–215.

Shapiro, J., Lammarra, V., Lynch, M. (1975) Biomanipulation: an ecosystem approach to lake restoration. *Limnology Research Centre, University of Minnesota* 143, 1–32.

Sinclair, A.R.E., Mduma, S., Brashares, J.S. (2003) Patterns of predation in a diverse predator-prey system. *Nature* 425, 288–290.

Slavík, O., Horký, P. (2012) Diel dualism in the energy consumption of the European catfish Silurus glanis. *Journal of Fish Biology* 81, 2223–2234.

Slavík, J. (2013) Charakteristiky chování sumce velkého v přírodních podmínkách a akvakultuře. Habilitační práce, *Česká zemědělská univerzita v Praze*, 126 pp (in Czech only).

Slavík, O, Horký, P, Maciak, M (2015) Ostracism of an Albino Individual by a Group of Pigmented Catfish. *Plos One* 10, e0128279. doi:10.1371/journal.pone.0128279.

Šmejkal, M., Baran, R, Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., Mrkvička, T., Kubečka, J. (2017) Early life-history predator-prey reversal in two cyprinid fishes. *Scientific Reports* 7, 6924. doi:10.1038/s41598-017-07339-w.

Specziár, A., Rezsu, E.T. (2009) Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. *Journal of Fish Biology* 75, 247–267.

Sumari, O. (1971) Structure of the perch populations of some ponds in Finland. Annales Zoologici Fennici 8, 406–421.

Suthers, I.M, Gee, J.H. (1986) Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 1562–1570.

Syväranta, J., Cucherousset, J., Kopp, D., Crivelli, A., Cereghino, R., Santoul, F. (2010) Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. *Aquatic Biology* 7, 137–144.

Terlecki, J. (1987) The diet of adult perch (*Perca fluviatilis* L.), in the Vistula dam reservoir in Wloclawek. *Acta Ichthyologica et Piscatoria* 17, 43–57.

Thorpe, J.E. (1977) Synopsis of biological data on the perch *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* Mitchill, 1814. *FAO Fisheries Synopsis No*. 113, Rome, 138 pp.

Tinbergen, L. (1960) The natural control of insects in pinewoods. 1: Factor influencing the intensity of predation by songbirds. *Archives neerlandaises se Zoologie* 13, 266–336.

Tonn, W., Magnuson, J., Ras, M., Toivenen, J. (1990) Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *American Naturalist* 13, 345–375.

Treasurer, J.W. (1988) The distribution and growth of lacustrine 0+ perch, *Perca fluviatilis*. *Environmental Biology of Fishes* 21, 37–44.

Vanderploeg, H.A., Ludsin S.A., Ruberg, S.A., Hook T.O., Pothoven, S.A., Brandt, S.B., Lang, G.A., Liebig, J.R., Cavaletto, J.F. (2009) Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology* 381, S92–S107.

Vašek, M., Kubečka, J. (2004) In situ diel patterns of zooplankton consumption by subadult/adult roach *Rutilus rutilus*, bream *Abramis brama*, and bleak *Alburnus alburnus*. *Folia Zoologica* 53, 203–214.

Vašek, M., Kubečka, J., Matěna, J., Seďa, J. (2006) Distribution and diet of 0+ fish within a canyon- shaped European reservoir in late summer. *International Review of Hydrobiology* 91, 178–194.

Wang, N., Eckmann, R. (1994) Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. *Hydrobiologia* 277, 135–143.

Wasserman, J.R., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., Weyl, O.L.F. (2016) Using functional responses to quantify interaction effects among predators. *Functional Ecology* 30, 1988–1998.

Whiteside, M.C., Swindoll, C.M., Doolittle, W.L. (1985) Factors affecting the early life history of yellow perch, *Perca flavescens*. *Environ. Biology of Fishes* 12, 47–56.

Wysujack, K., Mehner, T. (2005) Can feeding of European catfish prevent cyprinids from reaching a size refuge? *Ecology of Freshwater Fish* 14, 87–95.

Yamanaka, H., Kohmatsu, Y., Yuma, M. (2007) Difference in the hypoxia tolerance of the round crucian carp and largemouth bass: implications for physiological refugia in the macrophyte zone. *Ichthyological Research* 54, 308–312.

Research articles

Paper I

The pros and cons of the freshwater apex predator, European catfish *Silurus glanis*, and angling as a powerful mechanism for its regulation

The pros and cons of the freshwater apex predator, European catfish *Silurus glanis*, and angling as a powerful mechanism for its regulation

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Running title: Regulation of catfish by angling

Key-words: apex consumer, biomanipulation, economic impact, freshwater ecosystem, long-line

Summary

1. Catfish have spread across Europe and several countries out of this region within the last decades. Basic knowledge of this apex predator has revealed concerns of invasive behaviour and questions regarding its utilization as a biomanipulation species. However, a method enabling its regulation to a required level has not been developed so far.

2. We simulated the impact of angling on the catfish population by method of long-lines in two post-mining lakes with a monitored population consisting of tagged individuals and in two reservoirs as additional localities. Further, the efficiency of long-lines as a reducing device was examined and the economic aspects were determined.

3. Reduction of a catfish population to a harmless level may be efficiently provided by long-lines and angling (depending on the approach of anglers). It may be used in localities where this species is unwanted or invasive. Relatively low angling effort resulted in a reduction of the catfish population to a harmless level. Both angling and long-lines are very simple, they are financially and time bearable mechanisms of catfish reduction in any condition.

4. However, catfish play an important role as a biomanipulative species in many localities. In this case where catfish is beneficial, angling presents a real threat of population collapse and loss of the biomanipulative effect.

Introduction

Angling fundamentally affects water ecosystems, particularly the composition of the fish community, including its size and structure, drivers of evolution, overall changes in biota and water quality (Levin *et al*., 2006; Laugen *et al*., 2014). Similarly, fisheries-related activities such as stocking of hatchery-reared fish or fish introductions may radically change a fish community, other organisms and ultimately entire aquatic ecosystems (Pauly *et al*., 2001; Robinson & Frid, 2003; Allan *et al*., 2005; Frank *et al*., 2005; Mullon *et al*., 2005). Commercially important fish species are for the most part affected by commercial fishing (Jørgensen *et al*., 2007), whereas populations of apex predators are also considerably affected by angling (Hunt, 2005; Levin *et al*., 2006; Last *et al*., 2011). Pressure produced by a recreational activity may effectively lead to the disappearance of several species (Post *et al*., 2002; Hunt, 2005) and destabilisation of the ecosystem by changes to trophic cascades and trait-mediated effects (Arlinghaus *et al*., 2002; Myers *et al*., 2007). However, only limited information dealing with the impact of angling is known, particularly in freshwaters (Levin *et al*., 2006).

Apex predators play a key role in driving the aquatic ecosystem. They affect the entire food web due to their generalism (Sinclar *et al*., 2003; Vejřík *et al*., 2017a; Vejřík *et al*., 2017b). All parts of the food web are directly or indirectly affected by the presence of apex predators, including mesopredators (Prugh, 2009; Ripple *et al*., 2014). Lately, numbers of apex predators are generally decreasing and thus people have realized their non-substitutability in the ecosystem (Veit *et al*., 1997; Myers *et al*., 2007; Stone, 2007; Ferretti *et al*., 2010). The main freshwater apex predator in Europe is the European catfish (*Silurus glanis*) and its native area is Central and Eastern Europe (Copp *et al*., 2009). Catfish is the biggest freshwater fish in Europe and the third biggest freshwater fish in the world (Stone, 2007; Copp *et al*., 2009). This may be the reason why there are a lot of myths connected with the catfish, also it is difficult to study, so practically no information was known about it for decades (Boulêtreau & Santoul, 2016). Knowledge about the ecology of catfish has been progressively revealed in the last years (Syväranta *et al*., 2010; Guillerault *et al*., 2015; Vejřík *et al*., 2017b). The insufficient number of studies focused on catfish is mainly caused by the low efficiency of standard capturing methods

(Alp *et al.*, 2003). It is difficult to capture catfish despite the fact that the number of catfish is generally increasing due to man-mediated spreading, in comparison to other apex predators (Carol *et al.*, 2007; Copp *et al.*, 2009; Cucherousset *et al.*, 2012; Cunico & Vitule, 2014). However, the populations of catfish in its native area cannot practically reach carrying capacity due to rather intensive angling (Copp *et al.*, 2009). In native localities, catfish is angled mainly due to its high quality meat (Linhart *et al.*, 2002).

Catfish has also been introduced to new localities such as Western and Southern Europe where it is regarded as an invasive species (Carol *et al.*, 2007; Cucherousset *et al.*, 2012). Invasions are in general serious threats to freshwater ecosystems (Dudgeon *et al.*, 2006). Recent work in Germany and the USA has shown that body size is a key determinant of angler motivation across a range of species (Arlinghaus *et al.*, 2014). The large body size of catfish is the main reason for illegal introduction outside its native range (Hutt *et al.*, 2013; Cucherrouset *et al.*, 2017). Catfish as an apex predator may dramatically affect localities such as Iberia and other countries in Southern Europe where high endemism of small-bodied fish species combines with an absence of native piscivorous fishes (Copp *et al.*, 2009). These species-unsaturated localities are more susceptible to invasion by non-native species because there is a vacant ecological niche and interspecific competition is less intense (Kennedy *et al.*, 2002). According to the Fish Invasiveness Scoring Kit (FISK), catfish poses a high risk in this situation (Almeida *et al.*, 2013). Considering the wide diet plasticity of catfish (Vejřík *et al.*, 2017b), it affects not only fishes, but also other vertebrates such as waterfowl (Carol *et al.*, 2009).

Catfish is a successful apex predator that fundamentally influences the ecosystem (Copp *et al.*, 2009; Vejřík *et al.*, 2017b). Thus, the impact may be profitable but also extremely unfavourable depending on the locality. Catfish has several unique characteristics that constitute it the position of an ideal species for biomanipulation, such as low requirements for water quality, longevity, tolerance to manipulation (Copp *et al.*, 2009), ability to form abundant population (Boulêtreau *et al.*, 2011), wide diet plasticity and lower gape limitations in comparison with other predators (Vejřík *et al.*, 2017b). Biomanipulation may be applied to obtain or maintain high water quality in reservoirs for drinking water (Vašek *et al.*, 2013) or in recreational water bodies such as post-mining lakes (Vejřík *et* *al.*, 2017b). High potential is assumed in a mild climate due to good prosperity of catfish in warmer water (Britton *et al.*, 2007).

The effect of angling can be perceived in two scenarios: i) environment where catfish possess a threat to native fauna, and ii) environment where catfish represents a fundamental and positive role in lowering the total fish biomass. In terms of the impact of angling on catfish, only two studies, to our knowledge, have been published so far (Britton *et al.*, 2007; Boulêtreau *et al.*, 2016), however these studies did not evaluate the impact of angling on the catfish population (Cadrin & Pastoors, 2008). Further, we evaluated the financial budget of a catfish fishery that is commonly ignored. In addition, we used long-lines, an efficient method for capturing catfish, which can be used for both scientific and manipulation purposes. Catfish individuals in the study sites were tagged, their abundances and biomasses were known and thus our study has a unique experimental design conducted under natural conditions.

Methods

Study sites

The study was conducted in two water bodies created after aquatic restorations of lignite mining pits, Milada and Most Lakes, Czech Republic (Fig. 1). The oligo- to mesotrophic Milada Lake (250 ha, 36×10^6 m^3, max. depth 25 m) was flooded with water between 2001 and 2010 when final water level was reached. Both lakes were naturally colonized by perch (*Perca fluviatilis*), rudd (*Scardinius erythrophthalmus*), roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernua*; for details see Vejříková *et al.*, 2016). European catfish was introduced in 2007 (316 individuals, mean weight 1.2 kg) for biomanipulation purposes. The oligotrophic Most Lake (311 ha, 70×10^6 m^3, max. depth 75 m) was flooded between 2008 and 2014. European catfish (694 individuals, mean weight 3.7 kg) was introduced in 2011, 2012 and 2013. In Most, all catfish individuals were individually tagged with a passive integrated transponder tag (PIT-tag, Oregon RFID, fullduplex, length 12 mm, diameter 2.15 mm, weight 0.11 g, 11784/11785 compatible). In Milada, catfish individuals were tagged when they were captured by long-lines. Both lakes present a new type of water body that appears throughout Europe nowadays (Sienkiewicz & Gasiorowski, 2017). Maintaining good water quality is an important feature of both lakes and fish predators play the main role in biomanipulation (Vejřík *et al.*, 2017b).

Angling is currently forbidden, however it is expected to be allowed in the future. Two dam reservoirs for drinking water were used as reference sites: Římov Reservoir (210 ha, 34×10^6 m^3, max depth 45 m) and Žlutice Reservoir (161 ha, 16×10^6 m^3, max. depth 23 m) (Fig. 1). Both reservoirs are eutrophic and catfish are stocked regularly (50 individuals, *i.e. ca.* 110 kg per year) for biomanipulation purposes (for more details see Vašek *et al.*, 2013).

Fish sampling

Animal treatment (including fish sampling and stomach content analysis) was performed in accordance with guidelines from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01679) and with permission of Palivový kombinát Ústí, state enterprise, the owner of Milada and Most Lakes, and the Vltava River Authority, administrator of Římov and Žlutice Reservoirs. The work was approved by the Ethics Committee of the Czech Academy of Sciences. The field study did not involve endangered or protected species.

European catfish from both lakes and both reservoirs were caught by long-lines during four day-and-night-long campaigns (Fig. 2). The main line was 60 m long with three main buoys situated at the ends and in the middle of the line. Anchoring ropes, 3.5–7 m long, with weights (32 kg each) were tied to the buoys and fixed to the main line in the right place. Every five metres between the main buoys, auxiliary buoys were placed with a hanging 2.5 m long snood made of two parts i) 2-m long fishing-line with maximum load of 50 kg and ii) more durable 0.5 m long fishing-line with maximum load of 100 kg. A swivel was placed between these two parts to prevent twisting and a 150 g sinker was hung on the snood to keep it at the appropriate depth. At the end of the snood, there was a multi hooks system with one single hook (size: 6/0–8/0) and one treble (size: 6/0–8/0). The bait was placed on the upper single hook (perch and rudd, total length: L_T=180–300 mm). We recommend using this multi hooks system to maximize the efficiency of long-lines, because it apparently reduces the number of spit-out baits (*i.e.*, catfish ingest the bait but spit it out before swimming away). 50% of attacked baits are spit-out when only a single hook is used (Boulêtreau *et al.*, 2016). When using this multi hooks system, the catfish is hooked by the fishing treble hanging under the baited hook. Altogether 30 individual bait fish on 3 long-lines were used each day of sampling. Most of the catfish were caught during the night. All individuals were measured and the codes of their pit-tags were recorded. We spent 32, 28, 12 and 8 days in Most, Milada, Římov and Žlutice, respectively.

To obtain reliable estimates of the fish biomass of the entire fish community, detailed sampling was conducted in all water bodies between 2012 and 2016; between July and September. Each water body was sampled during the course of 4–5 days in one year. Benthic and pelagic habitats were sampled with multimesh gillnets including 12 mesh sizes according to EU standard (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm; CEN, 2015). Each mesh size panel was 2.5 m long forming a 40 m long net in total. Benthic nets were 1.5 m high whereas pelagic nets were 4.5 or 3.0 m high. The nets were placed at three depth ranges from the surface up to 9 m (e.g. 0–3, 3–6, 6–9 m) and the number of nets was set according to the representative water volume (6–24 in the first, 6–12 in the second and 6–9 in third strata; for details see Blabolil *et al*., 2017). Nets were set before dusk and lifted the next day after dawn and covered the usual evening and morning peaks in fish activity (Vašek *et al*., 2009). All captured fish were anaesthetised using a lethal dose of tricaine methanesulfonate (MS–222, Sigma Aldrich Co.), identified to species and weighed (wet mass). For each water body, catch per unit effort was calculated in terms of fish wet mass (BPUE; kg 1,000 m^{-2} multimesh gillnetnight^{-1}) separately for benthic (*i.e.* water layer of 1.5 m above the bottom) and pelagic habitats (open water). To combine catches from the two different habitats into a water body-wide CPUE, benthic and pelagic CPUE data were weighted according to estimated volumetric habitat proportions in each water body (benthic habitat: 6–20%, pelagic habitat: 80–94 %).

Simulation of anglers

Long-lines authentically simulate angling with a supporting buoy that is commonly used for catfish angling (Fig. 2). The two baits simulate the two tips that are normally used by one angler. According to the Fishing regulations of the Czech Fishing Union (CFU, 2017), a single licensed person may practice angling with two rods. This means we simulated 15 anglers each day. To evenly cover the shore of the water body during the sampling campaign, over the time period of a day when angling is prohibited, long-lines were transported to a different place and reinstalled. Catching of catfish on long-lines was conducted only during hours allowed for angling in accordance with current fishing regulations of CFU (July and August: 04:00–00:00, September: 6:00–22:00, November: 07:00–18:00, and catching was always interrupted during the night interval). Hooks were checked in 08:00–10:00, before dusk (time depended on the season) and at the end of the catching time. Missing baits were replaced during checking times.

The bag limits according to rules in the Czech Republic are as follows: the angler may keep maximum of 7 kg of all species even if fisherman fishes in more localities in one day. In this catch there may be maximum of two catfish and 70 cm is the shortest minimum length of catfish that could be taken. If fisherman intends to keep the fish and the weight of the catch exceeds 7 kg with the first caught fish, angling that day must be finished. These restrictions were not obeyed in our case. On the other hand it was compensated by the difference that angler immediately notice and replace the missing bait when catfish tear down the bait without catching, whereas we checked the baits only three times per day. Baits torn off in the meantime were not replaced and thus there were "empty rods" that theoretically compensate situation of anglers finishing angling due to bag limit of 7 kg or two pieces of catfish.

Catfish larger than 70 cm were used to calculate the angling pressure. Angler would probably take such fish and thus these individuals would be removed from the lake. Simulations of angling pressure were conducted in June 23–27, August 18–22, September 1–5 and November 4–8 in Most Lake. Simulations were conducted in June–July 30–4, August 25–28, September 15–19 and November 17–21 in Milada Lake. The sampling campaigns covered basically the entire angling season that would last from June 16 to December 31, *i.e.* 199 days per year. Catches from May were not used for calculations due to prohibition of angling for predatory fish. It is impossible to catch all individuals of catfish from the locality on bait, thus it is practically impossible to reduce fish population to 0% of the previous size (Britton *et al.*, 2007). That is why our results show reduction to 10% as a terminal value.

Sampling campaigns in the reference reservoirs were conducted in 2017 in April 17–21, May 15–19 and July 17–21 in Římov Reservoir, and in May 22–26 and July 24–28 in Žlutice Reservoir.

Statistical analyses

Mark and Recapture calculations (Schnabel, 1938) were used to estimate the number of individuals in a population, *i.e.* population size in our study and reference sites:

$$N = \frac{\sum_{i=1}^{m} Mi\, Ci}{\sum_{i=1}^{m} Ri}$$

where N stands for population size, Mi for total number of previously marked animals at time i, Ci for number of individuals caught at time i, and Ri for number of marked animals caught at time i.

Survival rate of the catfish population per one visit (S) is calculated as:

$$S = \frac{\mathrm{N} - \mathrm{U_1}}{\mathrm{N}}$$

where U_1 is the catch per one visit calculated as the total number of catches within the month divided by 60, since catching effort applied in each month was equivalent to 30 visits of anglers with two rods.

Fishing mortality rate per one visit (z) was calculated as:

$$\mathrm{z} = -\ln \mathrm{S}$$

Efficiency of the catching differed during the year, thus z was calculated for each month separately (May, June-July, August, September and November). Values for the missing months were calculated as means of the previous and the following month.

The number of individuals in the population, with regard to mortality rate (caused by anglers or long-lines), was calculated as:

$$N_t = N_0 * e^{-z*E}$$

where N_0 stands for the number of individuals in the previous day, and E for expected catching effort in a given day (*i.e.* number of visit of anglers).

The decrease of the catfish population was modelled day by day in the fishing season for all sites. Natural mortality was considered as negligible in comparison to mortality caused by anglers, so we did not take it into consideration.

The mean cost of 1 kg of catfish sold as a live fish (7.5 €) was set in accordance with companies selling fish meat registered in The Czech Fish Farmers Association (www.cz-ryby.cz). A fishing licence in accordance with the Czech Fishing Union cost 44.5 € in 2017 and allows fishing in one region of the Czech Republic (CFU, 2017).

The effect of temperature and season on catfish catch rate was tested by general linear model (GLM), where lake identity was set as random factor.

Five variables– prey fish biomass (fish up to 2.5 kg weight), trophy (total Phosphorus), number of catfish in the water body, biomass of catfish in the water body and mean size of catfish– were used in a linear stepwise regression to identify the best model that explained catfish catch per 10 baits during a day, as determined by the lowest Akaike Information Criterion (AIC) value. All statistical analyses were conducted using R software version 3.4.2 (R Core Team, 2017).

Temperature

Water temperature was measured between 12:00 and 14:00 during the sampling campaign at each site. Measurements were made at 1 m depth intervals using a calibrated YSI 556 MPS probe (YSI Incorporated-Yellow Springs, Ohio, USA). The temperature of the epilimnion was used for the purpose of this study.

Results

Number of caught catfish, their lengths, weights and estimated size of their populations (individuals > 70 cm) in individual water bodies based on the Recapture method are summarized in Table 1.

Catch efficiency dependent on season

May (time before the opening of fishing season for predators in the Czech Republic) was the second most efficient month in both Milada and Most. The first half of the sampling campaign was more efficient than the second in both lakes. Water temperature ranged from 12.1 to 16.3°C during sampling in May (Fig 3). Catfish catch rate was significantly dependent on season (GLM, $F_{1,2} = 10.0$, $p<0.01$) contrary to temperature (GLM, $F_{1,1} = 0.8$, $p>0.05$). The most efficient time was June-July (water temperature 19.1–20.2°C). The mean efficiency was 2.8 and 5.4 individuals per 10 baits in one day for Milada and

Most, respectively. Efficiency of catching had a decreasing tendency in the following months, even in August when the water temperature was the highest (22.1–23.5 °C). In terms of the reference sites, the catch efficiency was 1.8 individuals per 10 baits in one day for Římov in April. In May it was 0.75 and 2.4 individuals per 10 baits in one day for Římov and Žlutice, respectively. In July it was 1.3 and 2.8 individuals per 10 baits in one day for Římov and Žlutice, respectively.

Parameters influencing the catfish catch

The most parsimonious model identified by stepwise linear regression for catfish catch per 10 baits during a day with the lowest AIC (Akaike information criterion) consisted of two parameters:

Catch . 10 baits^{-1}. Day $^{-1}$= 5.098* - 0.494 Mean length of catfish* + 0.177 Biomass of catfish

(AIC=-15.24, adj. R^2=0.988, p=0.063, length in mm, biomass in kg.ha^{-1}).

Asterisk indicates the significance levels at which the estimated parameters in the model formula differ from zero: * for $p < 0.05$. The model predicted a negative influence of mean size of catfish, and a positive effect of catfish biomass. The variables prey fish biomass, trophy and number of catfish in the locality were not chosen by the model. Model predictions closely matched observations with all observations falling in the 95% prediction confidence interval (Fig. 4).

Simulation of reduction of catfish population

In total, 3,582 bait-days would be needed to reduce the catfish population to 10% of the original size in Milada, *i.e.* 14.3 bait-days per 1 hectare. It corresponds to the visits of nine anglers each day during the entire season (Fig. 5a). If 20 anglers visited Milada each day, the catfish population would be reduced to 10% already on August 1, *i.e.* after 46 days of the fishing season.

In total, 4,776 bait-days would be needed to reduce the catfish population to 10% in Most, *i.e.* 15.4 bait-days per 1 hectare. It corresponds to the visits of 12 anglers each day during the entire season (Fig. 5b). If 20 anglers visited Most each day, the catfish population would be reduced to 10% already on August 21, *i.e.* after 66 days of the fishing season.

In terms of reference sites, 3,800 and 1,840 bait-days are needed to reduce the catfish population to 10% in Římov and Žlutice, respectively. It corresponds to 18 and 11 bait-days per 1 hectare in Římov and Žlutice, respectively. If 20 anglers visited Římov and Žlutice each day, the catfish population would be reduced to 10% after 95 and 46 days, respectively.

Economical analysis of catfish fishery

The pressure of anglers causing a reduction of the catfish population to 10% of the original size (daily visits of 9 and 12 anglers in Milada and Most, respectively) would represent a noticeable financial loss to the fishery. Comparing the income from licences and the costs of fish captured, the seasonal financial loss in Milada would be 10,295 € (41.2 € per ha) corresponding to 231 of sold annual fishing licences. The seasonal financial loss in Most would be 15,941 € (51.4 € per ha) corresponding to 358 of sold annual fishing licences.

At the beginning of the fishing season, each angler would catch on average 0.5 and 1.1 catfish per visit to Milada and Most, respectively. Considering the mean mass of catfish (8.2 kg and 4.1 kg in Milada and Most, respectively), it would correspond to an angler′s theoretical income of 30.75 € and 33.83 € per visit, which is 69% and 76% of the cost of the annual fishing licence. The fishing success would naturally quickly decrease depending on the visit rate and numbers of remaining catfish.

The cost of one multi hooks system used for long-line fishing (excluding bait fish) ranges from 5.5 € (medium quality) to 10 € (high quality) and a standard long-line contains 10 multi hooks systems. Its durability is between 5–11 of caught fish but the ideal time for replacement is after six caught fish. Thus profits from fish caught on one multi hooks system were 307.5–676.5 € and 153.8–338.3 € for Milada and Most, respectively.

Discussion

A new method for capturing catfish was described in this study. We evaluated its efficiency as a mechanism for catfish reduction. We compared it with angling and evaluated the financial impact of the issue. We focused on the benefits and threats connected with the presence of catfish depending on the locality.

Based on the Recapture method, the catfish population in Most was estimated at 576 individuals, this is 17% less than the total number of stocked individuals (694). Thus the estimation based on the Recapture method seems to be realistic considering the natural mortality of farmed and subsequently stocked fish (Copp *et al.*, 2009). Natural recruitment of catfish in Most Lake was not considered due to its short presence in the lake (3 years) and newly born individuals would not have reached sufficient length (Vejřík *et al.*, 2017b). Estimations of the catfish population in Milada, Žlutice and Římov were 186, 167 and 211, respectively. We assume that the estimations are as realistic as in the case of Most.

Access to anglers according to the rules of the Czech Fishing Union would cause a decrease in the catfish population to over 90% during the first season in both study sites. The consequences would be i) decrease of biomanipulation effect (Vejřík *et al.*, 2017b), ii) loss of ecologically stable population, and iii) substantial financial losses to the fishery (*ca*. 10,295 and 15,941 € in Milada and Most during the first fishing season, respectively). Basic economical calculations, taking into account cost of captured catfish versus cost of fishing licences, showed that this system would be unsustainable. Similar consequences can be expected for pike, the second biomanipulative species that is even easier to catch (Arlinghaus *et al.*, 2016b). As mentioned by Boulêtreau *et al.* (2016), different fish species vary in their reaction to attempts to recapture. For instance, hook avoidance induced by angling pressure was observed in brown trout (*Salmo trutta*; Young & Hayes, 2004) and in cod (*Gadus morhua*; Fernö & Huse, 1983). The opposite reaction was observed in white-spotted charr (*Salvelinus leucomaenis*), a caught and released wild individual was more likely to be caught than a fish never caught before (Morita & Tsuboi, 2004). The catchability of pike remained unaffected by previous captures with live baits (Beukema, 1970). The catchability of catfish seems to be either unaffected (Boulêtreau *et al.*, 2016), or to the contrary, it slightly increases with recapturing (Britton *et al.*, 2007; Boulêtreau *et al.*, 2016). The latter theory is also supported by the high frequency of recaptures in Most and Milada (32 and 34% respectively). Regarding the fact that catfish (Britton *et al.*, 2007) and pike (Beukema, 1970) do not react to angling pressure by hook avoidance and do not have timidity syndrome (Arlinghaus *et al.*, 2016) "Catch and Release" angling (Arlinghaus *et al.*, 2007a) practised by a part of the anglers would not ensure a sufficient number of predators. Most of the anglers in Central and Eastern

Europe still prefer taking the fish (Spurný *et al.*, 2017). Furthermore, the species is considered to be a culinary delicacy (Copp *et al.*, 2009). These reasons demonstrate that sustainable populations of predators including catfish in localities designed for recreational fishing can be maintained only with strict regulation of the angling and with regular stocking of new individuals (Johnston *et al.*, 2010). Thus the regular angling for predators should not be permitted in the post-mining lakes Milada and Most and in similar lakes that are newly appearing around Europe, nor in drinking water reservoirs such as Římov and Žlutice (Vašek *et al.*, 2013).

Wysujack and Mehner (2005) claimed that catfish is not efficient as a biomanipulative species. However their study is based on the diet of catfish of small sizes (mostly smaller than 80 cm), which is hardly sufficient considering the growth potential of this apex predator up to about 250 cm (Boulêtreau & Santoul, 2016). This is probably the reason why Vejřík *et al.* (2017b) presented entirely opposite results, *i.e.* clear impact of catfish on the whole fish community, including frequent consumption of large prey (up to ca. 70 cm and ca. 3 kg). The diet spectrum of catfish is wide, thus the entire fish community is affected by predation pressure which means more moderate pressure on a particular species (Syväranta *et al.*, 2010). Therefore, the high effect of biomanipulation provided by catfish may be achieved with a good-sized population (Vejřík *et al.*, 2017b). In contrast to other fish predators, catfish is able to maintain a high density in the ecosystem thanks to its low cannibalism (Vejřík *et al.*, 2017b), long lifespan (Copp *et al.*, 2009) and aggregations that have not been fully understood thus far but show gatherings of individuals that tolerate one another, this is not common for other predators (Boulêtreau *et al.*, 2011). Catfish is able to regulate practically the entire fish community thanks to its size (Boulêtreau & Santoul, 2016) and the width of its diet niche. Biomanipulation efficiency may be noticeably increased by a synergic predation effect, when pike and perch are the next predators present (Wasserman *et al.*, 2016).

Catfish is an invasive species in many areas located in Western and Southern Europe where it can affect native fish communities including endemic species (Copp *et al.*, 2009). Fast spreading is mediated mainly by anglers, even to localities with temperature-suboptimal conditions such as the United Kingdom (Britton *et al.*, 2007; Copp *et al.*, 2007), regardless of the fact that the spreading is illegal (Britton *et al.*, 2010a; Britton *et* *al.*, 2011). We can assume that the impact of catfish in localities such as the UK will be higher in the future due to increasing temperature caused by climate changes (Vejřík *et al.*, 2017a). According to available information, catfish probably presents the greatest threat in the Iberian Peninsula (Copp *et al.*, 2009; Almeida *et al.*, 2013). Catfish is an unwanted species also in Italy where it reaches maximum large sizes (Boulêtreau & Santoul, 2016). Therefore, release of catfish to aquatic ecosystems is forbidden by law (legge regionale n. 19 del 28 aprile 1998). Unfortunately, scientific results focusing on catfish impact in this locality are not available. In contrast, localities in France seem not to be negatively influenced so far, however long-term observations are necessary (Guilleraut *et al.*, 2015). When catfish is unwanted, the ability to extirpate a local population is practically impossible because catfish prefers large aquatic ecosystems with high connectivity (Britton *et al.*, 2010 b). However, a catfish population and its potential negative impact can be readily reduced by targeted capturing and thus intensive reduction of catfish abundance. 11–18 bait-days per 1 hectare are needed to reduce the local population of adult catfish to 10% of the original size (population size between 0.74 and 1.85 ind. ha^{-1}). Neither prey fish biomass, trophy, nor number of catfish in the locality had a significant impact on the catch efficiency. In contrast, the size of the catfish had a significant impact on the catch efficiency, as a small individual is more readily utilized than a large one. Further, efficiency increases with catfish biomass in a locality. Catfish populations in our study and reference sites are large in comparison to other aquatic ecosystems in the Czech Republic (Vašek *et al.*, 2013; Vejřík *et al.*, 2017a). The reasons are i) absence of anglers' activities and ii) man-mediated vast stocking programme at the study sites. Thus, we assume the presence of larger populations only in localities with more favourable conditions and with a warmer climate (Copp *et al.*, 2009). Unfortunately, estimates of total catfish populations in European localities are not available. However, catching effort intensified to 30–40 bait-days per one hectare for a year should be sufficient to reduce a catfish population to 10% of the original size in any European locality. Determination of the population size is necessary to calculate an accurate number of bait-days for a given locality. Spring and early summer seems to be the best time for the highest catch efficiency, *i.e.* time close to reproduction (Copp *et al.*, 2009). The efficiency decreases towards autumn and winter. Higher impact of season than temperature was statistically proved and was also assumed by Britton *et al.* (2007).

Anglers catching catfish in Western and Southern Europe commonly prefer the “Catch and Release“ method (Arlinghaus *et al.*, 2007a) in good faith to maximize welfare of fish (Arlinghaus *et al.*, 2007b). As such this capturing method can not be used for reduction of catfish populations. Consequently the catfish is still expanding its range and sizes of populations are increasing in Belgium, France, the United Kingdom and Spain despite fishing regulations aimed at the reduction of this species (Cucherrouset *et al.*, 2017).

We would recommend long-lines as an efficient method for catfish regulation for managing stakeholders in localities with unwanted presence of catfish. Because the long-lines efficiently reduce the number of predators in marine ecosystems (Cardinale *et al.*, 2015), it clearly must be even more efficient in much smaller freshwater ecosystems. Moreover, this was proved by our results. This method seems to be efficient also for other fish with similar body shape, such as burbot (*Lota lota*), where other capturing methods are not efficient (Blabolil *et al.*, 2017). Pressure provided by anglers or regulation by long-lines will not completely remove catfish from a locality. Nevertheless, the methods have substantial impacts on a catfish population from reduced abundance and biomass (Hutchings & Myers, 1994; Toresen & Østvedt, 2001), truncated age and size structure (Jørgensen, 1990), altered population genetic subdivision up to erosion of genetic diversity (Allendorf *et al.*, 2008). Therefore, the population is reduced down to a harmless level by these methods and the localities where catfish is invasive and unwanted will recover.

If we want to apply long-lines in the countries of the European Union, it is necessary to overcome the deep-rooted tradition that a lot of freshwater ecosystems serve only as an angling area and no other regulations are applied (Levin *et al.*, 2006). Further, the policy of each country will specify, whether ecologically sustainable management will be preferred opposed to the maintenance of hobby and relaxation facilities for many inhabitants, because big game fishing definitely provides satisfaction for anglers (Arlinghaus *et al.*, 2002; Matsumura *et al.*, 2011). Moreover, angling brings economical benefits thanks to the sale of licences and fishing equipment (Jørgensen *et al.*, 2007). We have to mention, that catfish can be beneficial in some cases in non-native localities, because it can reduce abundances of many other invasive species (Carol *et al.*, 2009). Thus an individual approach is necessary in each locality. Providing a study focused on catfish diet in the locality would be an ideal step before making a decision about catfish reduction or maintenance.

Acknowledgements

This study was supported by SoWa Research Infrastructure funded by MEYS CZ grant LM2015075, programme ‘‘Project of Large Infrastructure for Research, Development, and Innovations’’ and by European Regional Development Fund-Project „Research of key soil-water ecosystem interactions at the SoWa Research Infrastructure“, No. CZ.02.1.01/0.0/0.0/16_013/0001782. The work was also supported from ERDF/ESF project Biomanipulation as a tool for improving water quality of dam reservoirs (No. CZ.02.1.01/0.0/0.0/16_025/0007417). Further, it received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 677039" project CLIMEFISH. This publication reflects the views only of the authors, and the Commission cannot be held responsible for any use that may be made of the information contained therein. It was also supported by project No. 04-151/2016/P of the Grant Agency of the University of South Bohemia. We thank Ingrid Steenbergen for editing the English.

Authors contributions

L.V. conceived the project and designed the methodology, P.B. and J.K. conducted the statistical analysis, L.V., P.B. and Z.S. did the figures, L.V., L.K., Z.S., M.Š., T.J., P.B., D.B., I.V. and J.P. collected field data, J.P. and J.K. provided financial support, L.V., I.V., M.Č. and P.B. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Data will be available on request of the editor.

References

Allan, J. D., Abell, R., Hogan, Z., Revenga, C., Taylor, B. V., Welcomme, L. R. & Winemiller, K. O. (2005). Overfishing of inland waters. *BioScience*, 55, 1041–1051.

Almeida, D., Ribeiro, F., Leunda, P. M., Vilizzi, L. & Copp, G., H. (2013). Effectiveness of FISK, an invasiveness screening tool for non-native freshwater fishes, to perform risk identification assessments in the Iberian Peninsula. *Risk Analysis*, 33, 8.

Alp, A., Kara, C. & Buyukcapar, H. M. (2003). Reproductive biology in a native European catfish, *Silurus glanis* L., 1758, Population in Menzelet Reservoir. *Turkish Journal of Veterinary and Animal Science*, 28, 613–622.

Arlinghaus, R., Mehner, T. & Cowx, I. G. (2002). Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries*, 3, 261–316.

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C.,... Thorstad E. B. (2007a). Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science*, 15, 75–167.

Arlinghauss, R., Cooke, S. J., Schwab, A. & Cowx, I. G. (2007b). Fish welfare: a challenge to the feelings-based approach, with implications for recreational fishing. *Fish and Fisheries*, 8, 57–71.

Arlinghaus, R., Beardmoer, B., Riepe, C., Meyerhoff, J. & Pagel, T. (2014). Species-specific preferences of German recreational anglers for freshwater fishing experiences, with emphasis on the intrinsic utilities of fish stocking and wild fishes. *Journal of Fish Biology*, 85, 1843–1867.

Arlinghaus, R., Alós, J., Krefoth, T., Laskowski, K. L., Monk, C. T., Nakayama, S. & Schröder, A. (2016). Consumptive tourism causes timidity, rather than boldness, syndromes: a response to Geffroy. *Trends in Ecology and Evolution*, 31, 92–94.

Arlinghaus, R., Alós, J., Pieterek, T. & Klefoth, T (2016b). Determinants of angling catch of northern pike (*Esox lucius*) as revealed by a controlled whole-lake catch-and-release angling experiment—The role of abiotic and biotic factors, spatial encounters and lure type. *Fisheries Research*, 186, 648–657.

Beukema, J. J. (1970). Acquired hook-avoidance in the pike *Esox lucius* L. fished with artificial and natural baits. *Journal of Fish Biology*, 2, 155–60.

Blabolil, P., Boukal, D. S., Ricard, D., Kubečka, J., Říha, M., Vašek, M.,... Peterka, .J. (2017). Optimal gillnet sampling design for the estimation of fish community indicators in heterogeneous freshwater ecosystems. *Ecological Indicators*, 77, 368–376.

Boulêtreau, S., Cucherousset, J., Villéger, S., Masson, R. & Santoul, F. (2011). Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. *PLoS ONE* 6, e25732.

Boulêtreau, S. & Santoul, F. (2016). The end of the mythical giant catfish. *Ecosphere*, 7(11), e01606.

Boulêtreau, S., Verdeyroux, P., Lorthiois, E., Azémar, F., Compin, A., & Santoul, F. (2016). Do you eat or not? Predation behaviour of European catfish (*Silurus glanis*) toward live bait on a hook. *The Open Fish Science Journal*, 9, 8–14.

Britton, J. R., Pegg, J., Sedgwick, R. & Page, R. (2007). Using mark–recapture to estimate catch rates and growth of the European catfish *Silurus glanis* in a recreational fishery. *Fisheries Management and Ecology*, 14, 263–268.

Britton, J. R., Cucherousset, J., Davies, G. D., Godard, M. J. & Copp G. H. (2010a). Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshwater Biology*, 55(5), 1130–1141.

Britton, J. R., Davies, G. D. & Brazier, M. (2010b). Towards the successful control of the invasive *Pseudorasbora parva* in the UK. *Biological Invasions*, 12(1), 125–131.

Britton, J. R., Gozlan, R. E. & Copp, G. H. (2011). Managing non native fish in the environment. *Fish and Fisheies*, 12, 256–274.

Cadrin, S. X. & Pastoors, M. A. (2008). Precautionary harvest policies and the uncertainty paradox. *Fisheries Research*, 94, 367–372.

Cardinale, M., Bartolino, V., Svedäng, H., Sundelöf, A., Poulsen, R. T. & Casini, M. (2015). A centurial development of the North Sea fish megafauna as reflected by the historical Swedish longlining fisheries. *Fish and Fisheries*, 16 (3), 522–533.

Carol, J., Zamora, L. & García-Berthou, E. (2007). Preliminary telemetry data on the movement patterns and habitat use of European catfish (*Silurus glanis*) in a reservoir of the River Ebro, Spain. *Ecology of Freshwater Fish*, 16, 450–456.

Carol, J., Benejam, L., Benito, J. & Garcia-Berthou, E. (2009). Growth and diet of European catfish (*Silurus glanis*) in early and late invasion stages. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, 174, 317–328.

CEN (2015). Water Quality _ Sampling of fish with multimesh gillnets. European Committee for Standardization, EN 14757, Brussels.

CFU (2017). Fishing regulations of the Czech Fishing Union. https://www.rybsvaz.cz/?page=rybarsky_rad&lang=cz&fromIDS=&rybarsky_rad_rok=2017

Copp, G. H., Moffatt, L. & Wesley, K. J. (2007). Is European catfish *Silurus glanis* really becoming more abundant in the River Thames? *Aquatic Invasions*, 2, 113–116.

Copp, G. H., Britton, R., Cucherousset J., García-Berthou, E., Kirk, R., Beeler, E. & Skaténas, S. (2009) Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries*, 10, 252–282.

Cucherousset, J., Boulêtreau, S., Azémar, F., Compin, A. & Guillaume, M. (2012). “Freshwater Killer Whales”: beaching behavior of an alien fish to hunt land birds. *PLoS ONE*, 7, e50840.

Cucherousset, J., Horký, P., Slavík, O., Ovidio, M., Arlinghaus, R., Bouletreau, S.,... Santoul, F. (2017). Ecology, behaviour and management of the European Catfish. *Reviews in Fish Biology and Fisheries*, https://doi.org/10.1007/s11160-017-9507-9.

Cunico, A. M. & Vitule, J. R. S. (2014). First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). *BioInvasions Records*, 3 (2), 117–122.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Léveque C., … Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, 81, 163–182.

Fernö, A. & Huse, I. (1983). The effect of experience on the behaviour of cod (*Gadus morhua* L.) towards a baited hook. *Fisheries Research*, 2, 19–28.

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R. & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13, 1055–1071.

Frank, K. T., Petrie, B., Choi, J. S. & Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308, 1621–1623.

Guillerault, N., Delmotte, S., Bouletreau S., Lauzeral C., Poulet N. & Santoul, F. (2015). Does the non-native European catfish *Silurus glanis* threaten French river fish populations? *Freshwater Biology*, 60, 922–928.

Hunt, L. (2005). Recreational fishing site choice models: insights and future opportunities. *Human Dimensions of Wildlife*, 10, 153–172.

Hutchings, J. A. & Myers, R. A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 2126–2146.

Hutt, C. P., Hunt, K. M., Schlechte, J. W. & Buckmeier, D. L. (2013). Effects of catfish angler catch-related attitudes on fishing trip preferences. *North American Journal of Fisheries Management*, 33, 965–976.

Johnston, F. D., Arlinghaus, R. & Dieckman, U. (2010). Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. *Canadian Journal of Fisheries and Aquatic Science*, 60, 1507–1531.

Jørgensen, T. (1990). Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil International pour l'Exploration de la Mer*, 46, 235–248.

Jørgensen, C., Enberg, K., Dunlop, E. S.,Arlinghaus, R., Boukal, B., Brander, K., … Rijnsdorp, A. D. (2007). Managing evolving fish stocks. *Science,* 318, 1247–1248.

Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M. H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638.

Last, P. R., White, W. T., Gledhill, D. C., Hobday, A. J., Brown, R., Edgar, G. J. & Pecl, G. (2011). Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography,* 20, 58–72.

Laugen, A. T., Engelhard, G. H., Whitlock, R. Arlinghaus, R., Dankel, D. J., Dunlop, E. S.,… Dieckmann, U. (2014). Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish and Fisheries,* 15, 65–96.

Lewin, W. C., Arlinghaus, R. & Mehner, T. (2006). Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science,* 14, 305–367.

Linhart, O., Štech, L., Švarc, J., Rodina, M., Audebert, J. P.,Grecu, J. & Billard, R. (2002). The culture of the European catfish, *Silurus glanis,* in the Czech Republic and in France. *Aquatic Living Resources,* 15, 139–144.

Matsumura, S., Arlinghaus, R. & Dieckmann, U. (2011). Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*). *Evolutionary Ecology,* 25, 711–735.

Morita, K. & Tsuboi, J. (2004). Selectivity effects on wild white-spotted charr (*Salvelinus leucomaenis*) during a catch and release fishery. *Fisheries Research*, 69, 229–238.

Mullon, C., Fréon, P. & Cury, P. (2005). The dynamics of collapse in world fisheries. *Fish and Fisheries*, 6, 111–120.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315, 1846–1850.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolutions*, 10, 430.

Post, J. R., Sullivan, M., Cox, S., Lester, N., Walters, C. J., Parkinson, E. A. & Shuter, B. J. (2002). Canada's recreational fisheries: The invisible collapse? *Fisheries*, 27, 6–17.

Prugh, R. L., Stone, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S. & Brashares, J. S. (2009). The rise of the mesopredator. *BioScience*, 59, 779–791.

Ripple, W. J., Estes, J. A., Beschta, L. R., Wilmers, C. C., Ritchie, E. G., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.

Robinson, L. A. & Frid, C. L. J. (2003). Dynamic ecosystem models and the evaluation of ecosystem effects of fishing: can we make meaningful predictions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 13, 5–20.

Schnabel, Z. E. (1938). To estimation of the total fish population of a lake. *American Mathematical Monthly* 45:348–352. In: Amstrup, S. C., McDonald, T. L. & Manly, J. F. (2005) Handbook of Capture-Recapture Analysis. *Princeton*, 313 pp.

Sienkiewicz, E. & Gasiorowski, M. (2017). The diatom-inferred pH reconstructions for a naturally neutralized pit lake in south-west Poland using the Mining and the Combined pH training sets. *Science of the total environment*, 605–606, 75–87.

Sinclar, A. R. E., Mduma, S. & Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature*, 425, 288–290.

Spurný, P., Mareš, J., Kopp, R., Grmela, J., Mareš, L. & Malý, O. (2017). Socioekonomická studie sportovního rybolovu v České republice. Mendelova univerzita v Brně 40pp. (Only in Czech).

Stone, R. (2007). The last of the Leviathans. *Science*, 316, 1684–1688.

Syväranta, J., Cucherousset, J., Kopp, D., Crivelli, A., Céréghino, R. & Santoul, F. (2010). Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. *Aquatic Biology*, 8, 137–144.

Toresen, R. & Østvedt, O. J. (2001). Norwegian spring-spawning herring (*Clupea harengus*) and climate throughout the twentieth century. In: *University of Alaska Sea Grant College Program Report. Herring: Expectations for a new millennium*. (eds F. Funk, J. Blackburn, D. Hay, A. J. Paul, R. Stephenson, R. Toresen, D. Witherell), pp. 279–284.

Vašek, M., Kubečka, J., Čech, M., Draštík, V., Matěna, J., Mrkvička, T., … Prchalová, M. (2009). Diel variation in gillnet catches and vertical distribution of pelagic fishes in a stratified European reservoir. *Fisheries Research*, 96, 64–69.

Vašek, M., Prchalová, M., Peterka, J., Ketelaars, H.A.M., Wagenvoort, A. J., Čech, M., … Kubečka, J. (2013). The utility of predatory fish in biomanipulation of deep reservoirs. *Ecological Engineering*, 52, 104–111.

Veit, R. R., Mcgowan, J. A., Ainley, D. G., Wahl, T. R. & Pyle, P. (1997). Apex marine predator declines ninety percent in association with changing oceanic chmate. *Global Change Biology*, 3, 23–28.

Vejřík, L., Vejříková, I., Kočvara, L., Sajdlová, Z., Chung, S. H. T., … Čech, M. (2017a). Thirty-year-old paradigm about unpalatable perch egg strands disclaimed by the freshwater top-predator, the European catfish (*Silurus glanis*). *PLoS ONE*, 12(1), e0169000.

Vejřík, L., Vejříková, I., Blabolil, P., Eloranta, A. P., Kočvara, L., Peterka, J., … Čech, M. (2017b). European catfish *(Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability. *Scientific Reports*, 7, 15970.

Vejříková, I., Vejřík, L., Syväranta, J., Kiljunen, M., Čech, M., Vašek, M.,... Peterka, J. (2016). Distribution of herbivorous fish is frozen by low temperature. *Scientific Reports*, 6, 39600. doi: 10.1038/srep39600

Wysujack, K. & Mehner, T. (2005). Can feeding of European catfish prevent cyprinids from reaching a size refuge? *Ecology of Freshwater Fish*, 14, 87–95.

Wasserman, J. R., Alexander, M. E., Dalu, T., Ellender, B. L., Kaiser, H. & Weyl, O. L. (2016). Using functional responses to quantify interaction effects among predators. *Functional Ecology*, 30, 1988–1998.

Young, R. G. & Hayes, J. W. (2004). Angling pressure and trout catchability: behavioral observations of Brown trout in two New Zealand backcountry rivers. *North American Journal of Fisheries Management*, 24, 1203–1213.

Locality	Estimated size of the population	Ind. ha^{-1}	Biomass ha^{-1}	Mean mass (kg)	Mean length (cm)	No. of caught individuals	No. of recaptures
Milada	186	0.74	6.1	8.2	103	93	37
Most	576	1.85	7.6	4.1	85	232	74
Římov	211	1.00	11.8	11.7	116	47	3
Žlutice	167	1.04	8.5	8.2	102	57	6

Table 1. Abundance, biomass and mean size of catfish (individuals > 70 cm captured by long-lines) based on the Recapture method and number of recaptured individuals in Milada and Most Lakes, and Římov and Žlutice Reservoirs.

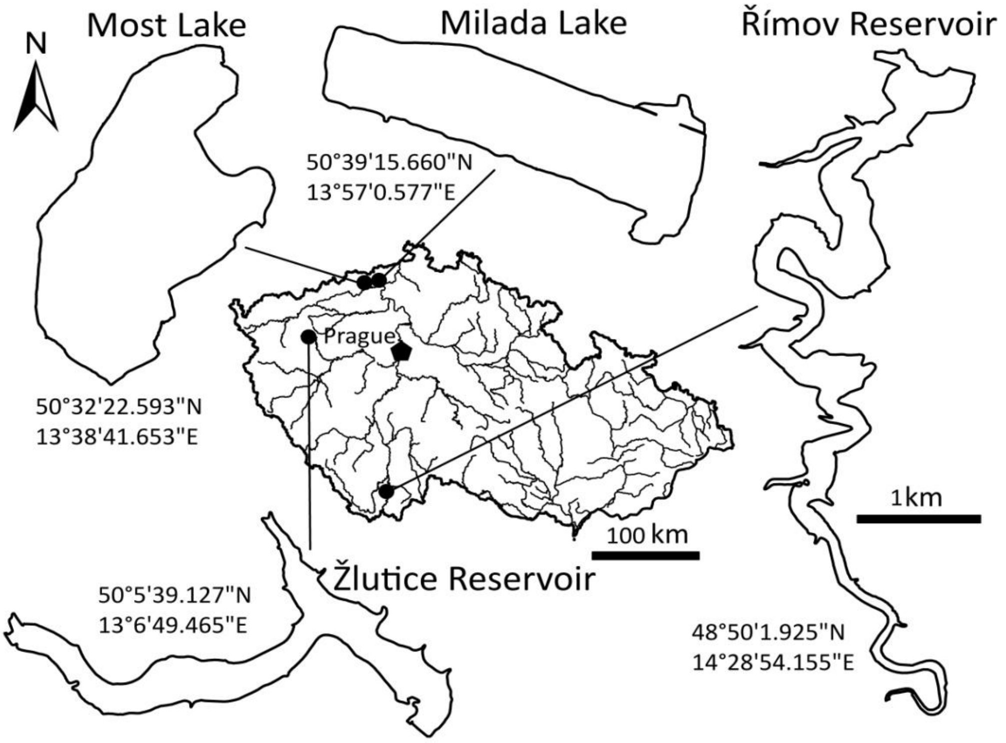

Figure 1. Study sites with GPS locations marked in the map of the Czech Republic (capital: Prague).

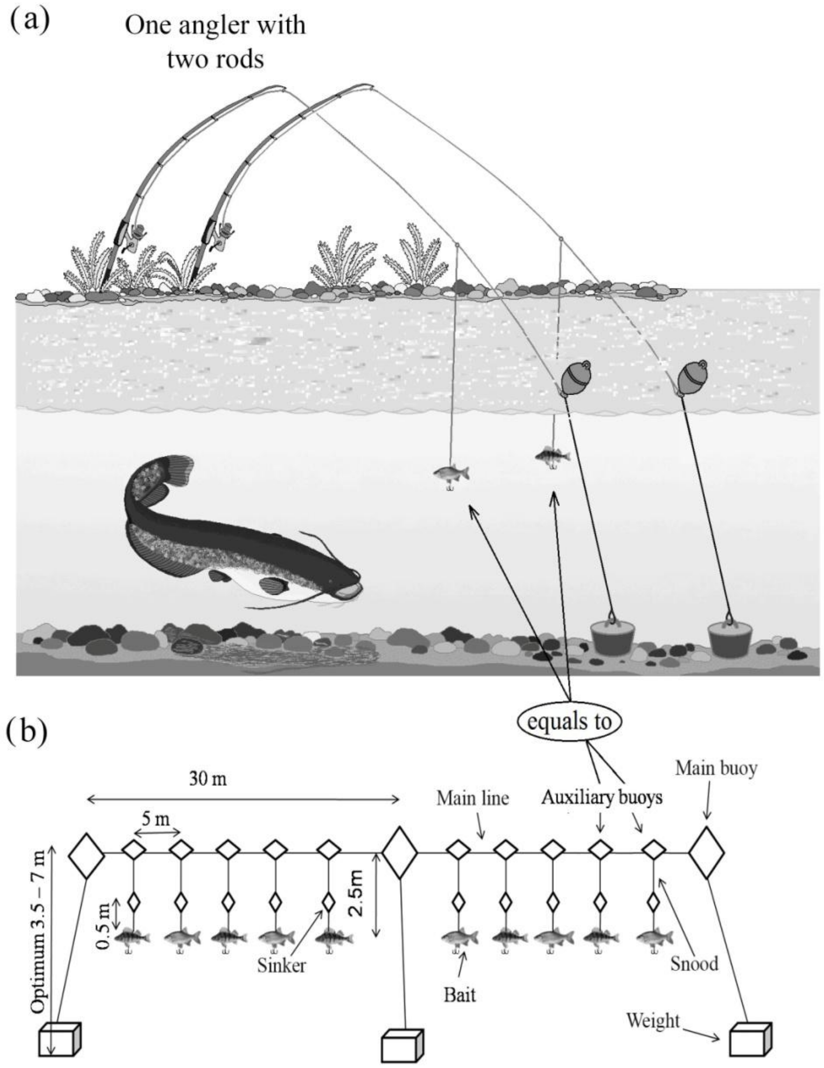

Figure 2. a) Catching efficiency of one angler with two rods (a) was simulated by the method of long-lines illustrated in the scheme b). Long-lines were used for capturing catfish in Milada and Most Lakes, and Římov and Žlutice Reservoirs.

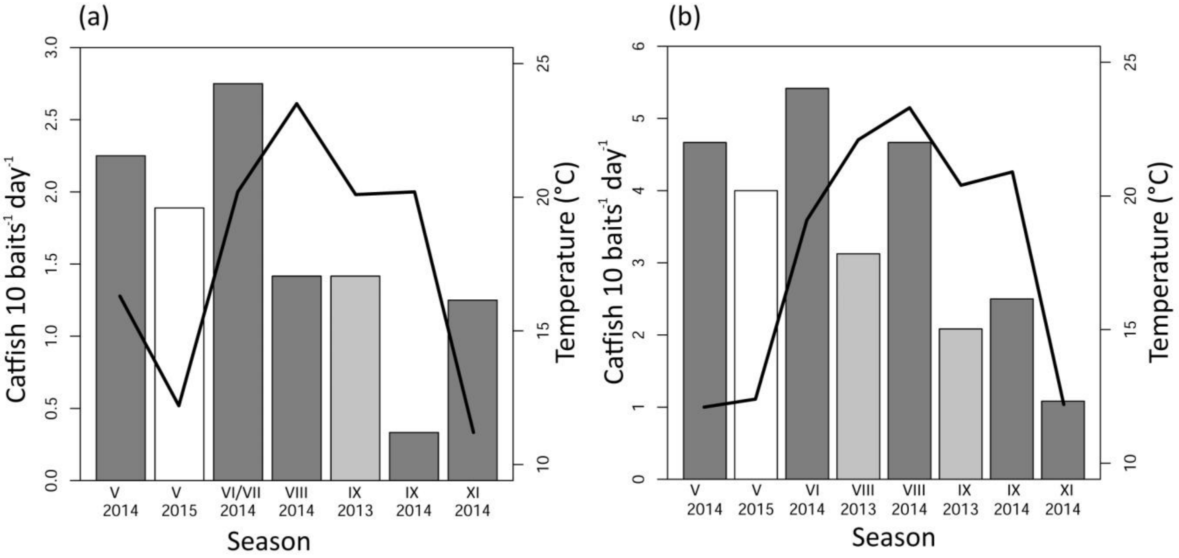

Figure 3. Catch efficiency of long-lines (catfish 10 baits^{-1} day^{-1}) for different months in years 2013 (light grey), 2014 (grey) and 2015 (white) in a) Milada and b) Most. Mean temperature of the epilimnion is represented by a curve.

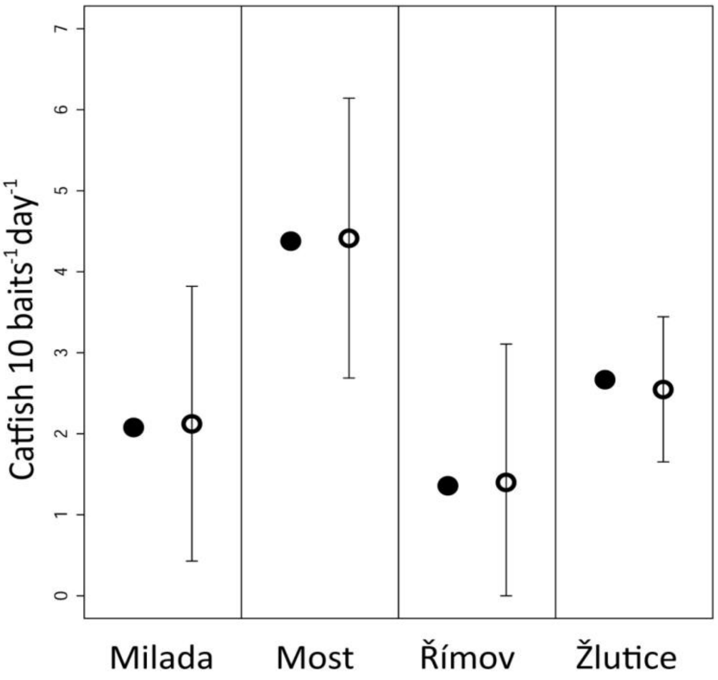

Figure 4. Comparison of observed catfish catch per 10 baits during a day (black dots) and model predictions (empty dots) with 95% confidence interval (error bars) in all study and reference sites.

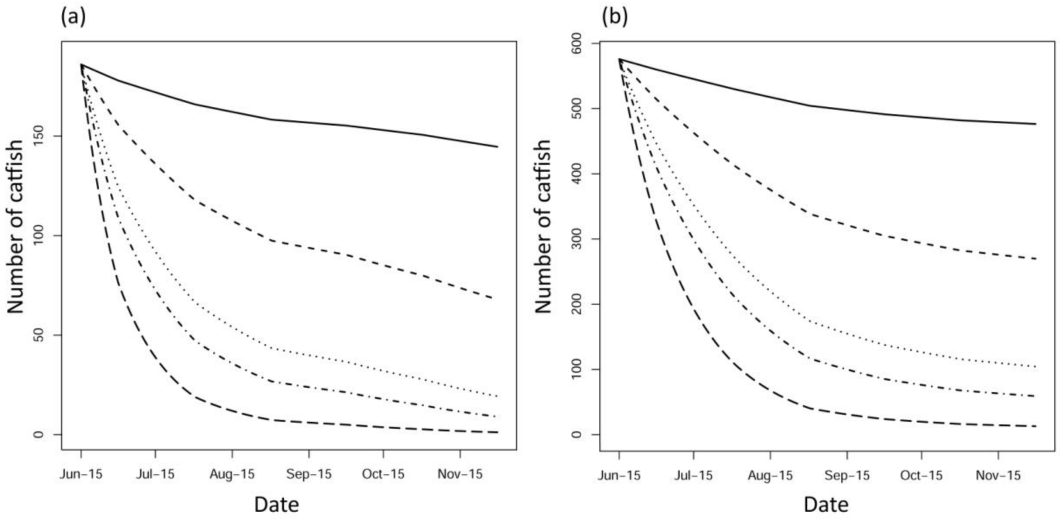

Figure 5. Modelled impact of anglers on the catfish populations in a) Milada and b) Most Lakes within one season depending on daily visit rate. The model demonstrates visits of one angler (solid line), three (dashed line), five (dotted line), eight (dot-dashed line), and 12 anglers for Milada and 20 anglers for Most (bold dashed lines). The last bold dashed lines correspond to number of anglers causing decrease of catfish population to 10% of the original size within one fishing season.

Paper II

European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability

SCIENTIFIC REPORTS

European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability

Received: 29 June 2017
Accepted: 8 November 2017

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Apex predators play a key role in ecosystem stability across environments but their numbers in general are decreasing. By contrast, European catfish (*Silurus glanis*), the European freshwater apex predator, is on the increase. However, studies concerning apex predators in freshwaters are scarce in comparison to those in terrestrial and marine ecosystems. The present study combines stomach content and stable isotope analyses with diet preferences of catfish to reveal its impact on the ecosystem since stocking. Catfish niche width is extremely wide in comparison to the typical model predator, Northern pike (*Esox lucius*). Catfish and pike have different individual dietary specialization that results in different functional roles in coupling or compartmentalizing distinct food webs. The role of both species in the ecosystem is irreplaceable due to multiple predator effects. The impact of catfish is apparent across the entire aquatic ecosystem, but herbivores are the most affected ecological group. The key feature of catfish, and probably a common feature of apex predators in general, is utilization of several dietary strategies by individuals within a population: long-term generalism or specialization and also short-term specialization. Catfish, similar to other large-bodied apex predators, have two typical features: enormous generalism and adaptability to new prey sources.

Large-bodied apex predators play a key role in community dynamics and ecosystem stability[1–3] due to their generalist foraging strategy on prey at different trophic levels and from different habitats[4–7]. In essence, these consumers tend to incorporate energy from a wide range of prey taxa and thereby often link multiple energetic pathways[8–10].

The difference among particular species of apex predators is whether all individuals are true generalists or whether they form specialized subpopulations[5,11] or even display individual niche specialization (INS)[12]. The wide diet plasticity of apex predators is driven by the requirement to satiate their large body and also by their ability to learn to utilize new food sources[13].

Therefore, the niche width of each apex predator is extremely broad[3,4]. Generalism of apex predators far exceeds dietary habits of other mesopredators in terrestrial[4] and marine ecosystems[6,14]. Thus the presence of apex predators influences lower situated members of food webs including mesopredators[3,7,15]. Decline or disappearance of an apex predator in an ecosystem causes a cascade effect of changes[2,16,17]. E.g. mesopredators can step in to the role of apex predator[15]. Nevertheless, a mesopredator has size and hunting limitations in comparison to an apex predator, and can therefore have a negative impact on ecosystem stability[18]. Therefore, understanding the role and potential impacts of apex predators is essential for management and protection of freshwaters that provide vital ecosystem services and contribute disproportionally to the global biodiversity[19]. Recently, numbers of apex predators have decreased in terrestrial[1,3], marine[16,20,21] and also in freshwater ecosystems[7,19,22]. The impact of the decline of apex predators is a topical ecological problem and has been widely studied[3]. However, comprehensive studies concerning the changes in freshwater ecosystems caused by the decline of apex predators are lacking. Global triggers inducing the trend of decline are climate changes[20], overexploitation and/or other anthropogenic

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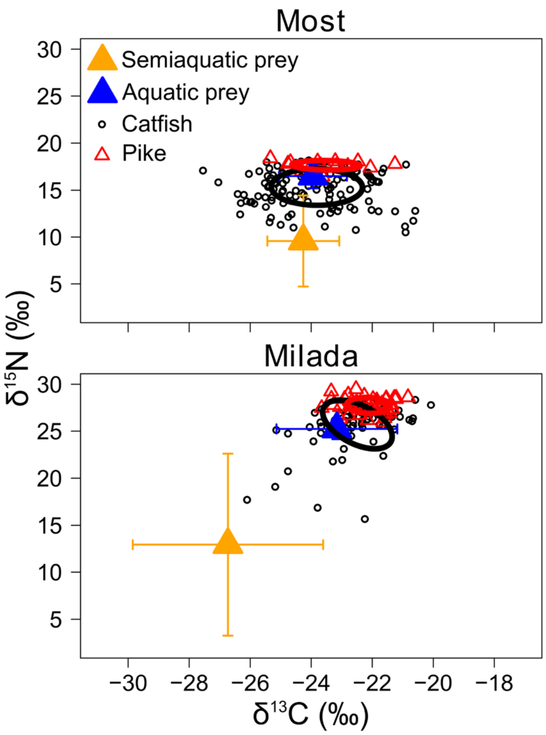

Figure 1. The δ^{13}C and δ^{15}N values of individual fish (muscle tissue) and the estimated isotopic niches of catfish (black) and pike (red) in Milada and Most lakes, illustrated as sample-size-corrected *SEA*c ellipse areas[36]. The mean ± SD δ^{13}C and δ^{15}N values of putative semiaquatic and aquatic food resources are also shown.

impacts[3,21]. Contrary to general apex predator decline, European catfish (*Silurus glanis*) metapopulation size and distribution range has increased in recent decades[23]. It is the largest freshwater fish in Europe and the third largest in the world (it reaches 2.7 m and 130 kg)[22,23]. The increase in number and dispersion to new localities is mainly induced by human activity[23–25]. Studies about European catfish focus mainly on diet specifications[26–28] or they are regional and only describe one characteristic (see review[23]). But the question about their role in an ecosystem, whether it is a key apex predator or not, has not been addressed yet. The main reason for the absence of studies dealing with European catfish is due to difficulties connected with capturing of this fish[29]. Due to the scarcity of information concerning this species, several myths about its unprecedented appetite have appeared among anglers and even among scientists[30,31].

The main goal of this study was to reveal whether catfish represents a true apex predator with some features known from terrestrial and marine ecosystems in spite of the structural and functional differences between these ecosystems and between life cycles of their species[3,10,15]. Attention has been paid whether it is a generalist species with broad dietary strategies, that stands above other members of the food web. We compared European catfish with Northern pike (*Esox lucius*), as it is a well-studied freshwater fish species and it is often used as a model predator in studies from freshwaters[32]. Pike is an ideal reference species because it is a high-level freshwater predator, the second biggest fish predator in Europe (it reaches 130 cm and over 25 kg), and it also has the widest extent of distribution in freshwaters[33].

The second goal was to use stable isotope analysis (SIA) of recaptured individuals and stomach content analysis of European catfish and Northern pike to fully understand dietary strategies and degree of specialization of these two freshwater predators. We investigated whether they exhibit individual trophic specialization and whether it is a short-term (seasonal) or a long-term specialization[10]. We focused on the total niche width of European catfish and Northern pike, and on the food origin, whether they utilize food sources only from the aquatic food web[7,35,36].

Last goal was to assess the impact of apex predators on lower-level members of the food web based on their diet preferences and long-lasting monitoring of fish communities in two study lakes and in the reference lake with similar fish community including pike but with absence of catfish in the system.

Results

Characterization of food webs, niche width and patterns of individual specialization. In both lakes, the semiaquatic vertebrates were isotopically distinct from aquatic food sources due to lower $\delta15$ N values (Fig. 1). However, differences in isotopic signatures of the semiaquatic and aquatic prey in Most Lake were smaller ("average differences here for both isotopes") than in Milada Lake ("average differences here for both isotopes") (Fig. 1), probably resulting SIAR (Stable Isotope Analysis in R) results for Most Lake to be slightly more diffused in contrast to Milada Lake (Fig. 2). The results from SIAR isotopic mixing model indicated that in both lakes, catfish utilized more semiaquatic vertebrates (mammals, frogs and birds) than pike (Fig. 2). Semiaquatic prey

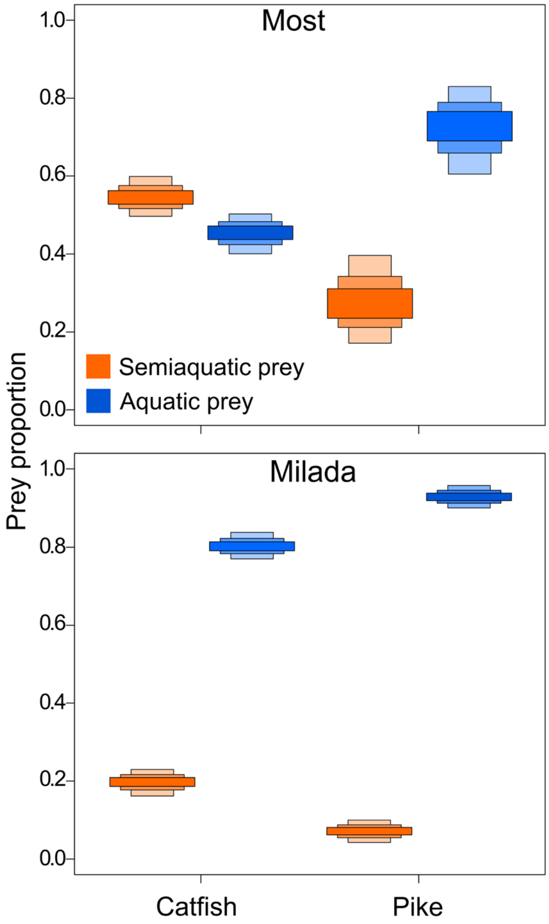

Figure 2. Relative contribution of semiaquatic and aquatic food resources in the long-term diets of catfish and pike in Most and Milada lakes. The boxes indicate the 95, 75 and 50% Bayesian credibility intervals for estimates based on SIAR model (Stable Isotope Analysis in R; version 4.2;[36]) isotopic mixing model.

Lake	Species	*SEA*	SEA_c	*TA*	SEA_c overlap
Most	Catfish	9.1	9.2	41.9	0.01
Most	Pike	1.7	1.9	3.9	
Milada	Catfish	8.0	8.2	48.9	0.07
Milada	Pike	1.9	2.0	6.9	

Table 1. Estimated isotopic niche widths of European catfish and pike in Most and Milada lakes, based on SIBER (Stable Isotope Bayesian Ellipses in R) estimates of standard ellipse (*SEA* and SEA_c) and total convex hull (*TA*) areas (for details see[35]). The SEA_c overlap indicates the proportional overlap between the sample-size corrected ellipse areas and hence the degree of niche segregation between European catfish and pike.

were a particularly important food for catfish in Most Lake (SIAR 95% credibility intervals: 50–61%) and to lesser extent in Milada Lake (SIAR 95% credibility intervals: 18–23%). In contrast, SIAR indicates that semiaquatic prey is not such an important food source for pike. In Most Lake, pike seem to feed on semiaquatic prey in some extent (SIAR 95% credibility intervals: 18–40%), but the contribution of semiaquatic prey is apparently low in Milada Lake (0–10%; Fig. 2).

In both lakes, the SIBER (Stable Isotope Bayesian Ellipses in R) results indicated a markedly (3–11 times) wider long-term dietary niche for catfish compared to pike (Table 1, Fig. 1). The wider isotopic niche of catfish was due to large individual variation in both carbon sources (δ^{13}C) and estimated trophic position (δ^{15}N). In both lakes, catfish individuals with exceptionally low δ^{15}N values were likely specialized on semiaquatic prey, whereas individual fish with high δ^{15}N values were probably specialized on piscivorous diets, possibly including also conspecifics.

The minor (1–7%) overlap between the SEA_c (corrected standard ellipse areas) isotopic niche areas (Table 1) indicate significant niche segregation between the species, with catfish occupying a "lower trophic position" (due to utilization of semiaquatic vertebrates, on average 2.0–2.3‰ lower δ^{15}N) than pike in both lakes (Most: $t = -10.6$, $df = 73.2$, $p < 0.001$; Milada: $t = -5.9$, $df = 92.5$, $p < 0.001$). No notable differences were found in

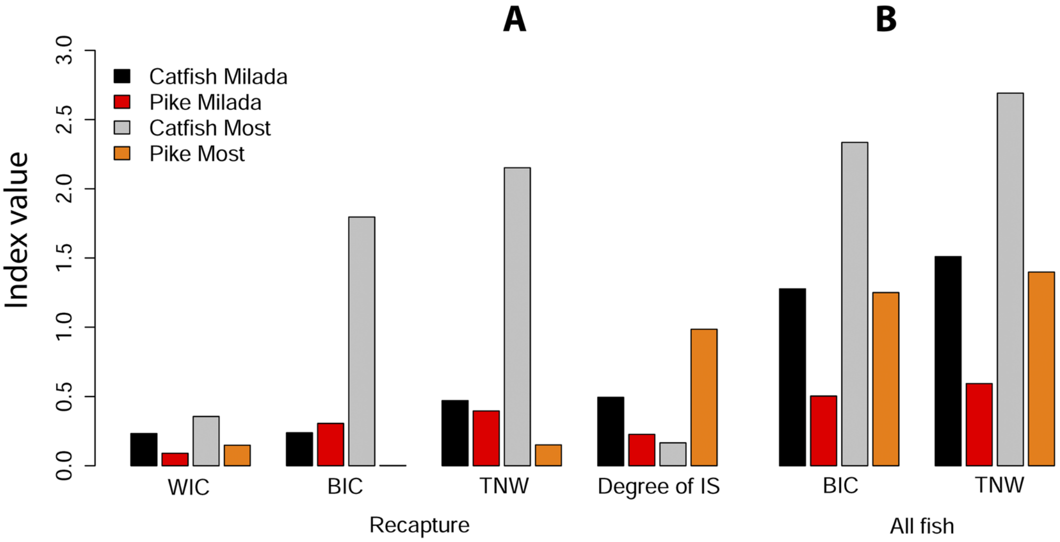

Figure 3. Total niche width (TNW) of catfish and pike population in Most and Milada lakes divided into two components: within-individual component (WIC) and between-individual component (BIC). Degree of individual specialization (IS) ranging from 0 to 1 shows whether each individual in a population utilizes the whole niche width of the population (then IS = 1). The calculations were provided for (**A**) recaptured individuals and for (**B**) all captured individuals.

carbon sources, although catfish had slightly (on average 0.4‰) lower $\delta^{13}C$ values than pike in Milada Lake (Most: $t = -0.9$, $df = 18.7$, $p = 0.370$; Milada: $t = -2.0$, $df = 1105.3$, $p = 0.044$).

According to analysis in Ind Spec programme based on $\delta^{13}C$, total niche width (TNW) of catfish in both lakes was approximately twice as high as that of pike. Moreover, TNW in Most with less potential food sources was twice as high as that in Milada, when considering all sampled individuals (Fig. 3). Similarly, the within individual component of variation (WIC) of catfish was 2.5 times higher than that of pike in both lakes and also higher in Most than in Milada for both species. The degree of individual specialization (IS) was 0.17 and 0.49 for catfish in Most and Milada Lakes, respectively. In terms of pike, the degree of IS was unexpectedly high in Most (0.98; but the value was probably biased by the low number of recaptures), and half the value in Milada (0.23) in comparison to catfish in Milada (Fig. 3).

Diet composition according to stomach content analysis and seasonal specialization. The prey fishes found in catfish stomachs included one herbivorous species (rudd: *Scardinius erythrophthalmus*), four omnivorous species (roach *Rutilus rutilus*, tench *Tinca tinca*, ruffe *Gymnocephalus cernuus* and whitefish *Coregonus* sp.), three species that we may call mesopredators (perch *Perca fluviatilis*, asp *Aspius aspius*, and pike) and European catfish itself indicating cannibalism. Among semiaquatic vertebrates, there were found five species of birds (great cormorant *Phalacrocorax carbo*, great crested grebe *Podiceps cristatus*, coot *Fulica atra*, great black-backed gull *Larus marinus*, and reed warbler *Acrocephalus scirpaceus*), two species of amphibians (marsh frog *Rana ridibunda* and edible frog *Rana esculenta*) and one species of mammal living on the shoreline (European water vole *Arvicola terrestris*). Among aquatic invertebrates, there were found spiny-cheek crayfish (*Orconectes limosus*) and larvae of Emperor dragonfly (*Anax imperator*).

In Most Lake, 72% of catfish had an empty stomach, 10% had our bait and 18% had their actual diet. Altogether, 65 food items were found in the catfish diet from Most Lake. It consisted of seven fish species, five species of waterfowl, one species of aquatic mammal, two species of amphibians, and perch egg strands. In Milada Lake, 40% of catfish had an empty stomach, 6% had our bait and 54% had their actual diet. Altogether, 117 food items were found in the catfish diet from Milada Lake. It consisted of eight fish species, two species of waterfowl, one species of aquatic mammal, two species of invertebrates, perch egg strands, and unidentified macrophytes. The mass ratio and percentage ratio of each food item in catfish diet is shown in Fig. 4.

Seasonal preferences for certain food sources were observed in catfish diet in both lakes. We found 63, 66 and 53 food items in catfish stomachs during spring, summer and autumn, respectively. Perch egg strands were found only during the perch spawning period in spring ($\chi^2 = 36.62$, $p < 0.001$). Aquatic invertebrates (crayfish and dragonfly larvae) were fully absent during spring and were present mainly during summer ($\chi^2 = 58.20$, $p < 0.001$; Fig. 5). In contrast, the contribution of omnivorous fish was the lowest during summer ($\chi^2 = 22.13$, $p < 0.001$ (Fig. 5) and the highest during spring (corresponding to the roach mass spawning period). Particularly in Most Lake in 2015, roach composed 88% of all food items found in catfish stomachs. Herbivorous fish were preferred particularly in spring and ignored in autumn, but neither was significant ($\chi^2 = 4.53$, $p > 0.05$). Differences in the contribution of mesopredators ($\chi^2 = 2.28$, $p > 0.05$) and semiaquatic vertebrates ($\chi^2 = 1.05$, $p > 0.05$) in catfish diet among seasons were not statistically significant (Fig. 5).

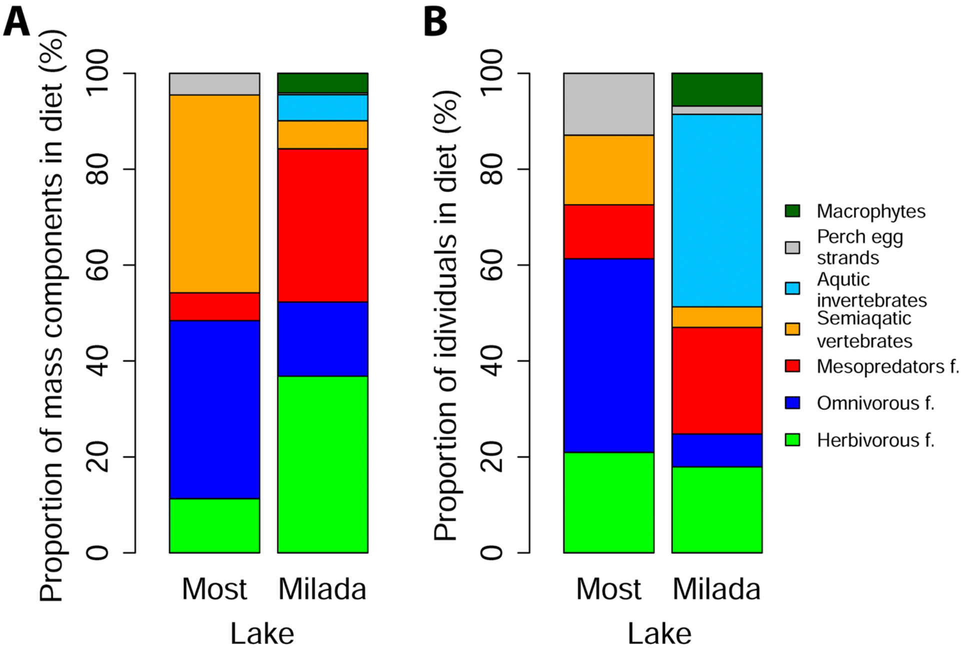

Figure 4. Diet composition of catfish in Most and Milada lakes based on stomach contents divided into seven basic groups of food sources. Prey fish is represented in three groups: herbivorous fish, omnivorous fish and fish mesopredators. Mass ratio and percentage ratio of each food item in the catfish diet are shown in part (**A**) and part (**B**), respectively.

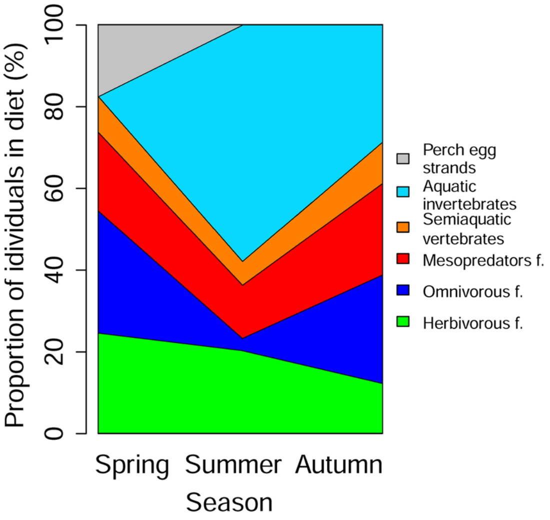

Figure 5. Percentage ratio of each food source found in catfish diet along the seasons pooled from both Most and Milada lakes. Food items found in stomachs were divided into seven basic groups. Macrophytes are not presented due to inability of separation into individuals and due to probable accidental suction with another food items.

In terms of pike, 7 and 12 food items were found in their stomachs from Most and Milada Lakes, respectively. In Most Lake, we identified roach five times, one perch and one whitefish. In Milada Lake, we identified roach nine times, perch twice and one tench. Evidently, only prey fish was found in pike stomachs.

The prey-to-predator length ratio (PPR) for catfish ranged from 0.04 to 0.51 (mean ± SD: 0.24 ± 0.08) in Most Lake and from 0.05 to 0.57 (mean ± SD: 0.17 ± 0.11) in Milada Lake. The size and mass of prey found in catfish stomach ranged from 4 cm and 0.5 g (larvae of dragonfly) to 68 cm and 2,750 g (asp). PPR for pike ranged from 0.14 to 0.29 (mean ± SD: 0.25 ± 0.07) in Most Lake and from 0.15 to 0.30 (mean ± SD: 0.22 ± 0.04) in Milada Lake (for details see Supplementary Table S1). The size and mass of prey found in pike stomachs ranged from 10 cm and 9.5 g (roach) to 30 cm and 351 g (roach).

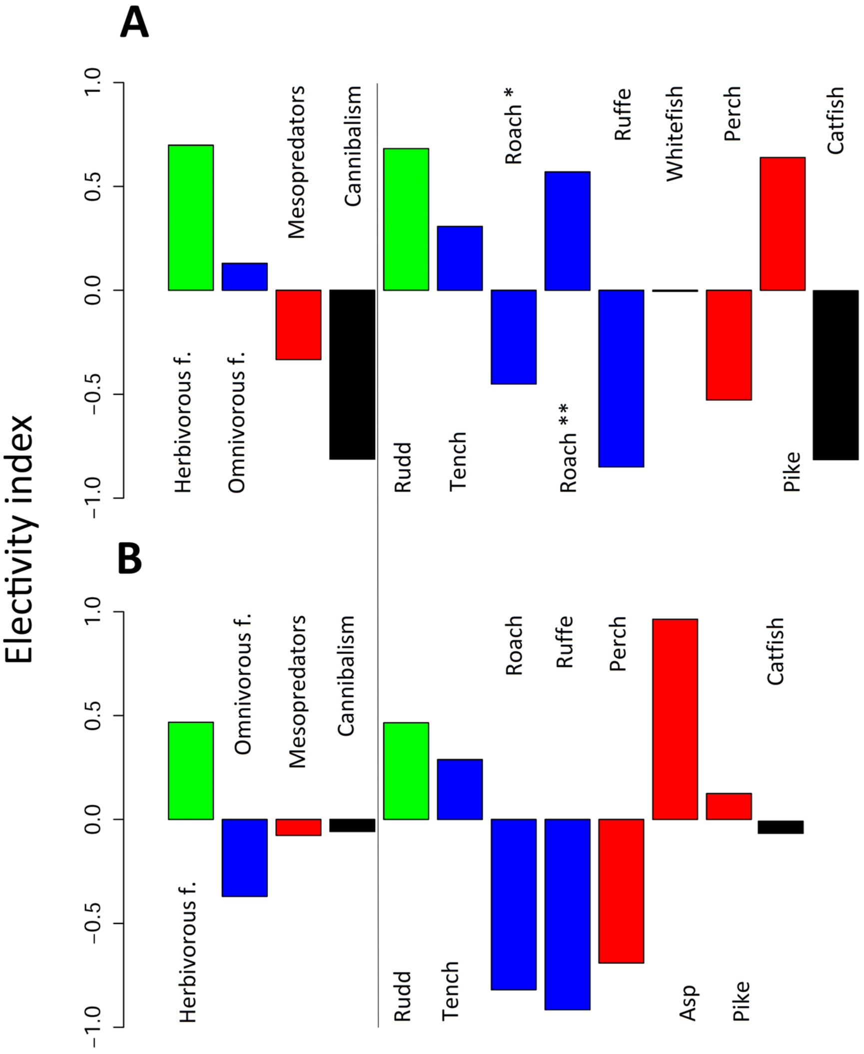

Figure 6. Electivity index of catfish (defined as ratio of relative biomass of a prey in a predator's diet and relative biomass in the ecosystem based on mean gillnet catches in 2013–2015) for (**A**) Most and (**B**) Milada. Green colour stands for herbivorous fish (only rudd), blue colour for omnivorous fish (tench, roach and ruffe in both lakes and whitefish in Most Lake), red colour for fish mesopredators (perch and pike in both lakes and asp in Milada Lake) and black colour for cannibalism, *i.e.*, utilizing of catfish. Value 1 responds to full preference and −1 to total ignorance of food item in the diet. One asterisk stands for E_i of roach in Most Lake obtained from seven sampling campaigns except May 2016 during spawning period and two asterisks stand for E_i only from May 2016.

Food preferences and impact on the ecosystem. The electivity index (*Ei*) concerning only prey fish in catfish diet revealed marked preferences for herbivorous fish (rudd) in catfish diet. The *Ei* reached 0.68 and 0.47 in Most and Milada, respectively. Positive values of *Ei* were also reached for mesopredators, namely pike, 0.64 and 0.12 in Most and Milada, respectively. Although asp was found only twice in catfish diet in Milada Lake, the *Ei* was the highest (*Ei* = 0.96) due to its low biomass in the lake. A lower *Ei*, but still with positive values, was reached for omnivorous tench, 0.31 and 0.29 in Most and Milada, respectively. Omnivorous roach in Most Lake was the last type of fish with a positive *Ei*, this was mainly due to sampling provided in May 2015 during roach reproduction. If we exclude this sampling campaign, the index is negative (Fig. 6). The *Ei* for other fish was negative in both lakes. Therefore, herbivorous species were in both lakes the most preferred fish out of four fish groups, i.e. herbivores, omnivores, mesopredators and cannibalism (Fig. 6).

Pike markedly preferred roach in the diet. The *Ei* for roach was 0.44 and 0.45 in Most and Milada, respectively. However, the highest index was recorded for whitefish in Most Lake (*Ei* = 0.70). A positive value was recorded also for tench in Milada Lake (*Ei* = 0.12). All three mentioned species were grouped in omnivorous fish, and this group was generally the most preferred food source by pike, the *Ei* reached 0.24 and 0.40 in Most and Milada, respectively. Out of the mesopredators, we found perch in the diet, but the *Ei* was negative, −0.36 and −0.51 in Most and Milada, respectively. Neither herbivorous fish nor European catfish were found in pike stomachs.

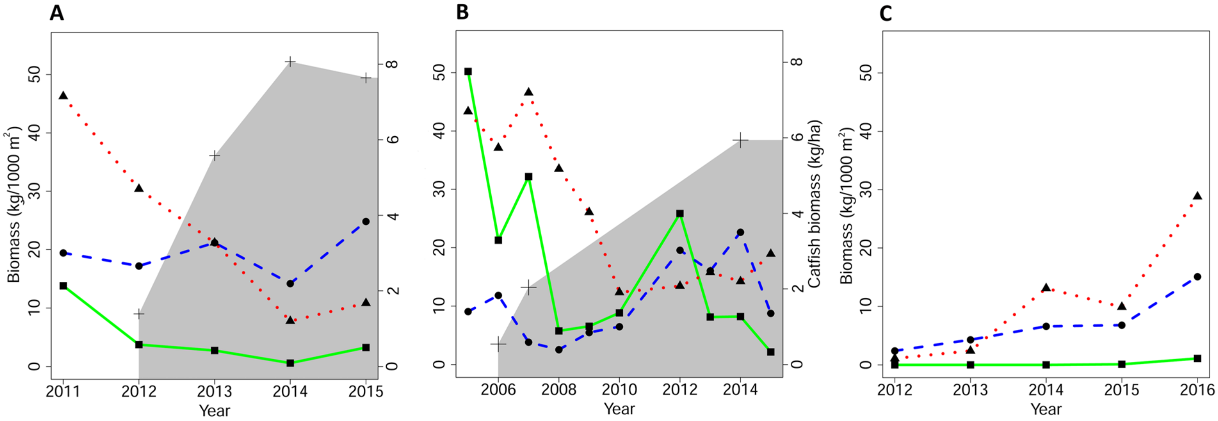

Figure 7. Biomass of three fish groups (herbivores: green, omnivores: blue, mesopredators: red) in gillnet catches (fish older than 0 +; kg per 1,000 m^2 of gillnets) of (**A**) Most, (**B**) Milada and (**C**) Medard. Pike was stocked in 2011–2013 (855 kg each year) and 2005 (237 kg) to Most and Milada, respectively. In Medard, pike occurred from the beginning (*i.e.* 2008). Beginning of grey part shows the first relevant presence of catfish in the lakes (2012 for Most and 2006 for Milada) and subsequently represents estimated biomass of catfish population (kg ha^{-1}). Catfish were stocked in autumn of previous years (2011 for Most and 2005 for Milada), in all cases well after individual gillnet sampling campaigns. This is the reason why illustrations of catfish presence begin one year later, when gillnet catches reflect (for the first time) potential impact of catfish on populations of herbivorous, omnivorous and mesopredatory fishes. Biomass for years 2012–2014 in Most and 2006–2007 in Milada is based on cumulative amount of stocked fish. Biomass for year 2015 in Most and 2014–2015 in Milada is calculated from recaptures.

The fish community has changed dramatically since European catfish and Northern pike were stocked in the lakes (Fig. 7). We recorded lower catches of herbivorous fish and mesopredators by gillnets. In Most Lake, the decrease in herbivores was of 72% during the first year and the abundance of herbivores, compared to the former population, was 16% in the following years. In Milada Lake, the direct decrease of herbivores was 50% and abundance of herbivores was approximately 20% of the former population in the following years. In terms of mesopredators, numbers in Most Lake decreased by 34% and abundance was 29% compared to the former population. In Milada Lake, mesopredators also decreased rapidly and the abundance after five years stabilized at 35% compared to the former population (Fig. 7). In contrast, the population of omnivorous fish did not apparently change. In Most Lake, practically no changes were recorded in the abundance of omnivorous fish in spite of slight fluctuation. In Milada Lake, the abundance of omnivorous fish increased by 17% (Fig. 7). In contrast to study lakes, fish biomass was gradually increasing in the reference Medard Lake with no catfish. Abundance of omnivorous fish and mesopredators increased six and 26 times, respectively. Unfortunately, herbivorous rudd was primarily absent in the reference lake, its presence was evidenced in 2015 (0.1 kg per 1,000 m^2 of gillnets) and its biomass increased markedly in 2016 (1.1 kg per 1,000 m^2 of gillnets). However, increase of mesopredators is apparent in Medard in comparison to other two study lakes, exceeding omnivorous fish since 2014 with almost twice as high population in 2016 (mesopredators 28.8 kg and omnivores 15.1 kg per 1,000 m^2 of gillnets).

According to feed conversion ratio (FCR), catfish population consume annually 528–1,232 kg (1.7–4 kg ha^{-1}) and 475–1,109 kg (1.9–4.4 kg ha^{-1}) of food in Most and Milada, respectively (considering selected FCR). Detailed specification of food items and their masses consumed annually by catfish is shown in Table 2.

Discussion

Terrestrial and many marine predators have visual and olfactory prey detection[37]. Visual prey detection is probably crucial even for freshwater predators such as pike and perch[32,34]. In contrast, European catfish have an entirely different method of detection by hydrodynamic traces[27,38]. Thus, catfish more easily detects a moving prey item than a static one. Despite the various hunting strategies of apex predators across a clade, their eventual impact on the ecosystem is very similar. The strategy of catfish naturally influences hunting activity, which takes place predominantly at night[24]. This is supported also by our catches, because the majority of catches (87%) were made during the night. It seems also to be the reason why catfish frequently utilizes prey that are active at night, such as rudd[39], tench[40], or crayfish[41].

In contrast, pike hunts for food mainly during the day, which is reflected in the composition of its diet[32,33,42]. Therefore, interspecific competition for food between catfish and pike is of low relevance. This is apparent also from the stomach contents and minor niche overlap. Hence it seems that an ecosystem can be shared by both predators without major problems. European catfish is a true generalist, but roach is rare in its diet, whereas it is the main food item of pike. A similar situation also occurs in the marine ecosystem, where tiger shark (*Galeocerdo cuvier*) is a generalist, whereas bull shark (*Carcharhinus leucas*) has specialist individuals[10].

According to high values of $\delta^{15}N$, pike seems to be at higher trophic level than catfish. However this is misleading information. Pike is a piscivorous species preferring a limited number of species (mainly roach and usually perch but not in our case) with a tendency to cannibalism[32]. The niche width of pike proves narrow specialization

	Most Lake		Milada Lake	
Food item	Lower limit	Upper limit	Lower limit	Upper limit
Rudd	58.5	136.6	182.4	425.8
Roach	120.5	281.1	12.7	29.7
Tench	65.9	153.7	63.7	148.6
Ruffe	0.7	1.7	0.2	0.5
Whitefish	4.4	10.2	X	X
Perch	17.1	39.8	20.1	46.9
Pike	26.0	60.7	52.9	123.6
Asp	X	X	75.6*	176.5*
Catfish	1.4	3.4	9.5	22.3
Perch egg strand	23.1	53.9	1.8	4.3
Crayfish	X	X	12.4	28.9
Dragonfly	0.0	0.0	27.0	63.0
Waterfowl	189.4	442.0	16.6	38.8
Mammal	6.5	15.2	12.4	28.9
Frog	17.3	40.5	0.0	0.0
Total	530.9	1238.7	487.3	1137.8

Table 2. Estimated mass (kg) of each food item consumed annually by catfish population in Most and Milada lakes. Green colour: herbivores, blue: omnivores, red: mesopredators, black: cannibalism, light blue: aquatic invertebrates, orange: semiaquatic vertebrates. X stands for food items that do not occur in the lakes. The estimation marked with asterisk was based only on two observations but with high mass of the prey.

of this species. In contrast, lower values of $\delta^{15}N$ may seem to indicate a lower trophic level of catfish but the main reason is the utilization of semiaquatic vertebrates with low $\delta^{15}N$.

Based on the electivity index of catfish, there is relatively intensive predation on pike. The opposite predation is most probably low. We did not find catfish in any pike stomachs. The reason is probably that pike are active during the day[42], whereas catfish are active during the night already from small sizes and are hidden in a refuge during the day[24]. This fact puts European catfish in the position of apex predator in freshwater ecosystems. Beside Northern pike, European catfish is also able to utilize other mesopredators, such as perch and asp. Differences in populations of mesopredators between lakes with and without catfish are apparent. Populations of mesopredators started to decrease after stocking of catfish and their abundances were lower than abundances of omnivores in most of the monitored years (Most, Milada). I n contrast, marked increase of abundances of mesopredators with time was observed in the reference lake (Medard). Their abundances significantly exceeded the abundances of omnivores with time. The fundamental impact of apex predators on mesopredators is well known[15]. The impact is induced by i) direct competition for food or territory[3,15], ii) killing of weaker mesopredators as unwanted competitors[3], and also iii) hunting for mesopredators as a food source[3]. In the case of European catfish, the latter impact seems to be the most relevant, because preference for mesopredators is low (−0.33 and −0.08 for Most and Milada, respectively) and hence the mesopredators are not killed to get rid of competitors. In spite of the low presence of mesopredators in catfish diet, decrease of their abundances is caused by their lower resistance to the predation pressure in comparison to that of omnivores. The catfish theoretically consume only 17.1–39.8 kg and 20.1–46.9 kg of perch per year in Most and Milada, respectively. However, the predation pressure on perch is raised by the consumption of their egg strands[28]. The predation pressure on mesopredators is sufficient to reduce their biomass to a tolerable level in the ecosystem that consequently stagnates, therefore mesopredators are able to coexist with the European catfish. We are well aware of differences in life cycles and strategies between freshwater and terrestrial predators, but similar coexistence relationships may be observed in several terrestrial predators from the order carnivora[4].

Regarding human management in aquatic ecosystems with natural occurrence of both European catfish and Northern pike, it is advisable to maintain the coexistence of both species. Multiple predator effects provide high stability and well-balanced biodiversity in the ecosystem[43]. Cannibalism in European catfish was proved in both lakes, but it was quite a rare phenomenon. Thus catfish is a less cannibalistic species than pike or perch[32,34]. It probably occurs only for the purpose of food intake, not as an evolutionary strategy. This strategy is often observed in the order Carnivora where cannibalism or even infanticide is connected with an attempt to increase their fitness and thus to decrease the fitness of an intraspecific competitor[44].

The high contribution of herbivores (mainly rudd) in catfish diet was a surprising finding, considering their relatively low biomass in the lakes. In addition, rudd was definitely a preferred food item. The nocturnal activity of these potential preys is presumably the main reason (see the description above). In terms of rudd, predation occurs also during the day due to its inefficient antipredation behaviour[39]. Similarly, a fundamental part of the diet of terrestrial apex predators is composed of herbivores. It is closely linked to the key impact of apex predators on ecosystem structure, that is commonly shaped by herbivores[3,11]. The cascade effect, called top down effect, has been documented in the freshwater ecosystem long before[45], and this effect leads to a final impact on phytoplankton as a primary producer. Whether an apex predator may also affect species richness and cover of macrophytes, the main food item of aquatic herbivores[46], has still not been answered. Nevertheless, our preliminary results indicate this mentioned effect (Vejříková, in prep.). Due to insufficient comparison of herbivorous rudd in lakes with and without catfish, we cannot make confident conclusions on the impact of catfish on its population. However, substantial impact is very probable due to the strong preference of rudd in catfish diet, high number of rudd individuals consumed every year in both study lakes (see Table 2) and apparent decrease of rudd abundances in both lakes after catfish stocking.

Although predator-prey interactions depend on density of prey[47], the most numerous species, roach, was avoided in the diet for most of the year. It is probably due to roach sleeping at night (SCUBA observations; L. Vejřík, J. Peterka, M. Čech, unpubl. data) and various antipredation mechanisms during the day[39]. In contrast, a strong preference for roach in catfish diet near its spawning area during reproduction in Most Lake clearly illustrates the rapid ability of European catfish to learn and directly utilize a new, easily available food source. During reproduction, cyprinids gather at spawning areas in abundant shoals and their alarm cues (chemical substance released from injured fish skin that provides warning for surviving individuals) are suppressed[48]. Risk perception is generally lower for all animals during reproduction[49]. European catfish were also observed close to spawning areas of rudd in Milada Lake (F. Uhlíř, pers. comm.) and of bream in Římov Reservoir (J. Seďa, pers. comm.). Therefore, visiting and hunting on cyprinids spawning grounds seems to be a common and very efficient strategy for catfish to meet their dietary needs. Their great ability to adapt to currently available food sources is also proved by the occurrence of perch egg strands in the diet[28].

Macrophytes were the most unexpected food item found in the catfish stomach. It composed 7% of total diet biomass in Milada Lake. Plants have already been recorded in catfish diet[23], nevertheless, accidental ingestion of these items during suction of benthic prey (larvae of dragonflies, crayfish etc.) is a more probable explanation for the presence of macrophytes in catfish stomachs than intentional feeding on them. The question is whether ingested plant material may provide energy to the catfish. The fish digestive tract works differently than that of higher vertebrates. Tracts of closely related carnivorous and herbivorous fish may be very similar but differ in digestive biochemistry that plays a key role[50]. Microorganisms responsible for digestion of plant material get into the tract mainly from detritus[46]. Hence, we may assume that European catfish also has the potential to digest plants. This presumption is supported by videos recorded in Chernobyl cooling pond, where European catfish are intensively fed with bread (check YouTube: www.youtube.com/watch?v=3cEj8R5m3AI; www.youtube.com/watch?v=qf7n2kLubUQ and others). It sheds new light on the generalist behaviour of this apex predator. In relation to habitat, the dietary niche of European catfish extends from primarily marine food sources[26], to terrestrial prey[27], semiaquatic prey and freshwater prey across clades of freshwater animals[23] and plant material.

An analogical apex predator in a terrestrial ecosystem would be the grizzly bear (*Ursus arctos horribilis*). It is also a true generalist with a similarly wide diet spectrum and short-term individual specialization[51]. In the marine environment, the most similar generalist would probably be the tiger shark[10]. Unusually wide niche of catfish is also proved by extra-large PPR (0.04–0.51 and 0.05–0.57 for Most and Milada Lakes, respectively) in contrast to narrow PPR of Northern pike (0.14–0.29 and 0.15–0.30) and PPR of other freshwater predators[52] and related studies.

The relatively high number of European catfish individuals with empty stomachs (40 and 72%) is not surprising, because the strategy "run on empty" is very common for predators[53]. Common frequency of empty stomachs of catfish is 20–78%[23]. In case of Most where the estimated mean annual mass increase of catfish is c. 381 g, sufficient amount of food for catfish specialized on waterfowl (*i.e.* abnormal prey in size) seems to be two or three

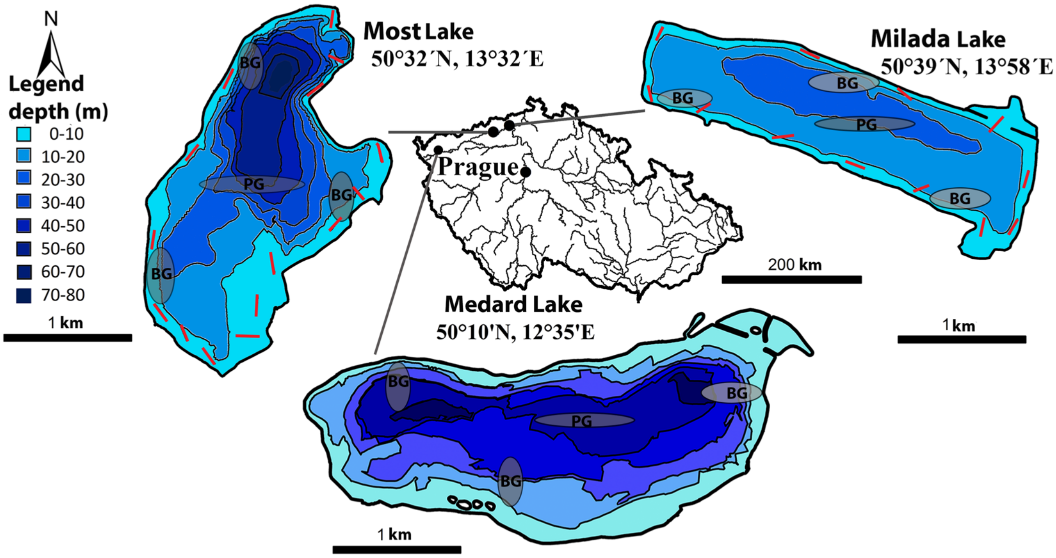

Figure 8. Map showing the location and relevant depths of the two study lakes, Most and Milada, and the reference Medard Lake, Czech Republic. Localities sampled by longlines are shown by red lines along the lake shores, and localities sampled by gillnets by grey ellipses with BG and PG for benthic and pelagic gillnets, respectively. The figure was generated by the software ArcMap, version 10.2.2[65].

individuals of waterfowl per year. In Milada with estimated mean annual mass increase of catfish c. 1.1 kg, six individuals of waterfowl should be sufficient. However, mean mass of the prey consumed in Most and Milada was 269 and 242 g, respectively. Individuals would have to utilize eight and 25 of these average preys per year in Most and Milada, respectively. Although, such irregular food intake has not been sufficiently recorded among fish, it is a common phenomenon found among aquatic apex predators from ectothermic vertebrates[54]. Nevertheless, the reason of such high occurrence of catfish with empty stomachs and such high frequency of our baits in the stomachs in Most is also caused by the low food availability in the lake. It is also evident from the low trophic status of the lake. The distinctly lower degree of IS for European catfish in Most Lake, which signifies high individual niche specialization (INS), is probably induced by higher intraspecific and conversely lower interspecific competition[12]. The other reasons are i) biomass of catfish is 28% higher in Most than Milada, ii) the biomass of pike is according to catches much lower in Most than Milada, and iii) the other mesopredator, asp, is totally absent in Most Lake[55].

WIC and TNW of pike are distinctively lower than that of catfish. As mentioned above, pike prefers only a few prey species. Its partial utilization of semiaquatic prey in Most Lake is presumably due to low food availability in this oligotrophic lake. In contrast, the stomach contents of catfish indicate the true generalist behaviour of this species. However, SIA showed marked differences among individuals. It proves that the generalist population contains many specialist individuals, specializing on semiaquatic or terrestrial prey[27]. Similarly, the population of alligator (*Alligator mississippiensis*), the main apex predator of freshwaters in North America, is composed of both generalist and specialist individuals, specializing on difficult to catch prey[7]. INS aimed at large and high-energy prey is an advantageous target for apex predators. The learned ability to utilize one type of large prey[13] considerably shortens handling time[56]. This is probably the reason why some individuals from our lakes focused on semiaquatic prey. Catching and handling of this type of prey is difficult and learning how to do it is more complicated and challenging in comparison to utilization of aquatic prey[11,27].

According to WIC and seasonal preferences of certain food sources, the majority of catfish individuals seem to have high short-term INS. This phenomenon for apex predators has already been described[7]. Hence the widely accepted paradigm stating that generalist populations are composed of specialist individuals[12] may be in some cases biased by short-term specialist individuals that appear to be long-term generalist individuals when the whole year is taken into consideration. The effects of prey composition on short-term INS are particularly important to investigate for large apex predators. They generally move long distances and thus inhabit various ecosystems with different types of prey[7]. Hence apex predators need to be ready to turn a profit from a new niche and utilize food sources that were until recently unfamiliar to them. This situation may be observed in killer whales (*Orcinus orca*) that, besides forming a highly specialized population across the world, are also able to switch to a different food source when the preferred source is absent[14]. In addition, killer whales are spreading to polar regions due to climate changes, where they utilize completely new food sources[6]. The ability to learn efficiently and become specialized on newly available prey[13] plays a key role in becoming a successful apex predator for these reasons i) it is probably the most efficient method to satisfy the energy requirements of a large body, and ii) this ability enables the maintenance of a relatively numerous population of the apex predator species. However, nowadays the second reason mostly cannot be realized because of the negative impact of humans[2]. This scenario is not true for European catfish thanks to its popularity among anglers[23].

Comparison of fish community in the lakes with catfish (Most and Milada) and without catfish (Medard) shows that catfish markedly affect the ecosystems. Although the study and reference lakes have very similar characteristics, uncertain distinctness should be also taken into account in the fish community development. However, catfish had a great impact on the populations of rudd and mesopredators. The total amount of consumed food per year calculated using annual mass increase of catfish and feed conversion ratio (FCR)[57] is 530.9–1,238.7 kg and 487.3–1,137.8 kg for Most and Milada, respectively. The values in the upper limits are more probable considering the low trophy of the lakes and necessarily longer time for searching the prey. Then, catfish population annually utilize 3.7 kg and 5 kg of prey per 1 hectare of Most and Milada, respectively. In case of fish prey (excluding cannibalism), it is 2.2 kg and 3.8 kg per 1 ha of Most and Milada, respectively. Fish biomass (excluding catfish) in 2013–2015 was estimated at 11.3–27.5 kg and 14.9–28.3 kg per 1 ha of Most and Milada, respectively[55,58]. Thus the fish preys consumed by catfish make 8–20% and 13–26% of total fish biomass in Most and Milada, respectively. However, the values are not totally accurate and have only information character.

Conclusion and recommendation for future studies.

The European catfish niche width widely exceeds the niche width of Northern pike, the second biggest fish predator in Europe. In the presence of catfish, pike fulfils the role of mesopredator. Nevertheless, the position of pike is still irreplaceable due to multiple predator effects.

European catfish has many behavioural features in common with other apex predators[2]. Catfish is raised to the position of successful apex predator thanks to features such as wide diet plasticity and good adaptability to new food sources[26–28] associated with distribution of various food sources among individuals. These features, in conjunction with a low level of cannibalism, allow catfish to establish highly abundant populations[23]. This is the reason why European catfish is an ideal species to study the impact of an apex predator in an ecosystem in real time. Further, thanks to its human-mediated spread to new localities (particularly by anglers), future studies may focus on continuous changes in communities from all trophic levels in the ecosystem, such as phytoplankton or macrophytes.

Broad adaptability and learning ability to utilize various food sources may be an important feature of the trophic dynamics of an apex predator. It should be considered in studies focused on freshwater food webs and the ecological role of apex predators.

As far as we know, our study is based on the largest dataset collected in natural conditions among studies focused on the diet of European catfish. Hence, we would recommend the spread of gained information among the public, particularly among anglers, to avoid inaccurate conclusions concerning the dietary behaviour of catfish.

Methods

Study site.

The study was conducted in two lakes created after aquatic restorations of mining pits, Most and Milada Lakes, Czech Republic. The oligotrophic Most Lake has an area of 310 ha, volume of 70×10^6 m^3 and maximum depth of 75 m, and the oligo to mesotrophic Milada has an area of 250 ha, volume of 36×10^6 m^3 and max. depth of 25 m (Fig. 8). Aquatic restoration in Most lasted six years (2008–2014) and in Milada ten years (2001 to 2011). Fish community is similar in both lakes. Fishes occurring already in retention pool of the mining pit were rudd (herbivore), roach, ruffe, tench (omnivores) perch (mesopredator) in both lakes, and rarely asp and pikeperch (*Sander lucioperca*) (mesopredators) in Milada Lake. Whitefish (*Coregonus sp*., omnivorous fish) was introduced to Most Lake in 2011–2013[46]. European catfish (apex consumer) and Northern pike (mesopredator) were stocked for biomanipulation purposes because absence of large predators raised concerns about expansion of zooplanktivorous fish that may have a negative impact on the water quality. In Most, Northern pike (2,332 individuals, mean mass 1.1 kg) and European catfish (694 individuals, mean mass 3.7 kg) were both introduced in 2011, 2012 and 2013. In Milada, Northern pike was introduced in 2005 (789 individuals, mean mass 0.3 kg) and low number of small European catfish in 2005 (12 individuals, mean mass 7.7 kg) but the catfish was introduced mainly in 2007 (316 individuals, mean mass 1.2 kg), In both lakes, all introduced catfish and pike were individually tagged with a PIT-tag (passive integrated transponder tag, Oregon RFID, full-duplex, length 12 mm, diameter 2.15 mm, mass 0.11 g, 11784/11785 compatible).

The reference lake, Medard, was also created after aquatic restorations of mining pits. It is an oligotrophic lake with an area of 493 ha, volume of 50×10^6 m^3 and maximum depth of 55 m. Aquatic restoration lasted eight years (2008–2016). Fish community occurring already in retention pool of the mining pit was composed of roach, ruffe (omnivorous fish) and Northern pike (mesopredator). In contrast to Most and Milada, pike occurred from the beginning of the water restoration. During water filling in 2012–2014, new species came from the river: perch, pikeperch (mesopredators) tench, European chub (*Squalius cephalus*), common bream (*Abramis brama*) and silver bream (*Blicca bjoerkna*) (omnivorous fish). In 2015, rudd (herbivorous fish) occurred in the lake. Whitefish (omnivorous fish) were introduced to Medard Lake in year 2012-2014. Catfish was not stocked to the lake (J. Peterka, unpubl. data).

Fish sampling and stomach content analysis.

Animal treatment was performed in accordance with guidelines from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01679) and with permission of the owners of the study sites, Palivový kombinát Ústí, státní podnik (Most, Milada) and Sokolovská uhelná a.s. (Medard). The Experimental Animal Welfare Commission approved all experimental protocols.

European catfish and Northern pike from both lakes were caught by longlines from August 2013 to May 2015 always during a 4-day-and-night-long campaign. Eight campaigns were conducted on each lake from spring to late autumn (May to November), i.e. 32 days in each lake. See[28] for details about the longline method. Three lines, each with 10 bait fish, were used and were moved every day of sampling to a new place to cover the shore evenly. They were checked three times per day (before dusk, soon after midnight, and shortly after dawn). Each caught predatory fish was measured, weighed, a small part of fin was cut for SIA and non-invasive stomach content analysis was provided[46]. Stomach content of catfish was extracted by hand through opened mouth and gullet. Stomach content of pike was washed out through a larger tube into a jar, while water was pumped through a small tube into the pike's stomach. The latter method was not fully effective as we tried to prevent any harm to fish. All fish were released back into the lake as soon as possible. The stomach contents were subsequently identified, or fixed with 70% ethanol for laboratory identification using diagnostic elements such as fish bones see [S1[59],]. Only fish stocked at least 660 days ago were used for SIA due to turnover of isotopic signal[10].

Prey fishes were sampled in September 2011–2015 in Most and 2005–2015 in Milada by both benthic and pelagic multi-mesh gillnets in both lakes for details see[46]. 36 gillnets (24 benthic and 12 pelagic) were set in each lake and year, summing to a total of 144 gillnet nights and 8,640 m^2 gillnet area. Fish biomass (kg of fish > 0 + per 1,000 m^2 of gillnets) in Fig. 7 was calculated as the weighted average of each depth zone using both littoral and pelagic gillnets. In total, 4,876 and 6,753 individuals of eight fish species found in catfish diet were captured in Most and Milada, respectively. Prey samples for SIA were sampled in 2014, it means the same year as the most of the predators.

All captured fish were immediately anaesthetized by a lethal dose of tricainemethanesulfonate (MS–222, Sigma Aldrich Co.). Mammals, birds, amphibians and large-sized benthic odonates were collected during campaigns of catfish sampling. From each fish (randomly chosen fish individuals of all potential prey species) and other potential prey sources, a small piece of muscle tissue was dissected and stored frozen at −20 °C prior to final preparation for SIA. Six to eight replications of each prey sample found in catfish stomachs were used for SIA.

Size of captured individuals, time period of the catch and mass increase of recaptures.

Altogether we captured 232 and 93 catfish individuals in Most and Milada, respectively. Out of these individuals, there were 74 and 37 recaptures in Most and Milada, respectively. Mean size and mean mass were 85 cm and 4.1 kg (min: 55 cm and 0.65 kg, max: 128 cm and 11.8 kg) in Most Lake, and 103 cm and 8.4 kg (min: 67 cm and 2.2 kg, max: 158 cm and 23.5 kg) in Milada Lake. The majority of individuals (87%) were captured during the night. All captured individuals were stocked and tagged. Individuals born in the lakes did not reach the sizes of individuals that are caught by long-lines ($L_T > 70$ cm), moreover, due to the predation pressure and competition they are extremely scarce in both lakes (J. Peterka, unpubl. data). Annual mass increase of recaptured individuals was approximately 381 g and 1,100 g in Most and Milada, respectively.

We captured 18 and 84 pike individuals in Most and Milada, respectively. Out of these individuals, there were 2 and 10 recaptures in Most and Milada, respectively. Mean size and mean mass were 84 cm and 4.2 kg (min: 69 cm and 1.8 kg; max: 97 cm and 6.1 kg) in Most Lake, and 84 cm and 5.1 kg (min: 48 cm and 0.55 kg, max: 120 cm and 14.3 kg) in Milada Lake. All individuals were captured during the day. All pikes from Most Lake were stocked and tagged. In Milada Lake, 28% of captured pikes were tagged, other individuals originated from the natural reproduction in the lake.

Stable Isotope Analysis.

All frozen SIA samples were later dried at 60 °C for 48 h and ground into a homogenous powder using a ball-mill Retsch MM 200 (Retsch GmbH, Haan, Germany). Small subsamples (0.52–0.77 mg) were weighed into tin cups for the analysis of $\delta^{13}C$ and $\delta^{15}N$. All SIA were conducted using a FlashEA 1112 elemental analyser coupled to a Finnigan DELTA^{plus} Advantage mass spectrometer (Thermo Fisher Scientific Corporation, Waltham, MA, U.S.A.) at the University of Jyvaskyla, Finland. Stable nitrogen and carbon isotope ratios are expressed as $\delta^{15}N$ and $\delta^{13}C$ relative to the international standards for nitrogen (atmospheric nitrogen) and carbon (Vienna PeeDeeBelemnite). Analytical precision was ± 0.20‰ for both isotopes, and was determined by repeated analysis of a working standard (pike white muscle tissue) inserted in each run after every five samples. As C:N ratios were consistently lower than 3.5 (i.e., > 90% of cases), obtained stable isotope values of fish were not lipid corrected[60].

Statistical analysis.

The SIAR package (Stable Isotope Analysis in R; version 4.2;[35]) was used to estimate the relative contributions of semiaquatic and aquatic prey in the long-term diets of catfish and pike. The SIAR input data included individual $\delta^{13}C$ and $\delta^{15}N$ values from catfish and pike fin, mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values of muscle tissue from potential semiaquatic and aquatic prey sources, and the commonly used trophic fractionation corrections of 0.4 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 1.0‰ for $\delta^{15}N$[61]. Finally, the SIBER package (Stable Isotope Bayesian Ellipses in R; version 2.0.3;[36]) was used to estimate sample-size corrected standard ellipse areas (SEA_c), total convex hull areas (*TA*), and proportional overlap of the SEA_c areas. The estimated SEA_c and *TA* areas indicate the long-term dietary niche widths of catfish and pike, whereas the proportional overlap between SEA_c areas measures the degree of dietary niche segregation between the two predatory fishes. For SIAR and SIBER analyses, 74 and 69 of catfish samples, and 18 and 32 of pike samples were used from Most and Milada, respectively. No recaptures were used in SIAR and SIBER analyses and both were done in R 3.1.1[62].

Trophic specialization is calculated as dietary variation within individuals (WIC: within individual component of variation) and between individuals (BIC: between individual component of variation) of a population. The WIC of a population measures how variable an individual's diet is over time period. It is typically expressed as a mean value for an entire population, but can be similarly assessed for individuals. It was calculated from 16 and 16 recaptured catfish, and 2 and 8 recaptured pikes from Most and Milada, respectively. The BIC of a population measures how different each individual's diet is from the other members of the population[63]. Low values of WIC indicate individuals and populations that are more specialized, as individual diets show little variation and should be consistent over time, and vice versa[63]. The BIC varies based on total niche width (TNW). IS (degree of individual specialization) is calculated as WIC/TNW ratio and reaches values from 0 to 1. A high value means that all individuals utilize the entire niche of the species, whereas low values signify low intraspecific overlap and thus greater individual niche specialization (INS)[10]. WIC, BIC, TNW and degree of IS were calculated from $\delta^{13}C$ in the Ind Spec1 program[64].

The prey-to-predator length ratio (PPR) was calculated as:

$$PPR = L_TPy/L_TPr$$

where L_TPy represents L_T (total length) of prey and L_TPr represents L_T of a predator[52]. Perch egg strands and macrophytes were excluded from the calculations, whereas fish baits, that were found in the stomachs, were included. In total, 101 and 106 diet samples from catfish stomachs, and 6 and 12 diet samples from pike stomachs were used from Most and Milada, respectively.

Electivity index, E_i defined for a group (i) as:

$$E_i = (r_i - P_i)/(r_i + P_i)$$

where r_i represents the relative biomass of a prey in a predator's diet and P_i represents the prey's relative biomass in the ecosystem. $E_i = -1$ means total avoidance of, $E_i = 0$ means non-selective feeding on, and $E_i = 1$ means exclusive feeding on a given prey *i*.

Estimated size of the catfish biomass from stocking to 2015 shown in Fig. 7 was calculated from stocked biomass in the years 2011–2013 for Most, and 2005 and 2007 for Milada. Gillnet sampling in a given year was always conducted prior to the stocking of predators, thus biomass and potential impact of fish predators on fish communities was considered for the following year. Estimated size of population for Most in 2015 and for Milada in 2014–2015 was calculated from recaptures (Vejřík unpubl. data). Year 2011 in Milada, when sampling was not conducted, was spaced with a straight line. The size of pike biomass was not estimated due to an insufficient number of recaptures. Fish biomass (kg per 1,000 m^2 of gillnets) in Fig. 7 was calculated as the weighted average for each depth zone using both littoral and pelagic gillnets. A chi-square test (χ^2) was used to compare the contribution of each food item among the seasons. For the analyses, we used 48 and 53 fish samples found in catfish stomachs from Most and Milada, respectively.

Total consumption (TC) of food utilized by catfish was calculated as:

$$TC = N * FCR$$

where *FCR* represents feed conversion ratio showing total biomass of each food item utilized annually, and ranges from 2.4 to 5.6 kg of food per 1 kg of mass increase in natural ecosystems[57] and related studies. *N* represents total number of adult catfish and was estimated (using recaptures) at 577 and 180 individuals in the populations of Most and Milada, respectively[28]. The contribution of each food item was then calculated from the percentage ratio of all food items found in catfish stomachs, see Fig. 2A. Differences in nutrition values were not taken into account.

Data availability. All data analysed during this study are included in this published article (and its Supplementary Information files).

Ethics. Animal treatment was performed in accordance with guidelines from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01679) and with permission of the owner of the study sites, Palivový kombinát Ústí, státní podnik. The Experimental Animal Welfare Commission approved all experimental protocols.

References

1. Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *J. Appl. Ecol.* **43**, 1049–1055 (2006).
2. Estes, J. A. *et al.* Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).
3. Ripple, W. J. *et al.* Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484 (2014).
4. Sinclair, A. R. E., Mduma, S. & Brashares, J. S. Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288–290 (2003).
5. Foote, A. D., Newton, J., Piertney, S. B., Willerslev, E. & Gilbert, M. T. P. Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Mol. Ecol.* **18**, 5207–5217 (2009).
6. Ferguson, S. H., Higdon J. W. & Westdal, K. H. Prey items and predation behavior of killer whales (*Orcinus orca*) in Nunavut, Canada based on Inuit hunter interviews. *Aquat. Biosyst.* **8**, https://doi.org/10.1186/2046-9063-8-3 (2012).
7. Rosenblatt, A. E. *et al.* Factors affecting individual foraging specialization and temporal diet stability across the range of a large "generalist" apex predator. *Oecologia* **178**, 5–16 (2015).
8. Rooney, N., McCann, K. S., Gellner, G. & Moore, J. C. Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269 (2006).
9. Rooney, N., McCann, K. S. & Moore, J. C. A landscape theory for food web architecture. *Ecol. Lett.* **11**, 867–881 (2008).
10. Matich, P., Heithaus, M. R. & Layman, C. A. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *J. Anim. Ecol.* **80**, 294–305 (2011).
11. Baird, R. W. & Whitehead, H. Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* **78**, 2096–2105 (2000).
12. Araújo, M. S., Bolnick, D. I. & Layman, C. A. The ecological causes of individual specialisation: the causes of individual specialisation. *Ecol. Lett.* **14**, 948–958 (2011).
13. Dall, S., Bell, A. M., Bolnick, D. I. & Ratnieks, F. L. W. An evolutionary ecology of individual differences. *Ecol. Lett.* **15**, 1189–1198 (2012).
14. Estes, J. A., Tinker, M. T., Williams, T. M. & Doak, D. F. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476 (1998).
15. Prugh, R. L. *et al.* The rise of the mesopredator. *BioScience* **59**, 779–791 (2009).
16. Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. & Peterson, C. H. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846–1850 (2007).
17. Baum, J. K. & Worm, B. Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* **78**, 699–714 (2009).
18. Brashares, J. S., Prugh, L. R., Stoner, C. J. & Epps, C. W. Ecological and conservation implications of mesopredator release. In Terborgh, J., Estes, J. A., eds. *Trophic Cascades. Island Press. Forthcoming* (2010).

19. Dudgeon, D. *et al*. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* **81**, 163–182 (2006).
20. Veit, R. R., Mcgowan, J. A., Ainley, D. G., Wahl, T. R. & Pyle, P. Apex marine predator declines ninety percent in association with changing oceanic chmate. *Glob. Change Biol.* **3**, 23–28 (1997).
21. Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R. & Lotze, H. K. Patterns and ecosystem consequences of shark declines in the ocean. *Ecol. Lett.* **13**, 1055–1071 (2010).
22. Stone, R. The last of the leviathans. *Science* **316**, 1684–1688 (2007).
23. Copp, H. G. *et al*. Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish. Fish.* **10**, 252–282 (2009).
24. Carol, J., Zamora, L. & García-Berthou, E. Preliminary telemetry data on the movement patterns and habitat use of European catfish (*Silurus glanis*) in a reservoir of the River Ebro, Spain. *Ecol. Freshw. Fish.* **16**, 450–456 (2007).
25. Cunico, A. M. & Vitule, J. R. S. First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). *BioInvasions Rec.* **3**, 117–122 (2014).
26. Syväranta, J. *et al*. Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. *Aquat. Biol.* **8**, 137–144 (2010).
27. Cucherousset, J., Boulêtreau, S., Azémar, F., Compin, A. & Guillaume, M. "Freshwater Killer Whales": beaching behavior of an alien fish to hunt land birds. *PLoS One* **7**, e50840 (2012).
28. Vejřík, L. *et al*. Thirty-year-old paradigm about unpalatable perch egg strands disclaimed by the freshwater top-predator, the European catfish (*Silurus glanis*). *PLoS One* **12**, e0169000 (2017).
29. Alp, A., Kara, C. & Buyukcapar, H. M. Reproductive biology in a native European catfish, *Silurus glanis* L., 1758, population in Menzelet Reservoir. *Turk. J. Vet. Anim. Sci.* **28**, 613–622 (2003).
30. Slavík, O. Behaviour of European catfish in natural conditions and aquaculture (Habilitation Thesis), Czech University of Life Sciences (2013).
31. Boulêtreau, S. & Santoul, F. The end of the mythical giant catfish. *Ecosphere* **7**, e01606 (2016).
32. Forsman, A. *et al*. Pike *Esox lucius* as an emerging model organism for studies in ecology and evolutionary biology: a review. *J. Fish Biol.* **87**, 472–479 (2015).
33. Kottelat, M. & Freyhof, J. Handbook of European freshwater fishes. *Cornol: Publications Kottelat*. 646 pp. (2007).
34. Svanbäck, R. & Persson, L. Individual diet specialization, niche width, and population dynamics: implications for trophic polymorphisms. *J. Anim. Ecol.* **73**, 973–982 (2004).
35. Parnell, A. C., Inger, R., Bearhop, S. & Jackson, A. L. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* **5**, e9672 (2010).
36. Jackson, A. L., Inger, R., Parnell, A. C. & Bearhop, S. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **80**, 595–602 (2011).
37. Ferrero, D. M. *et al*. Detection and avoidance of a carnivore odor by prey. *Proc. Natl. Acad. Sci. USA* **108**, 11235–11240 (2011).
38. Pohlmann, K., Atema, J. W. & Breithaupt, T. The importance of the lateral line in nocturnal predation of piscivorous catfish. *J. Exp. Biol.* **207**, 2971–2978 (2004).
39. Hölker, F. *et al*. Species-specific responses of planktivorous fish to the introduction of a new piscivore: implications for prey fitness. *Freshw. Biol.* **52**, 1793–1806 (2007).
40. Herrero, M. J., Madrid, J. A. & Sánchez-Vázquez, F. J. Entrainment to light of circadian activity rhythms in tench (*Tinca tinca*). *Chronobiol. Int.* **20**, 1001–1017 (2003).
41. Musil, M., Buřič, M., Policar, T., Kouba, A. & Kozák, P. Comparison of day and night activity between noble (*Astacus astacus*) and spiny-cheek crayfish (*Orconectes limosus*). *Freshwater Crayfish* **17**, 189–193 (2010).
42. Cook, M. F. & Bergersen, E. P. Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Trans. Am. Fish. Soc.* **117**, 495–502 (1988).
43. Wasserman, J. R. *et al*. Using functional responses to quantify interaction effects among predators. *Funct. Ecol.* **30**, 1988–1998 (2016).
44. Ebensperger, L. A. Strategies and counterstrategies to infanticide in mammals. *Biol. Rev. Camb. Philos. Soc.* **73**, 321–346 (1998).
45. Brooks, J. L. & Dodson, S. I. Predation, body size, and composition of plankton. *Science* **150**, 28–35 (1965).
46. Vejříková, I. *et al*. Distribution of herbivorous fish is frozen by low temperature. *Sci. Rep*. **6**, https://doi.org/10.1038/srep39600 (2016).
47. Abrams, P. A. The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Evol. Syst.* **31**, 79–105 (2000).
48. Smith, R. J. F. Testosterone eliminates alarm substance in male fathead minnows. *Can. J. Zool.* **51**, 875–876 (1973).
49. Magnhagen, C. Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**, 183–186 (1991).
50. Day, R. *et al*. Enzymatic digestion in stomachless fishes: how a simple gut accommodates both herbivory and carnivory. *J. Comp. Physiol.* **181**, 603–613 (2011).
51. Munro, R. H. M., Nielsen, S. E., Price, M. H., Stenhouse, G. B. & Boyce, M. S. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *J. Mammal.* **87**, 1112–1121 (2006).
52. Vejřík, L. *et al*. Who is who: an anomalous predator-prey role exchange between cyprinids and perch. *PLoS One* **11**, e0156430 (2016).
53. Arrington, D. A., Winemiller, K. O., Loftus, W. F. & Akin, S. How often do fishes "run on empty". *Ecology* **83**, 2145–2151 (2002).
54. Nakano, S. & Murakami, M. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl. Acad. Sci. USA* **98**, 166–170 (2001).
55. Peterka, J. Complex fish stock assessment of Most Lake in year 2014. Report of the Biology Centre CAS, Institute of Hydrobiology (in Czech) (2015a).
56. Kislalioglu, M. & Gibson, R. N. Prey "handling-time" and its importance in food selection by the 15-spined stickleback, *Spinachi spinachia* (L.). *J. Exp. Mar. Biol. Ecol.* **25**, 151–158 (1976).
57. Zaikov, A., Iliev, I. & Hubenova, T. Investigation on growth rate and food conversion ratio of wels (*Silurus glanis* l.) in controlled conditions. *Bulg. J. Agric. Sci.* **14**, 171–175 (2008).
58. Peterka, J. Complex fish stock assessment of Milada Lake in year 2014. Report of the Biology Centre, CAS, Institute of Hydrobiology (in Czech) (2015b).
59. Čech, M., Čech, P., Kubečka, J., Prchalová, M. & Draštík, V. Size selectivity in summer and winter diets of great cormorant (*Phalacrocorax carbo*): Does it reflect season-dependent difference in foraging efficiency? *Waterbirds* **31**, 438–447 (2008).
60. Post, D. M. *et al*. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–189 (2007).
61. Post, D. M. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703–718 (2002).
62. R Core Team R: a language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria (2014).
63. Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M. & Svanbäck, R. Measuring individual-level ressource specialization. *Ecology* **83**, 2936–2941 (2002).
64. Ind Spec1: Bolnick D. Center for population biology Store Hall University of California, Davis, USA 530–752–6784 (2002).
65. Esri, Working with ArcMap. ArcGIS Help 10.2.2. (2016). Available at: http://resources.arcgis.com/en/help/main/10.2/#/Mapping_and_visualization_in_ArcGIS_for_Desktop/018q00000004000000/ (Accessed: 26th June 2017).

Acknowledgements

The study was supported by projects No. CZ.1.07/2.3.00/20.0204 (CEKOPOT) of the Ministry of Education, Youth and Sports, No. 7F14316 of the Norwegian Financial Mechanism 2009–2014 under contract number MSMT-28477/2014 and No. 04-151/2016/P of the Grant Agency of University of South Bohemia. This work has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 677039″ project CLIMEFISH. This publication reflects the views only of the authors, and the Commission cannot be held responsible for any use that may be made of the information contained therein. Further, it was supported by the SoWa Research Infrastructure funded by MEYS CZ grant LM2015075, programme "Project of Large Infrastructure for Research, Development, and Innovations" and CZ.02.1.01/0.0/0.0/16_013/0001782, operational programme "Research, Development and Education". We thank two anonymous reviewers for their comments and Ingrid Steenbergen for editing the English.

Author Contributions

L.V. designed the study. L.V., I.V., P.B., L.K., J.P., Z.S., S.H.T.C., M.Š. and M.Č. participated in the field work. I.V. and M.K. did the stable isotope analyses. L.V. and M.Č. did the laboratory work. L.V., P.B. and A.P.E. conducted the statistical analysis. L.V. and I.V. wrote the first draft. All authors contributed substantial comments during manuscript preparation.

Additional Information

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-017-16169-9.

Competing Interests: The authors declare that they have no competing interests.

Paper III

Who is who: an anomalous predator-prey role exchange between cyprinids and perch

PLOS | ONE

RESEARCH ARTICLE

Who Is Who: An Anomalous Predator-Prey Role Exchange between Cyprinids and Perch

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Citation: Vejřík L, Matějíčková I, Seďa J, Blabolil P, Jůza T, Vašek M, et al. (2016) Who Is Who: An Anomalous Predator-Prey Role Exchange between Cyprinids and Perch. PLoS ONE 11(6): e0156430. doi:10.1371/journal.pone.0156430

Editor: Hideyuki Doi, University of Hyogo, JAPAN

Received: March 31, 2016

Accepted: May 15, 2016

Published: June 8, 2016

Data Availability Statement: The basic dataset used for the manuscript is attached as a supplemental file. In case of need, detailed data can be obtained on request from the database called fishecu.db (inventor: Daniel Ricard; current manager: Vilem Ded) created in pgAdmin III.

Funding: The study was supported by projects no. CZ.1.07/2.3.00/20.0204 (CEKOPOT) of the Ministry of Education, Youth and Sports (http://www.msmt.cz/), 7F14316 of the Norwegian Financial Mechanism 2009–2014 under contract number MSMT- 28477/2014 (http://nfm.mjs.bg/NFMs/EN/SitePages/Home.aspx), 206/09/P266 and 15-24309S of the Czech Science Foundation (http://www.udu.cas.cz/en/), and

Abstract

Piscivory in cyprinids (Cyprinidae) is extremely rare. Specifically, common bream (*Abramis brama*) and common carp (*Cyprinus carpio*) are zooplanktivorous fish in deep lentic waters. Nevertheless, we observed predation by these two cyprinids under natural conditions in the Vír Reservoir, Czech Republic. We conducted diet analysis for cyprinids caught by trawling and gillnets and the large amount of young-of-the-year (YOY) perch (*Perca fluviatilis*), with sizes of 37–52 mm standard length, were found in their digestive tracts. In 2010, a large amount of YOY perch caused a significant decrease in *Daphnia* spp. size and abundance in the reservoir. Hence, a food deficit was induced for the cyprinids, apparent also from the poor nutritional condition of common bream which was much worse than the condition of those in similar reservoirs. Common carp and common bream shifted to forced piscivory, and they utilized the YOY perch as an alternative food source. In contrast, smaller species, such as roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*), widely utilized planktonic cyanobacteria. In the following year, YOY perch occurred in significantly lower numbers and conversely, *Daphnia* spp. size and abundance were significantly higher. The forced piscivory was not observed. Our results indicate a switch to forced piscivory by cyprinids, which was caused by a shortage of their natural food source. Moreover, this phenomenon presents an effective mechanism for reduction in the numbers of YOY perch, ensuring the stability of the ecosystem.

Introduction

In freshwater ecosystems, two basic interactions between perch (*Perca fluviatilis*) and cyprinids (Cyprinidae) are commonly described. The first is the predator-prey interaction where adult perch prey on cyprinids [1–3]. In addition to the predatory role of adults, young-of-the year

159/2013/P of the Grant Agency of University of South Bohemia (http://www.jcu.cz/). D. Ricard was supported by project no. CZ.1.07/2.3.00/30.0032 of the Postdok BIOGLOBE co-financed by the European Social Fund and the state budget of the Czech Republic (http://alfa.bc.cas.cz/Postdok-BIOGLOBE/ (http://alfa.bc.cas.cz/Postdok-BIOGLOBE/)).

Competing Interests: The authors have declared that no competing interests exist.

(YOY) perch have also been documented to prey on YOY common bream (*Abramis brama*) [4], although zooplankton is their dominant prey item [5–8]. The second interaction is the interspecific competition. Although cyprinids are primarily omnivores [9,10], they are usually zooplanktivores in deep lentic waters [11,12]. Therefore, zooplankton, namely *Daphnia* spp., are an essential food source for both perch and cyprinids [3,12–15]. The competition for *Daphnia* spp. is indirectly emphasized by fish kairomones produced by abundant YOY perch. The presence of kairomones induces the shift of *Daphnia* spp. into deeper pelagic water layers, resulting in them being inaccessible to the fish [7,16–18].

Usually, extremely large YOY perch populations are effectively reduced by intercohortal cannibalism [19–23] or by other typical predators, such as pike (*Esox lucius*) and pikeperch (*Sander lucioperca*) [24–26]. A less studied mechanism for reducing YOY perch population is auto-reduction. In this case, the strong predation pressure on zooplankton causes depletion of the food source, and YOY perch consequently die from starvation [27]. No information about reduction of YOY perch by cyprinids has been previously presented.

Although cyprinids are known for their diet plasticity [9–11,28], piscivorous feeding is very rare. Except for asp (*Aspius aspius*) [29] and the *Labeobarbus* species flock [30], piscivory in cyprinids has only been observed to limited extent in common carp (*Cyprinus carpio*) [31,32] and rudd (*Scardinius erythrophthalmus*) [33–35].

Our study describes a reversal of the typical predator-prey interaction between perch and cyprinids. Specifically, it is focused on (a) the impact of an extremely numerous YOY perch cohort on zooplankton and the effect this has on the population of cyprinids, (b) the highest rate of cyprinids piscivory observed to date and the first proof of piscivory by the common bream, and (c) a general discussion of the significance of piscivorous feeding by omnivorous cyprinids.

Methods

Study area

The main part of the present study was conducted in the canyon-shaped Vír Reservoir located in the eastern part of the Czech Republic (49°34′ N; 16°18′ E; Fig 1). The maximum surface altitude is 464 m a.s.l. The reservoir has a surface area of c. 224 ha, a length of 9.3 km and total water volume of c. 56 × 10^6 m^3. Maximum and mean depths are 64 m and 25 m, respectively. It is characterized as eutrophic, and since 1992, cyanobacterial blooms have increasingly occurred, dominated mainly by *Microcystis* sp. [8].

As a comparison, two reference reservoirs (Vranov and Římov) were used for the length-mass relationship in common bream and for the size and abundance of *Daphnia* spp. The eutrophic Vranov Reservoir is a canyon-shaped reservoir located in the southeastern part of the Czech Republic (48° 54′ N, 15° 48′ E; 352 m a.s.l.). The reservoir has a surface area of 761 ha, a length of 28 km and total water volume of c. 133 × 10^6 m^3. The maximum and mean depths are 45 m and 15 m, respectively [36]. The meso- to eutrophic Římov Reservoir is a narrow, canyon-shaped reservoir located in the southern part of the Czech Republic (48°50′ N, 14°30′ E; 472 m a.s.l.; Fig 1). The reservoir has a surface area of 210 ha, a length of 9 km and total water volume c. 34 × 10^6 m^3. The maximum and mean depths are 45 m and 16 m, respectively [11].

Abiotic factors

In the Vír Reservoir, water temperature and transparency were measured 10:00–14:00 (day sampling) in conjunction with the zooplankton sampling. To distinguish the epi-, meta- and hypolimnion, temperatures were measured at 1-m intervals throughout the entire water column of a dam section of the reservoir (to a maximum depth of 55 m, or when the probe

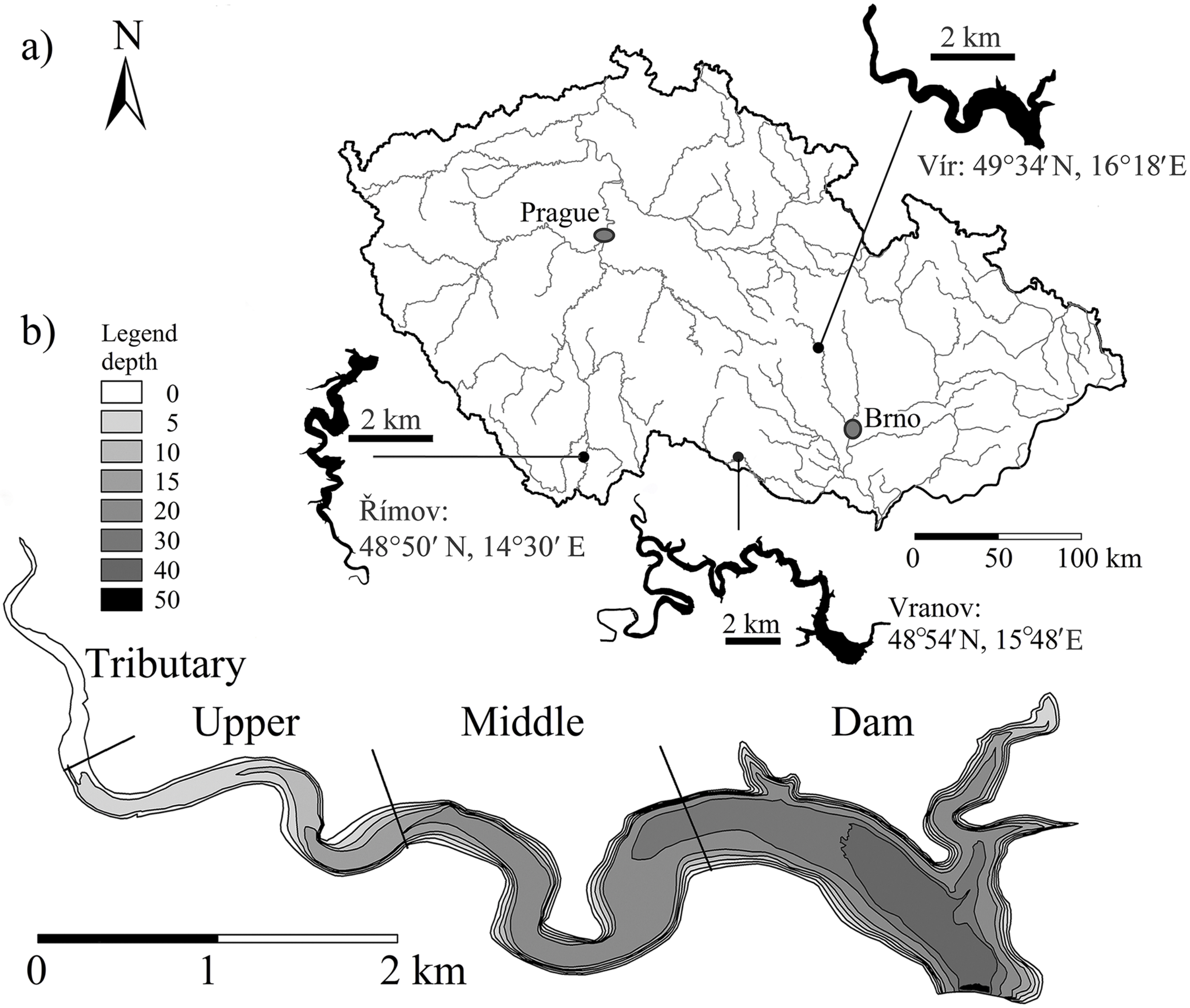

Fig 1. A map showing the location of the Vír, Vranov and Římov Reservoirs in the Czech Republic (a) and a detailed view of the bathymetric map of the Vír Reservoir (b). In (b), 0 corresponds to the surface level in late July 2010. The legend shows contour lines with relevant depths. The sampling design of the Vír Reservoir consisted of four sections (Tributary, Upper, Middle and Dam) along its longitudinal gradient.

doi:10.1371/journal.pone.0156430.g001

reached the bottom) using a calibrated YSI 556 MPS probe. A Secchi disk was used to measure the water transparency.

Trawl sampling

In the Vír Reservoir, trawling for adult fish was conducted during the night of July 27, 2010 (22:00–03:00). A pelagic trawl with a mouth opening of 13×8 m was used to sample adult fish. The trawl was towed approximately 100 m behind the research vessel, usually for 10–25 minutes, at speeds of 1.1–1.5 m s^{-1}. For technical details, see Vejřík *et al.* [8]. The reservoir was divided into four approximately equidistant sections along its longitudinal axis, the dam, middle, upper and tributary sections; each section was approximately 2 km in length (Fig 1). Five tows were conducted in the dam and middle sections of the reservoir. It was not possible to conduct tows in the open water layers of the upper and tributary reservoir sections due to insufficient depth in these sections. All fish from each trawl tow were immediately anaesthetized by a lethal dose of tricaine methanesulfonate (MS–222, Sigma Aldrich Co.). The fish were identified to the species level, counted, measured (SL–standard length, and TL–total length) and weighed. The adult trawling was not repeated in 2011 due to incredibly demanding and time-consuming sampling campaign involving financial and manpower limitations. Trawling for YOY fish was carried out on July 26 (night) and July 27 (day), 2010, and on July 31 (night) and August 1 (day), 2011. A pelagic, fixed-frame fry trawl with a mouth opening of 3×3 m was used to sample the YOY fish. The trawl was towed approximately 100 m behind the research vessel, usually for 10 minutes, at speeds of 0.8–1.1 m s^{-1}. A total of 63 tows were conducted. For technical details, see Vejřík *et al.* [8]. All of the juvenile fish from each trawl tow were immediately anaesthetized by a lethal dose of MS–222 and subsequently preserved in 4% formaldehyde. In the laboratory, the fish were identified to the species level and counted. SL was measured on 1,000 individual YOY perch from both years. The catch was expressed as the number of fish per 100 m^3 of water volume sampled.

Pelagic gillnet sampling

In addition to adult trawling, pelagic gillnets were used to sample adult cyprinids in the open water of the Vír Reservoir in 2010 and 2011. They were also used to sample the common bream used as reference from the Římov Reservoir in 2010 and the Vranov Reservoir in 2011.

Gillnets were placed from the surface to a depth of 4.5 m and between 5 and 9.5 m. The design of the pelagic gillnets followed the European standard [37] and was supplemented by gillnets with larger mesh sizes according to [38]. Gillnets (n = 3 per section for both types) were set one hour prior to sunset and collected one hour after sunrise to cover the highest peaks in fish activity [39] in the dam, middle and upper reservoir sections on July 28 in 2010 and August 2 in 2011 in the Vír Reservoir, on July 27, 2011 in the Vranov Reservoir and on August 10, 2010 in the Římov Reservoir. In the upper section, gillnets were not set at 5–9.5 m depth due to shallow water. A total of 18 gillnets were set to the 0–4.5 m depth and 12 to the 5–9.5 m depth. The fish used for gut content analysis were taken out three hours after installation, and the remaining fish were taken out at the end of installation. All fish from the gillnets were immediately anaesthetized using a lethal dose of MS–222, identified to the species level, counted, measured (SL, TL) and weighed.

Zooplankton sampling

Zooplankton was sampled near the dam during the daytime on June 9 and July 27, 2010 and on June 3 and July 30, 2011 in the Vír Reservoir. In the reference reservoirs, zooplankton was sampled on June 6 and July 22, 2011 in the Vranov Reservoir and on June 7 and July 26, 2010 in the Římov Reservoir. Nighttime sampling was not conducted, as previous studies have confirmed no apparent diurnal vertical migration by zooplankton in manmade reservoirs [40] in contrast to results from natural lakes [7].Two different closing nets were used because the abundance of zooplankton differed by more than one order of magnitude between the upper and deep water layers. A net with an opening of 24 cm (diameter) was used for the epilimnion, and a net with an opening of 40 cm was used for the deeper water layers. Both nets had a 170-μm mesh size. The zooplankton samples were immediately preserved in 4% formaldehyde. Zooplankton samples were collected in four independent replications from the epi-, meta- and hypolimnion. Zooplankton specimens were identified to species level according to [41,42] using a microscope

(Olympus CX40), and counted according to [43]. Each zooplankton sample was diluted so that subsampling by a wide mouth pipette resulted in c. 200–250 individuals. Four subsamples were counted separately in a Sedgewick-Rafter counting chamber. When abundances in the bulk sample were low (usually from the deep water strata), the whole sample was processed. Abundance was calculated as an average per 1 L of water within each 3 m thick depth layer. Only the abundance of *Daphnia* spp. was used in this study because it dominates the diet of the fish. The *Daphnia* communities in the Vír and Vranov Reservoirs were identified as belonging to the *Daphnia longispina* complex and those in the Římov Reservoir to the *Daphnia galeata*. For more details, see [44,45]. A subsample of 300 individuals from each layer was digitally photographed under the microscope for subsequent measurement of carapace size. The minimum size for individuals capable of reproduction was determined to be 0.95 mm, according to [44].

Diet analysis

Diet analysis was conducted for randomly chosen individual common bream. Specifically, 100 individuals from the adult trawling and 50 individuals from the pelagic gillnets in 2010 and all individuals from the pelagic gillnets in 2011 were dissected. Diet analysis was conducted for all common carp, roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*) captured by the adult trawl in 2010 and for 50 randomly chosen individual bleak and 50 randomly chosen individual roach captured by pelagic gillnets in 2011.

The digestive tracts of cyprinids were dissected and preserved in a 10% formaldehyde solution for subsequent laboratory analysis. All three intestinal loops were examined. The percent composition of the diet by volume was visually estimated and the state of the food remains was evaluated (well-preserved, slightly digested, highly digested). Five categories of food were distinguished: YOY fish, zooplankton, insects or zoobenthos, planktonic cyanobacteria (mainly *Microcystis* sp.) and detritus. Species and size were directly determined in the case of well-preserved fish collected from the digestive tracts. The more digested fish from the digestive tracts were identified to the species level and size using a reference collection with diagnostic bones of each potential prey species [46,47].

The vertebrate work was approved by the Ethics Committee of the Czech Academy of Sciences. All sampling procedures and experimental manipulations were approved by the Czech Academy of Sciences, Morava River Authority and the Environmental Department of the Municipal Authority of the Town of Brno. The field study did not involve endangered or protected species.

Statistical analysis

The nonparametric Kruskal-Wallis test was used to compare the differences between YOY perch length found in common carp and common bream digestive tracts and between the YOY perch length in the Vír Reservoir in 2010. The same test was used to compare the differences of YOY perch abundances between 2010 and 2011.

One-way ANOVA was used to test the differences of YOY perch length between 2010 and 2011. The same test was used for one set of variables concerning the zooplankton data. A chi-square test (χ^2) was used to compare the contribution of piscivorous common bream in the population between 2010 and 2011. Further, the same test was used to compare the contribution of zooplankton and cyanobacteria in the roach and bleak diets between 2010 and 2011. A chi-square test (χ^2) was also used to compare the ratio of zooplankton abundance within the pelagic water layers between June 2010 and 2011 and between July 2010 and 2011.

A generalized linear model with a log link function was used to fit and compare the length-mass relationships of 188 common bream with SL larger than 260 mm (hereafter referred to as minimum length, min SL) obtained by sampling the three reservoirs (Vír, Vranov and Římov) in 2010 and 2011. Because of the length restriction (common bream $>$ 260 mm SL) the minimum size was set to zero. Therefore, intercepts and exponents for each model could be easily compared. Factorial ANOVA was used to test for differences in zooplankton sizes. Tukey's HSD post-hoc test was used to compare the differences in zooplankton sizes within the pelagic water layers (epi-, meta-, and hypolimnion).

Fulton's condition factor (*FCF*) [48] was calculated as:

$$FCF = \frac{m}{TL^3} \times 100$$

where m stands for fish mass (g) and TL for fish total length (cm).

The prey-to-predator length ratio (*PPR*) was calculated as:

$$PPR = \frac{SL_{Py}}{SL_{Pr}}$$

where SL_{Py} stands for SL of prey and SL_{Pr} for SL of a predator.

All statistical tests were performed in the R environment for statistical computing (version 3.2.2) [49].

Results

YOY fish

During the last week of July in 2010 and 2011, 45,047 YOY fish of seven species were caught by fry trawl in the Vír Reservoir: perch, pikeperch, common bream, bleak, roach, ruffe (*Gymnocephalus cernuus*) and European catfish (*Silurus glanis*). Percids made up 99% of the catch in both years and in all sampled reservoir sections at all depths, except at the 0–3 m depth in the upper section in 2011, where cyprinids were predominant. The most abundant species was perch followed by pikeperch. According to the averaged values from all tows, perch composed 98% (12.1 ind. 100 m^{-3}) of daytime and 99% (50.9 ind. 100 m^{-3}) of nighttime catches in 2010 and 84% (0.7 ind. 100 m^{-3}) of daytime and 99% (1.32 ind. 100 m^{-3}) of nighttime catches in 2011 (Fig 2). Significant decrease of YOY perch abundance between the years 2010 and 2011 was observed. Compared to situation in 2010, the mean daytime and nighttime YOY perch densities in 2011 declined by 94% and 98%, respectively. Both differences were statistically significant ($H_{2,34} = 4.7$ $P = 0{,}03$ for daytime catches and $H_{2,29} = 6.2$ $P = 0.01$ for nighttime catches). SL (mean ± SD) of YOY perch were 44.2 ± 3.3 mm in 2010 and 37.5 ± 4.1 mm in 2011. The length differences was statistically significant ($F_{1,2000} = 1622$, $P < 0.001$).

Adult fish and diet

During the adult night trawling in 2010, 1,042 fish of 11 species were caught in the Vír Reservoir. Four species of zooplanktivores were caught: common bream, common carp, bleak and roach. Common bream dominated the catch, making up in excess of 85% of the captured fish (886 individuals), followed by common carp (3.6%, 37 individuals), bleak (3%, 31 individuals) and roach (2%, 21 individuals). Typical fish predators, such as European catfish, European eel (*Anguilla anguilla*), pikeperch, asp and perch composed only 6.4% of the catch (a total of 67 individuals).

Another 1,082 individual fish older than YOY were caught by pelagic gillnets in the Vír Reservoir. Four species of zooplanktivores and benthivores were caught: common bream, bleak, roach and common carp. Bleak composed 64.1% of the total catch (693 individuals). Common bream was the second most common species at 15.1% of the total catch (164 individuals),

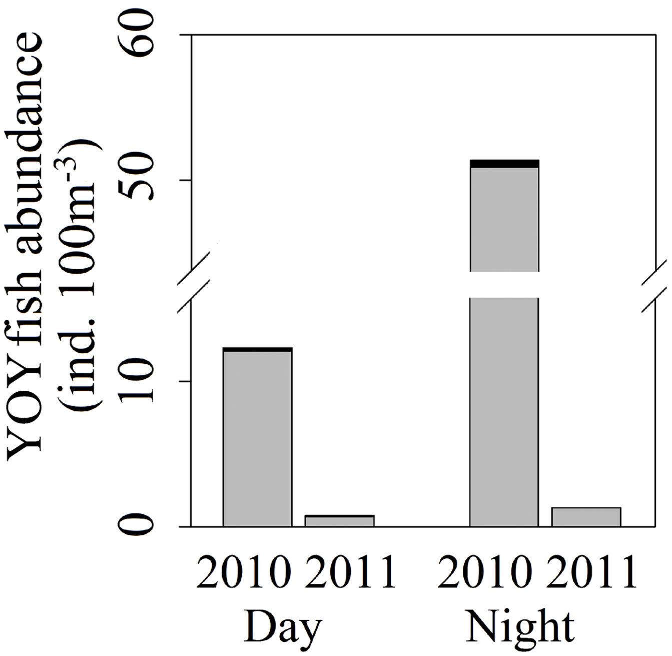

Fig 2. Abundance of YOY fish in pelagic water layer of the Vír Reservoir in 2010 and 2011. Mean abundance of YOY perch (grey colour)and other YOY fish (black colour)according to the fry trawl catches (Number of tows: 63, sampled water volume: 337.413 m^3).

doi:10.1371/journal.pone.0156430.g002

roach composed 9.1% of the total catch (99 individuals) and common carp composed only 0.4% of the total catch (4 individuals). Typical predators such as pikeperch, asp and perch composed 11.3% of the total catch (122 individuals).

In adult trawl catches in 2010, YOY fish were found in the diet of 72 individual common bream (48%) out of the 150 analyzed individuals within the SL range of 255 and 390 mm (mean ± SD: 304 ± 31.6 mm). In addition, YOY fish were found in 22 individual common carp (60%) out of the 37 individuals within the SL range of 155 and 285 mm (290 ± 26.7 mm). Neither roach (SL 100–260 mm, 180 ± 18.4 mm) nor bleak (SL 85–130 mm, 113 ± 10.1 mm) contained fish in their digestive tracts (Fig 3). All YOY fish found in common bream and common carp digestive tracts were identified as perch. YOY perch comprised 25–100% (mean 69%) and 33–100% (mean 73%) of the gut content in piscivorous common bream and common carp, respectively. The rest of the gut content in both fish species was composed primarily of zooplankton, with detritus also found in common carp. The roach diet was composed of zooplankton, planktonic cyanobacteria (*Microcystis* sp.) and detritus. The bleak diet consisted of planktonic cyanobacteria, zooplankton and terrestrial insects. Further, the diet analysis provided for 50 individual common bream and 4 individuals of common carp from gillnets revealed YOY fish in the diet of 25 individual common bream (50%) within the SL range of 230 and 385 mm (mean ± SD: 301 ± 25.6 mm). In common carp, YOY fish were found in 3 individual common carp (75%) within the SL range of 200 and 280 mm (227 ± 35.9 mm) (Fig 3). The contribution of piscivorous common bream and common carp in trawl catches and gillnet gatches did not statistically differ in 2010 ($\chi^2 = 0.46$, $P = 0.49$, and $\chi^2 = 3.6$, $P = 0.06$).

In 2011, 750 individual fish older than YOY were caught by pelagic gillnets in the Vír Reservoir. Three species of zooplanktivores and benthivores were caught: common bream, bleak and roach. Common carp were not caught in 2011. Bleak composed 70% of the total catch (520 individuals). Common bream was the second most common species at 11% of the total catch

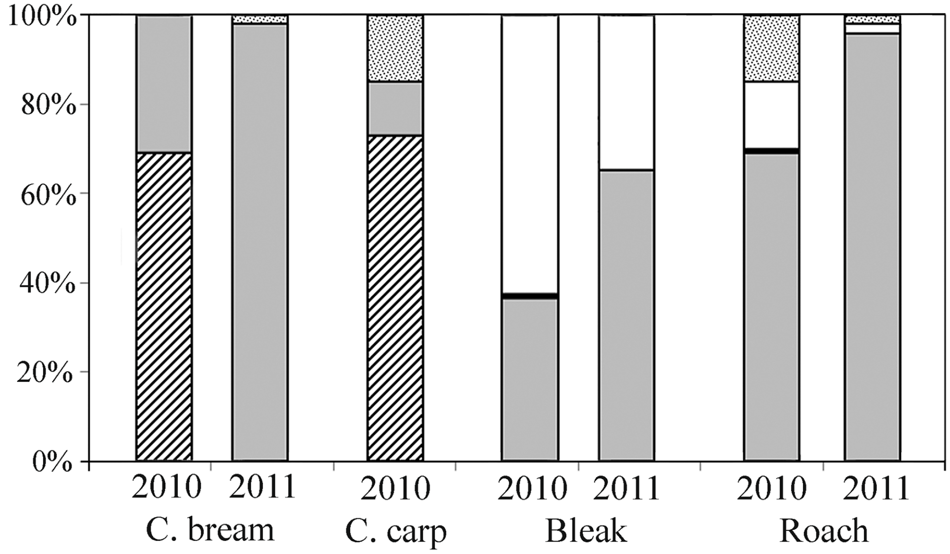

Fig 3. The gut contents of cyprinids from the Vír Reservoir in 2010 and 2011. The caught cyprinids were: common bream (*Abramis brama*), common carp (*Cyprinus carpio*), bleak (*Alburnus alburnus*) and roach (*Rutilus rutilus*). No common carp were caught in 2011. The gut content was divided into five categories: YOY fish (dashed), Zooplankton (grey), Insect and Zoobenthos (black), Planktonic Cyanobacteria (white), and Detritus (dotted).

doi:10.1371/journal.pone.0156430.g003

(85 individuals) and roach composed 10% of the total catch (78 individuals). Typical predators such as pikeperch, asp and perch composed 9% of the total catch (67 individuals). In 2011, no YOY perch were found in the digestive tract of common bream.

YOY fish found in the first intestinal loop of common bream and common carp in 2010 were well-preserved and easily identifiable and measurable. The preservation decreased in the second intestinal loop. White, highly digested emulsion was mostly found in the third loop. Ninety-four individual YOY perch from common bream digestive tracts could be measured. Their SL was between 37 and 52 mm (mean ± SD: 44.7 ± 2.8 mm). Although the size of YOY perch in common bream digestive tracts was slightly larger than in the overall reservoir, the difference was insignificant ($H_{2,195} = 2.27$, $P > 0.1$). Thirty-five individual YOY perch from common carp digestive tracts could be measured. Their SL was between 38 and 50 mm (44.3 ± 3.5 mm). The size difference between YOY perch in common carp digestive tracts and in the overall reservoir was insignificant ($H_{2,136} = 0.427$, $P > 0.5$). Prey-to-predator length ratios (PPR) ranged from 0.10 to 0.17 (mean: 0.13) for bream and from 0.14 to 0.24 (mean: 0.19) for common carp.

There was a significant decrease in the contribution of piscivorous individual common bream in the population between 2010 and 2011 ($\chi^2 = 85.4$, $P < 0.001$). In 2011, no YOY perch were found in digestive tracts of analyzed fish. The diet of common bream (SL 240–380 mm, mean ± SD: 311 ± 21.6 mm) was composed of zooplankton (98%) and detritus (2%). Zooplankton was also the main component of the diet for roach (SL 85–255 mm, 165 ± 21.1 mm). In the roach diet, the contribution of zooplankton significantly increased ($\chi^2 = 189.8$, $P < 0.001$), and in contrast, the contribution of planktonic cyanobacteria significantly decreased ($\chi^2 = 86.2$, $P < 0.001$) between 2010 and 2011. In the bleak diet (90–135 mm, 120 ± 11.4 mm), similar trend of increase of zooplankton ($\chi^2 = 26.1$, $P < 0.001$) and decrease of planktonic cyanobacteria ($\chi^2 = 36.1$, $P < 0.001$) was observed between 2010 and 2011.

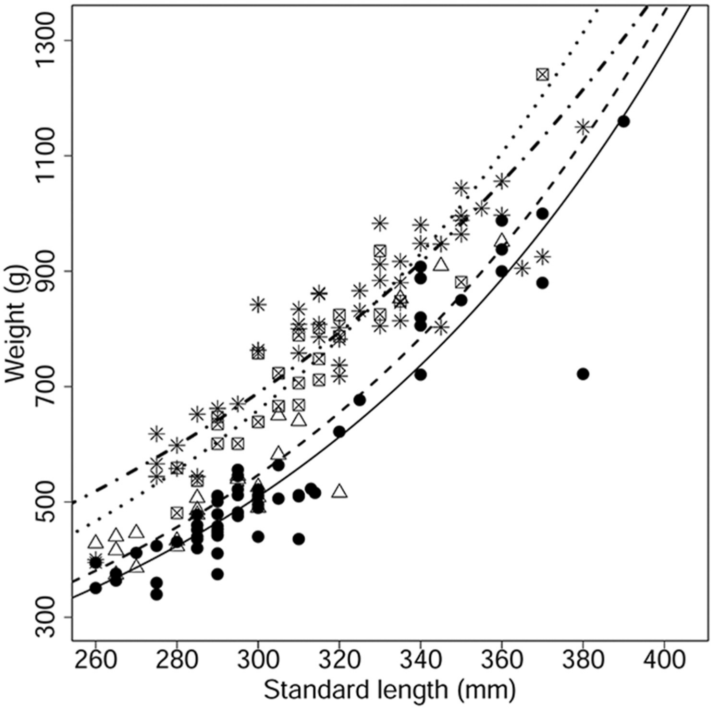

Fig 4. Comparison of length-weight relationships of common bream (*Abramis brama*). Data of 179 individuals with standard length > 260 mm were obtained by sampling from three reservoirs in 2010 and 2011. The comparison was performed by generalized linear model with a log link function. Legend: Vír Reservoir 2010 (designated with dots and solid line, $y = 5.864 \times e^{0.0092}$), Vír Reservoir 2011 (triangles and dashed line, $y = 5.942 \times e^{0.0090}$); Vranov Reservoir 2011 (crossed square and dotted line, $y = 6.146 \times e^{0.0086}$) and Římov Reservoir 2010 (asterisk and dash-dotted line, $y = 6.252 \times e^{0.0071}$).

doi:10.1371/journal.pone.0156430.g004

Bream condition

The poor nutritional condition of bream in the Vír Reservoir in 2010 was apparent from their length-mass relationship in comparison to the bream from the Vír Reservoir in 2011 and to those from the Římov and Vranov Reservoirs (Fig 4). The comparison of length-mass relationships by generalized linear models with log link functions revealed a significant difference between the intercepts for the Vír Reservoir bream from 2010 and those for the bream from the other sampling campaigns ($P < 0.05$). However, the changes in exponents were similar ($P > 0.05$), with the exception of those from the Římov Reservoir analysis ($P < 0.001$). This means that the growth curves of fish were similar in all reservoirs, but the mass at the same length was different. The lowest length-mass relationship was found for common bream from the Vír Reservoir in 2010. The following year the curve was higher, but it was still below the reference reservoirs (Fig 4).

Means of the Fulton's condition factor for common bream in particular reservoirs were as follows: $FCF_{(\text{Vír 2010})} = 0.975 \pm 0.091$ (mean ± SD), $FCF_{(\text{Římov 2010})} = 1.251 \pm 0.140$ (mean ± SD), $FCF_{(\text{Vranov 2011})} = 1.243 \pm 0.065$ (mean ± SD) and $FCF_{(\text{Vír 2011})} = 1.085 \pm 0.156$ (mean ± SD). Both analyses (results of length-mass relationships and Fulton's condition factors) indicate that the worst bream condition was found in 2010 in the Vír Reservoir and that there was an apparent improvement in 2011.

Zooplankton

The *Daphnia* community in the dam section of the Vír and Vranov Reservoirs was formed by the *Daphnia longispina* species complex, which was dominated by *D. longispina*, *D. galeata* and their hybrids. All specimens are subsequently referred to as *D. longispina* cp. The presence of *D. cucullata* was recorded in 2010 in the dam section of the Vír Reservoir. The *Daphnia* community in the dam section of the Římov Reservoir was formed by the *Daphnia galeata*.

Both the abundance and size of *D. longispina* cp in the Vír Reservoir differed among the depth layers and between the sampled months and years (Fig 5; Table 1). The carapace size in the upper layers (i.e., epi- and metalimnion) significantly decreased between June and July 2010 (epilimnion: $F_{1,608} = 290$, $P < 0.001$; metalimnion: $F_{1,604} = 1{,}091$, $P < 0.001$). In contrast, the size significantly increased in the hypolimnion ($F_{1,615} = 59$, $P < 0.001$). In 2011, the differences in the size of *D. longispina* cp in particular pelagic layers were less apparent between June and July. A significant decrease in size was noticed only in epilimnion ($F_{1,576} = 84$, $P < 0.001$; Fig 5; Table 1). In the reference reservoirs, a decrease in the size of *Daphnia* spp. in the epi- and metalimnion was observed also in the Vranov Reservoir between June and July, and an increase in size was observed in the Římov Reservoir. Nevertheless, the sizes in both reference reservoirs were significantly larger than in the Vír Reservoir in 2010 ($F_{2,1800} = 1225$, $P < 0.001$). In addition, the decrease in size in *Daphnia* spp. from the Vranov Reservoir was not as apparent as in those from the Vír Reservoir in 2010 (Table 1). In the Vranov Reservoir, a slight increase in the size of *D. longispina* cp in the hypolimnion was observed, but again it was apparently less than the size change in the Vír Reservoir in 2010.

The data come from sampling of dam sections in June and July of given years for particular pelagic water layers (epi-, meta- and hypolimnion). The extreme period with high predation pressure of YOY perch is shown in bold.

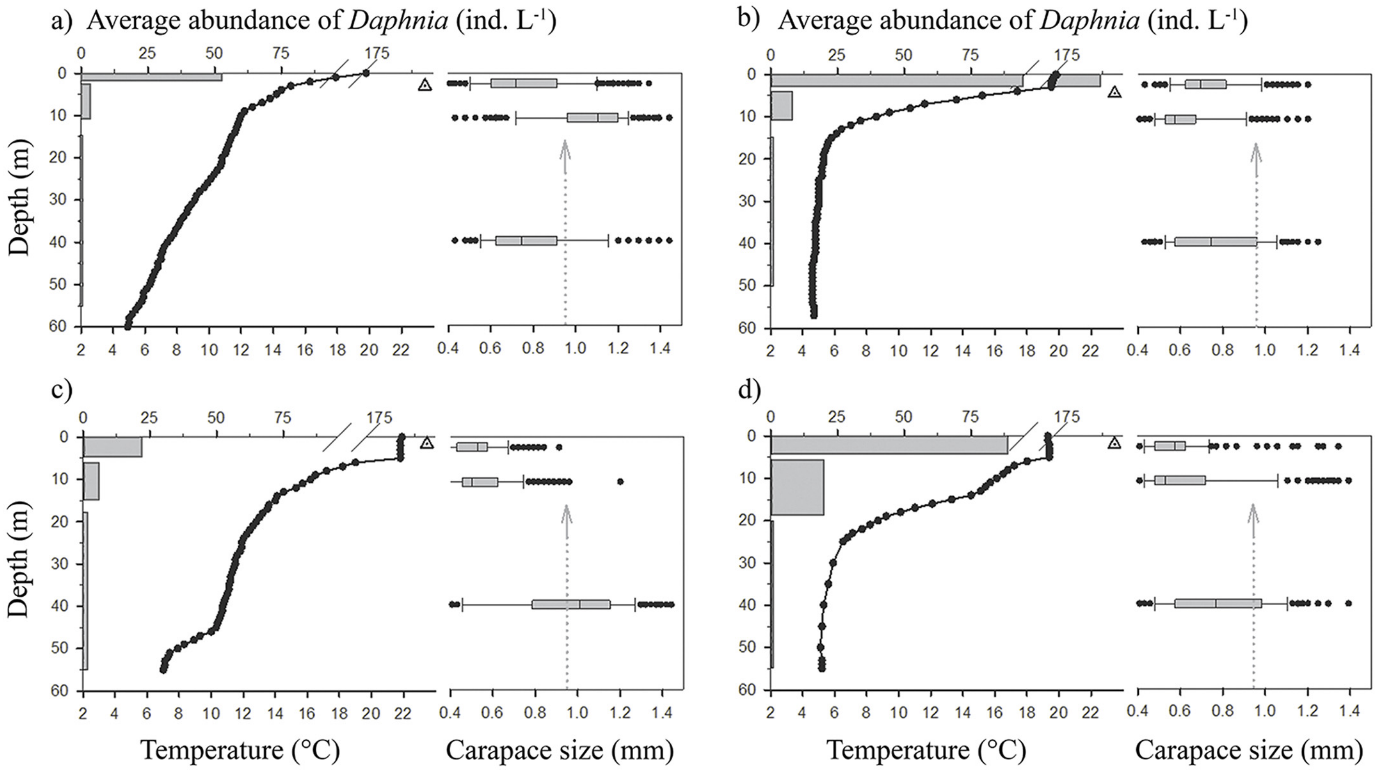

Fig 5. Vertical profile of abundance (horizontal bars for epi-, meta- and hypolimnion) and carapace size (box and whisker plots) of *D. longispina* cp. Data were obtained in the dam section of the Vír Reservoir in 2010 for a) June and c) July, and in 2011 for b) June and d) July. Black lines with black dots show the vertical temperature profiles. Box and whiskers plots: median values, upper and lower quartiles (boxes), maximum and minimum values (whiskers), and all outliers (dots) are shown. Arrows with dotted line indicate the minimum carapace size needed for reproduction according to Petrusek *et al*. [44]. The triangle in the center indicates water transparency measured by Secchi disk.

doi:10.1371/journal.pone.0156430.g005

Table 1. Mean carapace size (± S.D.), mean abundance (± S.D.) and population percentage share (PPS; i.e., relative *Daphnia* abundance from the entire water column) of *D. longispina* complex in the Vír, Římov and Vranov Reservoirs.

Water	Parameter	Vír 2010		Vír 2011		Římov 2010		Vranov 2011	
layer		June	July	June	July	June	July	June	July
Epi-	Mean carapace size	0.75	**0.51**	0.73	0.59	0.66	0.75	0.9	0.6
	±SD (mm)	±0.21	**±0.12**	±0.18	±0.17	±0.20	±0.30	±0.28	±0.20
	Mean abundance	53	**21.89**	191.8	88.8	60	35	40.5	46.3
	±SD (ind. L^{-1})	±5.08	**±1.27**	±14.7	±8.95	±6.01	±2.5	±4.98	±5.05
	PPS (%)	74	**51**	87	55	74	72	86	96
Meta-	Mean carapace size	1.04	**0.54**	0.62	0.63	0.93	0.64	0.72	0.57
	±SD (mm)	±0.22	**±0.14**	±0.17	±0.25	±0.31	±0.26	±0.21	±0.16
	Mean abundance	3.65	**5.9**	8.23	19.8	7	1	4	1.43
	±SD (ind. L^{-1})	±0.53	**±0.56**	±1.32	±1.50	±1.65	±0.2	±0.54	±0.15
	PPS (%)	20	**25**	9	40	17	18	10	3
Hypo-	Mean carapace size	0.79	**0.95**	0.77	0.78	0.94	0.83	0.77	0.81
	±SD (mm)	±0.22	**±0.29**	±0.21	±0.24	±0.32	±0.27	±0.22	±0.27
	Mean abundance	0.25	**1.35**	0.68	1.3	0.5	0.4	0.66	0.17
	±SD (ind. L^{-1})	±0.06	**±0.24**	±0.19	±0.1	±0.16	±0.09	±0,2	±0.05
	PPS (%)	6	**24**	4	5	9	10	4	1

doi:10.1371/journal.pone.0156430.t001

D. longispina cp sizes in the hypolimnion of the Vír Reservoir in July of both years were significantly larger than in the epilimnion and metalimnion ($P < 0.001$ for all tests). However, the size differences were more obvious in July 2010. That year, almost no epilimnetic and metalimnetic individuals reached the minimum size needed for reproduction. In contrast, *D. longispina* cp sizes in the hypolimnion were larger, indicating that individuals capable of reproduction found a refuge in the deeper water layer (Fig 5). Such a distinct size difference of *Daphnia* spp. was not observed in either reference reservoirs (Table 1).

The population percentage share (i.e., relative *Daphnia* abundance from the entire water column) in the metalimnion and in the hypolimnion was higher in July than in June in both years. The highest population percentage share in the hypolimnion was observed in July 2010 (24%) and the lowest was observed in June 2011 (4%). The population percentage share of *D. longispina* cp within the water layers was significantly different between July 2010 and 2011 ($\chi^2 = 24.4$, $P < 0.005$). The difference was also significant between June 2010 and 2011 ($\chi^2 = 9.0$, $P < 0.05$) but less so than in the July comparison (Table 1). The population percentage share in the hypolimnion was markedly higher in the Vír Reservoir in July 2010 than in all other observed periods and reservoirs (Table 1).

Discussion

Although Cyprinidae is one of the most species-rich (> 2000 species) and widespread freshwater fish family [50], piscivory is an extremely rare foraging strategy among this successful fish group [30]. Cyprinids are not well designed for piscivory because they lack teeth in their oral jaws, have a small slit-shaped pharyngeal cavity and lack a stomach with a low pH for digesting fish prey [30]. The only piscivorous cyprinids are the asp [29,51] and *Labeobarbus* species flock in Lake Tana, Ethiopia, where 8 of 15 species show signs of piscivory [30]. Facultative piscivory was rarely observed in introduced rudd and emerald shiner (*Notropis atherinoides*) in the Niagara River [34,35]. Furthermore, piscivory by rudd was probably observed in an experimental English lake with topmouth gudgeon (*Pseudorasbora parva*) as prey [33]. Piscivory was also observed for common carp on introduced topmouth gudgeon under experimental conditions [32] and for introduced common carp on small fish, probably tilapia (*Tilapia zillii*), in Naivasha Lake, Kenya [31]. Therefore, facultative piscivory has only been observed in introduced species or on introduced prey species where the natural species balance was affected in the ecosystem. In the situation presented here, perch, common bream and common carp are indigenous species in the Vír Reservoir of the Morava River catchment area [52].

Common bream and common carp diets consist mainly of zooplankton and zoobenthos in various proportions depending on the food availability and the location [11,14,29,53–55]. Hence, facultative piscivory by common bream and common carp in the Vír Reservoir is best explained as a reaction to the scarcity of invertebrate prey, specifically small sizes and low numbers of *D. longispina* cp in July 2010. During that piscivorous period, the average size of *D. longispina* cp was extremely small in the epilimnion (mean: 0.51 mm). Therefore, it did not reach the critical reproduction size. This was clear evidence of an extremely high predation pressure (*cf.* [44]). In contrast, *Daphnia* spp. sizes were apparently larger in the epilimnion layers of the Vír Reservoir in 2011 and of the reference reservoirs (Vranov, mean: 0.62 mm and Římov, mean: 0.75 mm). The presence of extremely high predation pressure in the Vír Reservoir in 2010 is supported by the occurrence of small-sized *Daphnia cucullata* in the dam section. This species commonly occurs only in the tributary section of reservoirs [44,56] where high fish biomass induces high predation pressure on zooplankton [57]. High predation pressure on zooplankton from YOY perch is also apparent from the gut content of other cyprinids. In 2010, a distinct share of planktonic cyanobacteria with a low nutritional value was found in bleak (mean: 60% of the gut content) and roach (mean: 15% of the gut content). In contrast, the share of planktonic cyanobacteria significantly decreased for both bleak (mean: 15% of the gut content) and roach (mean: 2% of the gut content) and the contribution of zooplankton increased in 2011. Utilization of cyanobacteria by cyprinids is typical for periods with significant food deficit [58,59].

In the Vír Reservoir in 2010, large individuals of *D. longispina* cp capable of reproduction occurred only in the hypolimnion refuge, which is avoided by cyprinids due to its low temperature, low oxygen concentration [8] and almost complete darkness [60]. This seeking of refuge by zooplankton in deep water layers due to intensive predation by YOY perch and the presence of YOY perch kairomones acting as a trigger is a well-known behavior [7,16,17]. Because *Daphnia* spp. were predominant in the YOY perch diet in the Vír Reservoir [8] and the number of YOY perch reached extreme values of 50.9 ind. 100 m^{-3} (mean) in 2010, the impact on zooplankton was substantial. The number of YOY perch was significantly lower in 2011 (1.32 ind. 100 m^{-3}) causing lower predation pressure on zooplankton. Nevertheless, the number of YOY perch is commonly even lower, averaging 0.1 ind. 100 m^{-3} for nine other Czech reservoirs, including both reference reservoirs [61,62]. Accordingly, predation pressure of YOY perch on zooplankton must have been extremely high in the Vír Reservoir in 2010. Forced facultative piscivory by common bream and common carp was probably induced by extreme conditions, specifically a short-term but substantial absence of their planktonic food source. This resulted in a poor nutritional condition of common bream in the Vír Reservoir in 2010. Additionally, the length-mass relationship for common bream was significantly lower in 2010 than in 2011 in the Vír Reservoir and it was lower than for bream from either reference reservoirs. In 2011, no forced piscivory by common bream was observed. This poor nutritional state in 2010 was caused either by drastic traditional food limitation or by an inability to fully digest fish as an alternative and easily accessible food source, as was described by De Graaf *et al.* [30]. In this case, it was probably a combination of both factors.

Considering no significant difference in share of piscivorous common bream and common carp between trawl catches and gillnet catches in 2010, the gillnet catches were representative enough for the year 2011 However, the share of common carp in total gillnet catches was very low in 2010 and no individual was caught in 2011. From that reason, we can not confirm or disconfirm the piscivory by common carp in 2011. Absence of common carp in 2011 could be caused by low catch efficiency by gillnets towards this species (*cf*. trawl catches and gillnet catches in 2010) or decrease of common carp abundance in Vír Reservoir between 2010 and 2011 (*e.g*. by poaching).

The PPR of piscivorous common bream and common carp were on average 0.13 and 0.19, with maximum values of 0.17 and 0.24, respectively, which are very low values in general. Similarly low values were found for piscivorous *Labeobarbus* of Lake Tana (mean: 0.15, max: 0.25) [63]. These low values are likely due to the physiological limitations of cyprinids, which tend to be severely gape limited. In contrast, PPRs of non-cyprinid freshwater piscivores reach mean values from 0.25 to 0.40 and maximum values from 0.40 to 0.70 [64,65]. No statistical differences between length of YOY perch in the reservoir and in the digestive tract of common bream and common carp in 2010 indicated any diet preferences towards smaller or bigger individuals. Thus, significantly smaller YOY perch in the Vír Reservoir in 2011 was not a reason for absence of the piscivory. Due to gape limit of cyprinids (theoretical PPR for bream = 0.12), smaller YOY perch would be more likely expected to support piscivory. Therefore, the piscivory in 2010 was clearly induced by absence of primary food sources for common bream and common carp and not by simple preference for abundant fish prey.

The predation strategy of common bream and common carp remains as an unanswered question. According to Sibbing & Nagelkerke [66], some of Lake Tana's piscivores of the *Labeobarbus* group likely use a variety of strategies (e.g., ambush hunters versus pursuit hunters). Based on the common bream and common carp mouth morphology, the strategy of a pelagic ambush hunter using velocity suction with protrusion is most probable [67]. This strategy has been demonstrated by *Labeobarbus megastoma* and *L. macrophthalmus* in Lake Tana [30]. Although the strategy of cyprinids is not fully clear, the lack of a significant difference between the length of YOY perch found in cyprinid digestive tracts and of those caught in the reservoir indicates that common bream and common carp did not prefer any particular sizes and that the prey selection likely depended on random encounters.

Despite of no information about common bream piscivory and scarce information about common carp piscivory in the scientific literature [31,32], this phenomenon may not be rare and may just be under studied. Common bream and common carp piscivory in the Vír Reservoir in 2010 occurred to a great extent and was apparently induced by extreme conditions caused by a large amount of YOY perch, as no piscivory was observed in 2011. Considering the numbers of traditional piscivorous fish (6.4% of trawl catch) relative to the numbers of common bream and common carp (88.6% of trawl catch) in the reservoir, we can conclude that piscivorous cyprinids may induce a much higher predation pressure on YOY perch than traditional piscivorous species.

The findings presented here highlight the key role of YOY perch in freshwater ecosystems. They can affect and change the behaviour of many species in fundamental ways. In the present case, YOY perch triggered (a) the shift of mature individuals of *D. longispina* cp into a hypolimnetic refuge and (b) the forced piscivory of cyprinids. Hence, our study under natural conditions illustrates that extreme situations require extreme solutions.

Supporting Information

S1 Dataset. Data file. Spreadsheet containing basic data required to reproduce the analyses, figures and table presented in the manuscript.
(XLS)

Acknowledgments

We thank to all FishEcU members for their help during sampling, and two anonymous reviewers for valuable comments on an earlier version of the manuscript.

Author Contributions

Conceived and designed the experiments: LV MČ TJ JS. Performed the experiments: LV MČ JS TJ PB MV JF JK MŘ JM. Analyzed the data: LV PB DR. Contributed reagents/materials/analysis tools: JK JS MČ. Wrote the paper: LV IM MČ.

References

1. Winfield IJ. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus* and perch, *Perca fluviatilis*. J. Fish Biol. 1986; 29: 37–48.
2. Diehl S. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 1988; 53: 207–214.
3. Persson L. Asymmetries in competitive and predatory interactions in fish populations. In: *Size-structured populations Ecology and Evolution* (Eds. Ebenman B. & Persson L.. Berlin: Springer-Verlag; 1988. pp. 203–218.
4. Borcherding J, Maw SK, Tauber S. Growth of 0+ perch (*Perca fluviatilis*) predating on 0+ bream (*Abramis brama*). Ecol. Freshw. Fish 2000; 9: 236–241.
5. Vašek M, Kubečka J, Matěna J, Seďa J. Distribution and Diet of 0+ Fish within a Canyon- Shaped European Reservoir in Late Summer. Inter. Rev. Hydrobiol. 2006; 91: 178–194.
6. Kratochvíl M, Čech M, Vašek M, Kubečka J, Hejzlar J, Matěna J, et al. Diel vertical migrations of age 0+ percids in shallow, well-mixed reservoir. J. Limnol. 2010; 69: 305–310.
7. Ringelberg J. Diel Vertical migration of zooplankton in Lakes and Oceans, Netherlands: Springer Science & Business Media. 2010.
8. Vejřík L, Matějíčková I, Jůza T, Frouzová J, Seďa J, Blabolil P, et al. Hypoxic pelagic zone as a refuge for small fish in a freshwater ecosystem. Freshwater Biol. 2016
9. Persson A, Hansson LA. Diet shift in fish following competitive release. Can. J. Fish. Aquat. Sci. 1998; 56: 70–78.
10. Persson A, Brönmark C. Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. Oikos 2002; 97: 271–281.
11. Vašek M, Jarolím O, Čech M, Kubečka J, Peterka J, Prchalová M. The use of pelagic habitat by cyprinids in a deep riverine impoundment: Římov Reservior, Czech Republic. Folia Zool. 2008; 57: 324–336.
12. Jarolím O, Kubečka J, Čech M, Vašek M, Peterka J, Matěna J. Sinusoidal swimming in fishes: the role of season, density of large zooplankton, fish length, time of the day, weather condition and solar radiation. Hydrobiologia. 2010; 654: 253–265.
13. Olin M, Rask M, Ruuhijärvi J, Kurkilahti M, Ala-Opas P, Ylönen O. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundance of percids and cyprinids along a trophic gradient. J.Fish Biol. 2002; 60: 593–612.
14. Vašek M, Kubečka J. *In situ* diel patterns of zooplankton consumption by subadult/ adult roach *Rutilus rutilus*, bream *Abramis brama*, and bleak *Alburnus alburnus*. Folia Zool. 2004; 53: 203–214.
15. Olin M, Vinni M, Lehtonen H, Rask M, Ruuhij J, Saulamo K, Ala-Opas P. Environmental factors regulate the effects of roach *Rutilus rutilus* and pike *Esox lucius* on perch *Perca fluviatilis* populations in small boreal forest lakes. J. Fish Biol. 2010; 76: 1277–1293. doi: 10.1111/j.1095-8649.2010.02559.x PMID: 20537014
16. Ringelberg J. Enhancement of the phototactic reaction in *Daphnia-hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). J. Plankton Res. 1991; 13: 17–25.
17. Ringelberg J, Flik BJG, Lindenaar D, Royackers K. Diel vertical migration of *Daphnia hyalina* (sensus latiori) in lake Maarsseveen .1. aspects of seasonal and daily timing. Arch. Hydrobiol. 1991; 121: 129–145.
18. Mehner T, Thiel R. A review of predation impact by 0+ fish on zooplankton in fresh and brackish waters of the temperate northern hemisphere. Env. Biol. Fish. 1999; 56: 169–181.

19. Persson L. Behavioral response to predators reverses the outcome of competition between prey species. Behav. Ecol. Sociobiol. 1991; 28: 101–105.
20. Persson L. Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. Oikos 1993; 68: 12–22.
21. Olson MH., Mittelbach GG, Osenberg CW. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 1995; 76: 1758–1771.
22. Persson L, Eklöv P. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 1995; 76: 70–81.
23. Svänback R, Persson L. Individual specialization, niche width and population dynamics: implications for trophic polymorphisms. J. Anim. Ecol. 2004; 73: 973–982.
24. Hartman KJ, Margraf FJ. Evidence of predatory control of yellow perch *Perca flavescens* recruitment in Lake Erie, U.S.A. J. Fish Biol. 1993; 26: 109–119.
25. Frankiewicz P, Dabrowski K, Zalewski M. Mechanism of establishing bimodality in a size distribution of age- 0 pikeperch, *Stizostedion lucioperca* (L.) in the Sulejów Reservoir, Central Poland. Ann. Zool. Fenn. 1996; 33: 321–327.
26. Eklöv P. Effects of habitat komplexity and prey abundance on the spatial and temporal distribution of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. 1997; 7: 1520–1531.
27. Černý K, Pivnička K. Abundance and mortality of the perch fry (*Perca fluviatilis*, L 1758) in the Klíčava Reservoir. Věst. Česk. Spol. Zool. 1973; 37: 1–13.
28. Okun N, Mehner T. Distribution and feeding of juvenile fish on invertebrates in littoral reed (*Phragmites*) stands. Ecol. Freshw. Fish. 2005; 14: 139–149.
29. Specziár A, Rezsu ET. Feeding guilds and food ressource partitioning in a lake fish assemblage: an ontogenetic approach. J. Fish Biol. 2009; 75: 247–267. doi: 10.1111/j.1095-8649.2009.02283.x PMID: 20738494
30. De Graaf M, Weerd GH, Osse JWM, Sibbing FA. Diversification of prey capture techniques among the piscivores in Lake Tana's (Ethiopia) *Labeobarbus* species flock (Cyprinidae). Afr. Zool. 2010; 45: 32–40.
31. Britton JR, Boar RR, Grey J, Foster J, Lugonzo J, Harper DM. From introduction to fishery dominance: the initial impacts of the invasive carp *Cyprinus carpio* in Lake Naivasha, Kenya, 1999 to 2006. J. Fish Biol. 2007; 71: 239–257.
32. Britton JR. Testing Strength of Biotic Resistance against an Introduced Fish: Inter-Specific Competition or Predation through Facultative Piscivory? PLoS ONE 2012; 7: e31707. doi: 10.1371/journal.pone.0031707 PMID: 22363711
33. Britton JR, Davies GD, Harrod C. Trophic interactions and consequent impacts of the invasive fish Pseudorasbora parva in a native aquatic foodweb: a field investigation in the UK. Biol. Invasions. 2010; 12: 1533–1542.
34. Kapuscinski KL, Farrell JM, Wilkinson MA. Feeding patterns and population structure of an invasive cyprinid, the rudd *Scardinius erythropthalmus* (Cypriniformes, Cyprinidae), in Buffalo Harbor (Lake Erie) and the upper Niagara River. Hydrobiologia 2012; 693: 169–181.
35. Guinan ME Jr., Kapuscinski KL, Teece MA. Seasonal diet shifts and trophic position of an invasive cyprinid, the rudd *Scardinius erythrophthalmus* (Linnaeus, 1758), in the upper Niagara River. Aquat. Invasions 2015; 10: 217–225.
36. Vašek M, Jůza T, Čech M, Kratochvíl M, Prchalová M, Frouzová J, et al. The occurrence of non-native tubenose goby *Proterorhinus semilunaris* in the pelagic 0+ year fish assemblage of a central European reservoir. J. Fish Biol. 2011; 78: 953–961. doi: 10.1111/j.1095-8649.2011.02901.x PMID: 21366586
37. CEN Water Quality—Sampling of fish with multi-mesh gillnets. EN–14757; 2005.
38. Šmejkal M, Ricard D, Prchalová M, Říha M, Muška M, Blabolil P, et al. Biomass and abundance biases in European standard gillnet sampling. PLoS ONE 2015; 10: e0122437. doi: 10.1371/journal.pone.0122437 PMID: 25793776
39. Prchalová M, Mrkvička T, Peterka J, Čech M, Berec L, Kubečka J. A model of gillnet catch in relation to the catchable biomass, saturation, soak time and sampling period. Fish. Res. 2011; 107: 201–209.
40. Seďa J, Kolářová K, Petrusek A. *Daphnia galeata* in the deep hypolimnion: spatial differentiation of a "typical epilimnetic" species. Hydrobiologia 2007; 594: 47–57.
41. Flössner D. *Die Haplopoda und Cladocera Mitteleuropas*. Leiden: Backhuys Publishers. 2000.
42. Benzie AH. Cladocera—genus *Daphnia* including Daphniopsis. In: Guides to the identification of the microinvertebrates of the continental waters of the world (Ed. Dumont HJF.), pp 1–376. Vol. 21. Kenobi Productions and Backhuys Publishers, Ghent and Leiden. 2005.

43. McCauley E. The estimation of the abundance and biomass of zooplankton samples. In: *A manual on methods for the assessment of secondary productivity in fresh waters* (Eds. Downing JA., Rigler FH.). Oxford: Blackwell Publications, 1984; pp. 228–265.

44. Petrusek A, Seďa J, Macháček J, Ruthová Š, Šmilauer P. *Daphnia* hybridization along ecological gradients in pelagic environments: the potential for the presence of hybrid zones in plankton. Philos. T. Roy. Soc. B. 2008; 363: 2931–2941.

45. Petrusek A, Thielsch A, Schwenk K. Mitochondrial sequence variation suggests extensive cryptic diversity within the Western Palearctic *Daphnia longispina* complex. Limnol. Oceanogr. 2012; 57: 1838–1845.

46. Čech M, Čech P, Kubečka J, Prchalová M, Draštík V. Size selectivity in summer and winter diets of great cormorant (*Phalacrocorax carbo*): Does it reflect season-dependent difference in foraging efficiency? Waterbirds 2008; 31: 438–447.

47. Čech M, Vejřík L. Winter diet of great cormorant (*Phalacrocorax carbo*) on the River Vltava: estimate of size and species composition and potential for fish stock losses. Folia Zool. 2011; 60: 129–142.

48. Tesch FW. Age and growth. In: Fish production in fresh waters (Ed. Ricker WE),. London: Blackwell; 1971. pp. 98–130.

49. R Development Core Team R: A language and environment for statistical computing. 2015

50. Nelson JS. *Fishes of the World*. New York. Wiley; 1994.

51. Van Wassenbergh S, De Rechter D. Piscivorous cyprinid fish modulates suction feeding kinematics to capture elusive prey. Zoology 2011; 114: 46–52. doi: 10.1016/j.zool.2010.10.001 PMID: 21185704

52. Kottelat M, Freyhof J. Handbook of European freshwater fishes. Cornol: Publications Kottela. 2007.

53. Garcia-Berthou E. Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). Aquat.Sci. 2001; 63: 466–476.

54. Rahman MM, Kadowaki S, Balcombe SR, Wahab MA. Common carp (*Cyprinus carpio* L.) alters its feeding niche in response to changing food resources: direct observations in simulated ponds. Ecol. Res. 2010; 25: 303–309.

55. Specziár A, Bíró P, Tölg L. Feeding and competition of five cyprinid fishes in different habitats of the Lake Balaton littoral zone, Hungary. Ital. J. Zool. 2010; 65: 331–336.

56. Seďa J, Petrusek A, Macháček J, Šmilauer P. Spatial distribution of the *Daphnia longispina* species complex and other planktonic crustaceans in the heterogeneous environment of canyon-shaped reservoirs. J. Plankton Res. 2007; 29: 619–628.

57. Vašek M, Prchalová M, Říha M, Blabolil P, Čech M, Draštík L, et al. Fish community response to the longitudinal environmental gradient in Czech deep-valley reservoirs: implications for ecological monitoring and management. Ecol. Indic. doi: 10.1016/j.ecolind.2015.11.061

58. Vøllestad LA. Resource partitioning of roach *Rutilus rutilus* and bleak *Alburnus alburnus* in two eutrophic lakes in SE Norway. Holarctic Ecology. 1985; 8: 88–92.

59. Johansson L, Persson L. (1986) The fish community of temperate eutophic lakes. In: *Carbon Dynamics in Eutrophic Temperate Lakes* (Eds. Riemann B. & Søndergaard M.), Elsevier Science Publishers. 1986; pp. 237–266.

60. Čech M, Peterka J, Říha M, Vejřík L, Jůza T, Kratochvíl M, et al. Extremely shallow spawning of perch (*Perca fluviatilis* L.): the roles of sheltered bays, dense semi-terrestrial vegetation and low visibility in deeper water. Knowl. Manag. Aquat. Ecosyst. 2012; 406: 1–12.

61. Jůza T, Kubečka J. The efficiency of three fry trawls for sampling the freshwater pelagic fry community. Fish. Res. 2007; 85: 285–290.

62. Jůza T, Ricard D, Blabolil P, Čech M, Draštík V, Frouzová J, et al. Species-specific gradients of juvenile fish density and size in pelagic areas of temperate reservoirs. Hydrobiologia. 2015; 762: 169–181.

63. De Graaf M, Dejen E, Osse JWM, Sibbing FA. Adaptive radiation of Lake Tana's *Labeobarbus* species flock (Pisces, Cyprinidae). Mar. Freshwater Res. 2008; 59: 391–407.

64. Winemiller KO, Kelso-Winemiller LC. Comparative ecology of the African pike, *Hepsetus odoe*, and tigerfish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. J. Fish Biol. 1994; 45: 211–225.

65. Mittelbach GG, Persson L. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci. 1998; 55: 1454–1465.

66. Sibbing FA, Nagelkerke LAJ. Resource partitioning by Lake Tana Barbs predicted from fish morphometrics and prey characteristics. Rev. Fish Biol. Fisher. 2000; 10: 393–437.

67. Müller M, Osse JWM. Hydrodynamics of suction feeding in fish. Trans. Zool. Soc. Lond. 1984; 37: 51–135.

Paper IV

Small fish use the hypoxic pelagic zone as a refuge from predators

Freshwater Biology

Freshwater Biology (2016) **61,** 899–913 doi:10.1111/fwb.12753

Small fish use the hypoxic pelagic zone as a refuge from predators

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SUMMARY

1. Juvenile perch (*Perca fluviatilis*) often inhabit deep zones of lakes or reservoirs (metalimnion to hypolimnion). Using fry trawling and hydroacoustic measurements, we studied perch distribution to determine if juveniles are using deep hypoxic waters (oxygen concentration $\leq$3.5 mg L^{-1}) as a refuge from predation.

2. We found a heterogeneous depth distribution of perch, with the highest abundance of juveniles in the hypoxic pelagic zones. Distributions were better correlated with oxygen concentration than with depth or temperature.

3. Densities of *Daphnia* spp. were high in the deep hypoxic zones, likely related to avoidance of predation from zooplanktivorous cyprinid fish. Furthermore, *Daphnia* was found to be the dominant food source for juvenile perch in hypoxic zones and gut fullness was highest in areas with maximum hypoxia. Contrary to earlier studies suggesting a dietary advantage of fish inhabiting cooler hypoxic zones, our study, considering physiological benefits and limitations of juvenile perch digestion, found no support for temperature caused substantial changes in gastric evacuation rates.

4. Our finding that high juvenile perch abundance was associated with low oxygen concentration suggests that juvenile perch are mainly using deep hypoxic waters as a refuge from large predators. This behaviour is reinforced by the presence of zooplankton prey in this zone.

Keywords: hypoxia, *Perca fluviatilis*, perch, predator avoidance, zooplankton

Introduction

Deep water hypoxia is a symptom of cultural eutrophication (Carpenter *et al.*, 1998) in freshwater (Ludsin *et al.*, 2001; Klumb *et al.*, 2004) and marine (Diaz & Rosenberg, 2008) ecosystems throughout the world. Since oxygen concentrations below 2 mg L^{-1} are lethal for most fish (Suthers & Gee, 1986; Klumb *et al.*, 2004; Stanley & Wilson, 2004), hypoxic conditions are generally avoided. However, many zooplankton species tolerate oxygen concentrations below 1 mg L^{-1} (Weider & Lampert, 1985; Lass, Boersma & Spaak, 2000; Taylor, Rand & Jenkins, 2007), with tolerance inversely related to body size (Robb & Abrahams, 2003). Tolerance of low oxygen conditions allows zooplankton to use the hypoxic zone as a refuge from fish predation (Vanderploeg *et al.*, 2009; Larsson & Lampert, 2011).

Several studies have shown that fish may temporarily use hypoxic pelagic zones of fresh waters for feeding. Luecke & Teuscher (1994) found that rainbow trout (*Oncorhynchus mykiss*: Salmonidae) generally occupied waters immediately above the oxy-thermocline, briefly moving into the hypoxic pelagic zone to feed. Also, Roberts *et al.* (2012) referred to short hypoxic foraging forays by yellow perch (*Perca flavescens*: Percidae) in Lake Erie (U.S.A.), and laboratory results suggested that short-term exposure to low oxygen conditions did not impact the consumption potential of yellow perch.

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Taylor *et al.* (2007) suggested that the occurrence of juvenile anchovy (*Anchoa* spp.: Engraulidae) in the hypoxic pelagic zone was related to food consumption due to high densities of zooplankton.

As in the case of zooplankton, hypoxic habitats provide a refuge for a variety of other prey including small fishes (Chapman, Chapman & Chandler, 1996a; Chapman *et al.*, 1996b; Robb & Abrahams, 2002, 2003; Ekau *et al.*, 2010) due to their tolerance of low oxygen conditions. Conversely, body size is a limiting factor for several physiological characteristics of fish (Robb & Abrahams, 2003). For example, increasing the minute ventilation of gills, which increases with body size, is energetically expensive (Jones, 1971; Yamamoto, 1991, 1992). Furthermore, the negative allometric relationship for the mass-specific gill-surface area, results in a more efficient gas exchange in smaller individuals (Muir, 1969; Hughes, 1984). The oxygen-carrying capacity of blood also has an impact (Gallaugher & Farrell, 1998), due to the inverse relationship between haematocrit and body size (Lowe-Jinde & Niimi, 1983; Zanuy & Carrillo, 1985). Moreover, according to the fractal scaling model, independent of body size, fish are limited by the fixed size of the red blood cells used for gas exchange (West, Brown & Enquist, 1997). Hence, larger fish require a more complex branching of blood vessels and, subsequently, longer time and more energy for red blood cells to reach the tissues.

A number of studies have shown that fish use the hypoxic zones of littoral habitats as refuges from predation. Suthers & Gee (1986) showed that juvenile yellow perch use hypoxic conditions near littoral macrophytes as a refuge from cannibalism. Studying the fish community in the hypoxic macrophyte zone and well-oxygenated open area of Lake Nabugabo (Uganda), Chapman *et al.* (1996a,b) found that endemic species use the hypoxic conditions in macrophyte stands to avoid predation from the introduced Nile perch (*Lates niloticus*: Latidae). Similarly, Yamanaka, Kohmatsu & Yuma (2007) showed that round crucian carp (*Carassius auratus grandoculis*: Cyprinidae) use the hypoxic conditions associated with macrophytes as a refuge. In field and laboratory studies of predator – prey relationships between perch and fathead minnow (*Pimephales promelas*: Cyprinidae), Robb & Abrahams (2002, 2003) showed that fathead minnow utilised hypoxic conditions as a refuge from predation.

In contrast to the many studies on hypoxic littoral conditions, to our knowledge this is the first study to assess if small fish use the hypoxic pelagic environment (oxygen concentration $\leq$3.5 mg L^{-1}) as a refuge from predators. Using fry trawling and hydroacoustic measurements, we studied the distribution of juvenile perch (*Perca fluviatilis*: Percidae, smaller than 6 cm) in a deep canyon-shaped reservoir. We hypothesised that hypoxic conditions with sufficient food resources offer a refuge from predators.

Methods

Study area

The study was conducted in the canyon-shaped Vír Reservoir in Moravia, Czech Republic (Fig. 1). Mean annual inflow is 3.6 m^3 s^{-1} (minimum inflow is 0.4 m^3 s^{-1}, maximum 100-year inflow is 155 m^3 s^{-1}). The maximum surface water altitude is 464 m a.s.l. During sampling in 2010 and 2011, surface water altitude was between 460 and 457 m a.s.l., respectively, due to high runoff in late spring and summer. The reservoir has a surface area of *c.* 224 ha, a length of 9.3 km, a mean depth of 25 m (max 64 m) and a total water volume of *c.* 56 million m^3. The trophic state is characterised as eutrophic, and since 1992, algal blooms have increasingly occurred, mainly dominated by *Microcystis* sp. (Microcystaceae). The reservoir is dimictic. In summer, oxygen concentration of surface waters is usually 11 mg L^{-1} and temperatures average 21°C, while at depths below 25 m temperature decreases to 5°C. The thermocline depth in August is usually between 3 and 7 m, and oxygen concentration below the thermocline is low (less than 4 mg L^{-1}), but increases to 8 mg L^{-1} in hypolimnion (Morava River Authority, unpubl. data).

Trawl sampling

Trawling for juvenile fish, acoustic measurements and collection of water samples for measurements of abiotic variables was done on 26 July (night) and 27 July (day) in 2010 and on 31 July (night) and 1 August (day) in 2011. The reservoir was divided into four approximately equidistant sections along its longitudinal axis: dam, middle, upper and tributary sections; each section was *c.* 2 km in length (Fig. 1). The length of the tributary section varied depending on the water level.

A pelagic, fixed-frame fry trawl (length 10.5 m, opening 3 × 3 m, mesh size: 6 mm in the belly, 3 mm in the cod end, trawl volume 31.5 m^3) was used to sample juvenile fish. The trawl was equipped with a mesh funnel in the last third of the trawl to prevent fish from escaping (Jůza & Kubečka, 2007). Trawls

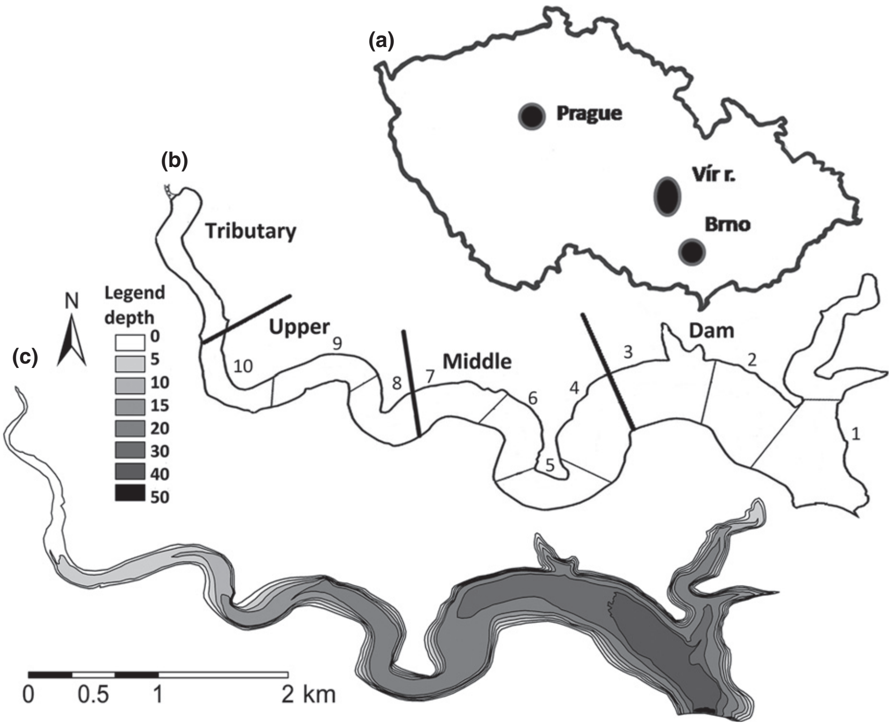

Fig. 1 (a) Map showing the location of the cities of Prague and Brno and the Vír Reservoir in the Czech Republic. (b) A detailed view of the Vír Reservoir divided into four sections (tributary, upper, middle and dam) along its longitudinal gradient. The sectors where fry trawling and hydroacoustic measurements were made are labelled by numbers 1–10. (c) A bathymetric map of the Vír Reservoir, where 0 corresponds to the surface level in late July 2010. The legend shows contour lines with relevant depths.

Table 1 Number of fry trawl tows in 2010/2011 for each depth layer and reservoir section of the Vír Reservoir. The first number corresponds to a day tow, second number in brackets to a night tow. In 2011, only the day tow was done in the dam section in a depth layer 12–15 m due to an early sunrise prior to the previous night's tow.

Depth layer (m)					
Reservoir section	0–3	3–6	6–9	9–12	12–15
Dam	2 (2)/2 (2)	2 (2)/2 (2)	2 (2)/2 (2)	2 (2)/2 (2)	1 (1)/1 (0)
Middle	2 (2)/2 (2)	2 (2)/2 (2)	2 (2)/0 (0)		
Upper	1 (1)/1 (1)	1 (1)/1 (1)			

were towed *c.* 100 m behind the research vessel (*Ota Oliva*, 64 hp diesel engine), usually for 10 min, at velocities of 0.8–1.1 m s^{-1}. The speed and position information was obtained from a GPS receiver (Garmin GPSMAP 60CSx; Garmin International, Inc., Olathe, KS). In total, 182 675 m^3 of water was filtered in 2010 and 154 738 m^3 in 2011. Five depth layers were sampled for juvenile fish (0–3, 3–6, 6–9, 9–12 and 12–15 m), with sampling depth regulated by a polystyrene float attached to the upper section of the frame. A total of 63 tows were conducted (sum of both years; for details see Table 1). No deep water tows were conducted in the upper reservoir section due to the risk of collision with submerged obstacles (stumps, logged trees, ruins of flooded buildings). Also, a shallow tributary section (depth ≤3 m) was not sampled.

The water volume sampled (V_W, m^3) was calculated as:

$$V_W = L \times S$$

where L is the tow length (m) and S is the area of the mouth of the trawl (m^2). Juvenile fish from each trawl tow were immediately anaesthetised by a lethal dose of Sandoz–MS 222 and subsequently preserved in a 4% formaldehyde solution. In the laboratory, the fish were identified to species and counted. The catch was expressed as the number of fish per 100 m^3 of water volume sampled.

Trawling for adult fish (fish larger than 15 cm, potential predators of juvenile perch) was conducted on the night of 27 July in 2010 (22:00–03:00 hours). Five tows were conducted in the dam and middle sections of the reservoir (sectors 1–7) using a pelagic trawl (length 38 m, opening 13 × 8 m (width × depth), mesh size in the main body 80/40/20 mm (half mesh, knot centre) from the opening towards the end and 10 mm in the cod end, trawl volume 1456 m^3). The funnel preventing fish escape was at the beginning of the cod end. Floats were attached to the headrope and lead weights to the footrope. Two 80 L buoys were attached to each side of the headrope to keep the trawl directly on the surface. A small barge was fixed to each side of the headrope, close to the buoys, to manipulate the footrope to avoid obstacles on the bottom of the reservoir. Two 80 kg weights were attached to each side of the footrope to keep it at a depth of 8 m during towing. Two research vessels: the *Ota Oliva* and *Thor Heyerdahl* (with 210 hp diesel engines) were used to tow the trawl. The duration of one tow was between 10 and 25 min. In total, 338 456 m^3 of water was sampled. All data from adult trawling are provided in detail in the work of Vejřík *et al.* (unpubl. data.).

Pelagic gillnet sampling

In addition to trawling, pelagic gillnets were used to sample the open water environment of the Vír Reservoir for potential predators of juvenile perch. Gillnets were placed from the surface to a depth of 4.5 m and between 5 and 9.5 m. The pelagic gillnets consisted of 2.5 m-long sections of varying mesh-sizes: 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm (Nordic type; Appelberg *et al.*, 1995). Gillnets (n = 3 per section) were set overnight (placement 18:00–20:00 hours, removal 06:00–08:00 hours) in the dam, middle and upper reservoir sections on 28–29 July in 2010 and 2–3 August in 2011. In the upper section, gillnets were not set at 5–9.5 m depth due to shallow water. A total of nine gillnets were set at 0–4.5 m depth and six at 5–9.5 m depth in both years (2010 and 2011). Fish were immediately anaesthetised by a lethal dose of Sandoz–MS 222, identified to species, counted and measured. The catch of individuals larger than 15 cm was expressed as number of adult fish per 1000 m^2 of pelagic gillnets.

Acoustic sampling

Acoustic measurements were made during night (23:00–03:00 hours) and day (11:00–15:00 hours) using a SIMRAD EK 60 split-beam scientific echosounder (frequency 120 kHz) (SIMRAD, Horten, Norway). The survey was conducted using a multiplexer, enabling the simultaneous operation of vertically and horizontally aligned transducers. The transducer used for vertical observation (SIMRAD ES120–7C) had a circular beam pattern with a nominal angle of 7.1°, while the transducer used for horizontal observation (SIMRAD ES120-4) had an elliptical beam pattern with nominal angles 9.1° × 4.3°. Both transducers were attached to a remotely controlled aluminium plate on the frame in front of the Thor Heyerdahl research vessel (survey speed *c.* 5 km h^{-1}). During sampling, the horizontal survey covered the part of the water column from the water surface to 2 m depth, while the vertical survey covered the water column from 2 m depth to the bottom. The pulse repetition rate was 6–10 pings s^{-1} (3–5 pings s^{-1} for each transducer) and the pulse length 0.128 ms. The echosounder was controlled using a Dell Latitude D820 personal computer. During each survey, over 16 million m^3 of water was sampled. Acoustic data were stored on a hard disk for later analysis. The whole sonar system was calibrated with a standard calibration copper sphere (diameter 23 mm) (Foote *et al.*, 1987). To detect all fish, the threshold for the primary noise filtering of the acoustic record during fieldwork was set to minimal target strength (TS; for definition see MacLennan & Simmonds, 1992) of −70 dB.

In the laboratory, the data were processed using the post-processing software, Sonar5 (Lindem Data Acquisition AS, Oslo). Vertical echograms were analysed from a depth of 2 m (near field of the transducer 0.97 m) down to the bottom (max. depth 55 m; bottom was detected automatically using a built-in algorithm in Sonar5 with a margin of error of 0.5 m and manually corrected to avoid any bottom echoes in the analyses). The water column was divided into 1 m thick layers, with each layer analysed separately. For calculation of fish abundance, echointegration (S_V/TS scaling method) was used. The TS distribution was established from *in situ* single echo detections. Horizontal echograms were analysed over a range of 4–25 m (maximally) from the transducer (near field of the transducer 3.75 m) to cover the upper 2 m of the water column. For calculation of the volume density of fish, the Sv/TS scaling method was used again. As the source of the TS distribution, catch baskets were used based on real fish catches from the pelagic multimesh gillnets during same period of summer (see above; Water Quality-Sampling of fish with Multimesh Gillnets, CEN TC 230, 2005). The TS was estimated from fish size using the relationship developed by Frouzová *et al.* (2005). Horizontal records were used to estimate abundance of adult fish only, since, in the case of juvenile fish, their low presence in surface layers (*cf.* fry trawl catches) in conjunction with high ambient noise would result in overestimating abundance using acoustic records. For the analysis with Surfer software (see below), juvenile fish abundance in the 0–2 m depth strata was recalculated from trawl catches using the ratio between trawl catches and the estimated acoustic fish abundance in deeper layers.

Due to the higher abundance of juvenile fish in the pelagic zone and more distinctive hypoxic conditions in the metalimnion of the Vír Reservoir in 2010 compared to 2011, only data from 2010 were used in statistical analyses. Furthermore, due to unsuitable acoustic conditions (intensive bubbling in the upper part of the reservoir, mainly in daylight hours), data were not analysed in sectors 8–10 during the day and in sector 10 during the night (*cf*. Fig. 1, Table 2).

Abiotic factors

Water temperature and dissolved oxygen measurements were made at 23:00–03:00 hours (night sampling) and 10:00–14:00 hours (day sampling) in both years (2010 and 2011). Measurements were made at 1 m depth intervals throughout the entire water column (to a maximum depth of 55 m or when the probe reached the bottom) using a calibrated YSI 556 MPS probe, at a single site in each of the three sections.

Zooplankton sampling

Zooplankton was sampled in conjunction with the daytime sampling of juvenile fish near the dam. Vertical stratification of zooplankton (surface to 21 m depth) was estimated using a closing net (mesh size 170 μm) to sample seven distinct depth layers (each layer was 3 m thick). As zooplankton abundance was low at depths greater than 21 m, an integrated hypolimnion sample was taken between 21 and 55 m.

Previous studies have shown no apparent diurnal vertical migration of zooplankton in man-made artificial reservoirs during the night (Sed’a, Kolářová & Petrusek, 2007a), thus only the upper 0–3 m depth layer in the dam section was sampled during the night. Two different closing nets were used because the abundance of zooplankton differed more than one order of magnitude between the upper and deeper strata: a net with an opening of 24 cm (diameter) was used for the epilimnion and a net with an opening of 40 cm was used for deeper strata. Zooplankton material was immediately preserved in 4% formaldehyde.

Zooplankton species were identified in the laboratory using a microscope (Olympus CX40), and counted according to McCauley (1984). Briefly, each zooplankton sample was diluted so that subsampling by a wide mouth pipette resulted in *c.* 200–250 crustaceans. Four subsamples were counted separately in a Sedgewick-Rafter counting chamber. When abundances in the bulk sample were low (usually from the deep water strata), the whole sample was processed. Abundance was calculated as the average number per 1 L of water within each individual 3 m thick depth layer.

All crustaceans were identified to species using regional keys (Šrámek-Hušek, 1953; Šrámek-Hušek, Straškraba & Brtek, 1962) with nomenclature from recent revisions (Einsle, 1996; Flössner, 2000; Ueda & Reid, 2003; Benzie, 2005). Previous studies have shown that all taxa from the *Daphnia longispina* sp. group occur in the Vír Reservoir, including the hybrid *D. galeata* × *D. longispina* (Sed’a *et al.*, 2007b), when *D. galeata* usually domi-

Table 2 Abundances of juveniles based on hydroacoustic measurements in 2010 and water volume in each section and depth layer of the Vír Reservoir to a depth of 30 m. Hypoxic conditions (oxygen concentration ≤3.5 mg L^{-1}) are highlighted by grey shading. Percentages of juveniles in hypoxic versus normoxic zones during day/night are in bold.

Water volume in each section and depth zone (10^6 m^3)					Number of juveniles during day			Number of juveniles during night			
Depth layer (m)	Dam	Middle	Upper	Sum	Dam	Middle	Sum	Dam	Middle	Upper	Sum
0–3	2.50	1.40	0.68	4.58	27	42	69	5988	3166	1927	11 081
3–6	2.37	1.32	0.52	4.21	881 910	689 389	1 571 299	489 202	257 185	29 662	776 049
6–9	2.24	1.23	0.37	3.85	620 092	74 768	1 360 860	1 116 898	729 713	88 720	1 935 331
9–12	2.12	1.15	0.20	3.47	195 766	255 552	451 318	508 560	294 556	14 804	817 920
12–15	2.00	1.07	0.24	3.30	3802	2210	6012	237 226	98 393	2920	338 540
15–18	1.89	0.98	0.08	2.95	755	49	804	65 780	20 326	525	86 631
18–21	1.78	0.89	0.02	2.70	0	0	0	15 761	2690	51	18 502
21–24	1.62	0.71	0.01	2.34	0	0	0	5164	0	15	5180
24–27	1.56	0.66	0	2.22	0	0	0	2231	0		2231
27–30	1.47	0.52	0	1.99	0	0	0	606	0		606
Percentage volume of hypoxic and normoxic pelagial (%)					Percentage of juveniles during day (%)			Percentage of juveniles during night (%)			
Hypoxic zone	33	35	0	31	48	59	**54**	76	80	0	**75**
Normoxic zone	67	65	100	69	52	41	**46**	24	20	100	**25**

nates (all in Daphniidae). For this study, genetic identification was not performed and all *Daphnia* were classified simply as *Daphnia* spp. Since *Daphnia* spp. was an important food source for perch (for details see section Results), only its abundance was used in the description of zooplankton distribution.

Diet analysis

For diet and gut fullness analyses, subsamples of juvenile perch from each depth layer (2010: 500 individuals, 2011: 150 individuals; at least 15 individuals were analysed for each depth layer) were used. In 2010, the diet analysis was done on juvenile perch caught during day, due to the lack of night-time feeding resulting in empty guts prior to sunrise (Vašek *et al*., 2006). Nevertheless, no juvenile perch were caught at depths from 0 to 9 m during the day in 2011 (*cf*. Fig. 2). Hence, the juvenile perch caught early after dusk (before night-time digestion) were used.

In the laboratory, gut fullness was estimated as empty (score 0) to fully distended (score 5) separately for stomachs and intestines, and the combined amount of stomach and intestine content scored between 0 and 10. The per cent composition of the diet by volume was visually estimated for the entire digestive tract. Seven categories

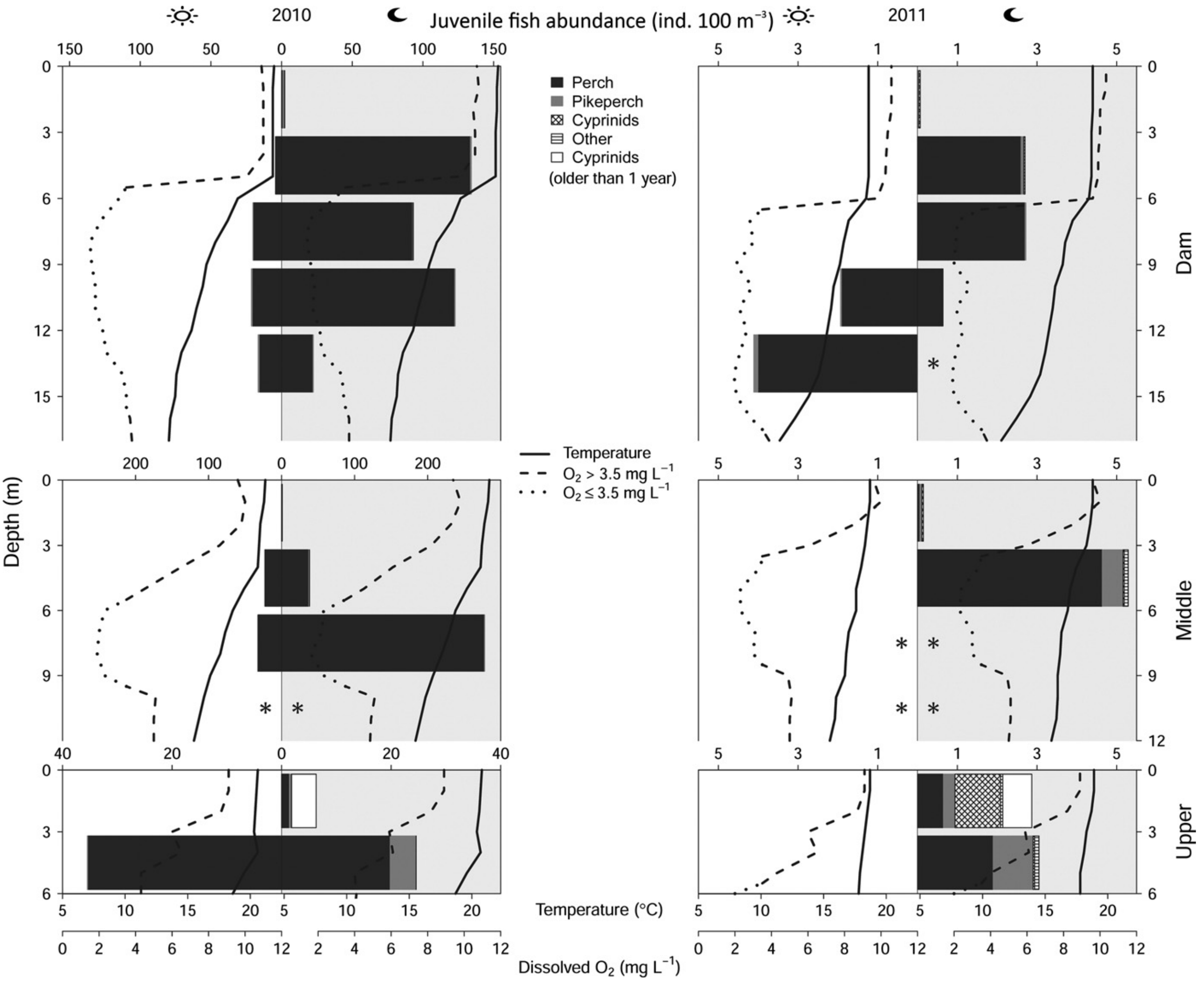

Fig. 2 Abundance estimates of juvenile fish obtained by day and night trawling at different depths of the Dam, Middle and Upper sections of the Vír Reservoir in 2010 and 2011. Estimates are given for different juvenile fish species ('other' is used for catfish and ruffe) and for cyprinid fish older than 1 year. Asterisks show depth layers which were not sampled. Lines correspond to vertical profiles of dissolved oxygen (dashed/dotted lines) and water temperature (solid lines).

of food sources were distinguished: *Dicrotendipes* (Chironomidae) and six zooplankton categories (*Daphnia* spp., *Leptodora kindtii* (Leptodoridae), *Diaphanosoma* sp. (Sididae), Bosminidae, Cyclopidae, other zooplankton).

Statistical analysis

A nonparametric Kruskal–Wallis test (Statistica 12; StatSoft Inc., Tulsa, OK) was used to test for differences in the abundance of juvenile perch from trawl samples in hypoxic (oxygen concentration 1.8–2.5 mg L^{-1}; depth layers 6–9, 9–12 and 12–15 m) and normoxic (oxygen concentration 5.3–11 mg L^{-1}; depth layers 0–3 and 3–6 m) pelagic zones in 2010; and in hypoxic (oxygen concentration 2.2–3.5 mg L^{-1}; depth layers 6–9, 9–12 m in the dam section and 3–6 m in the middle section) and normoxic (oxygen concentration 5–10.6 mg L^{-1}; depth layers 0–3 m in all sections and 3–6 m in the dam and upper sections) pelagic zones in 2011.

Ordination was used to test the effects of environmental factors on the abundance of fish during day and night in 2010 (ind. 100 m^{-3}; based on the acoustic survey). Constrained ordinations were done using the Canoco for Windows 5 software (Šmilauer & Lepš, 2014). Two fish groups, juvenile perch (1–6 cm; potential prey) and older fish (larger than 15 cm; potential predators) were used as response variables. The explanatory environmental variables were oxygen concentration, water temperature and depth (all quantitative). The length of the gradient (1.4 SD in detrended correspondence analysis) indicated that a linear model best fit the data; hence redundancy analysis (RDA) was used (Šmilauer & Lepš, 2014). Redundancy analysis was also used to test the effects of the oxygen concentration, depth and reservoir sections on the presence of different food sources in the guts of the juvenile perch. Seven food source categories were used as response variables. The explanatory environmental variables were the oxygen concentration (quantitative), depth layers (0–3, 3–6, 6–9, 9–12, 12–15 m) and sections of the reservoir (dam, middle, upper) (both qualitative). The environmental variables were tested by forward selection on centred response variables. Statistical significance was analysed using Monte Carlo permutation tests (number of permutations: 4999).

Gut fullness data were tested by a linear regression analysis (Statistica 12; StatSoft Inc.), with oxygen concentration was set as the independent variable and gut fullness as the dependent variable.

A contour map (applied in Fig. 4) was generated to provide a general distribution model of juvenile perch and fish larger than 15 cm, both of which were investigated by acoustics (Surfer software, Vision 10, Golden Software Inc.). The data entered in the Surfer software were assigned the numbers 1–7 (daytime data) and 1–9 (night-time data) for the sectors (x axis), 1–12 for water depth in metres (y axis) and the percentage value of the maximum fish abundance (the sector and depth with the highest observed abundance was assigned 100% and the percentage values of the remaining sectors and depths sampled were recalculated proportionally). Kriging was used as the gridding method. The isoline numbers in the Surfer model conformed to the mean percentage abundance in the relevant sector and relevant depth layer, recalculated from the area with the highest fish abundance (given as 100%) computed by the Surfer software.

The water volume of each pelagic depth layer (V_z) was calculated as:

$$V_z = \frac{1}{3} \times \mathrm{h}_z \times (S_1 + \sqrt{S_1 \times S_2} + S_2)$$

where h_z is the height of the pelagic depth layer (always 3 m), S_1 is the upper area of the layer (m^2) and S_2 is the lower area of the layer (m^2). The areas (S_1 and S_2 for each depth layer) from the water surface to a depth of 30 m (no occurrence of juvenile fish underneath) of the three sections (dam, middle, upper) in 2010 were calculated from the digital three-dimensional bathymetric model in ArcMap 10.2 (ESRI Inc., 2014). Using this method, the total numbers of juvenile fish were obtained in different sections and depth layers of the reservoir based on the acoustic investigations.

Results

In both years 2010 and 2011, the pelagic zone of the Vír Reservoir was characterised by metalimnetic hypoxia. In 2010, hypoxia occurred at depths of 6–17 m in the dam section and at 5–9 m in the middle section. In 2011, hypoxia occurred at depths of 7–17 m in the dam section and at 4–8 m in the middle section (Figs 2 & 3). In the epilimnion, oxygen concentration exceeded 10 mg L^{-1}, and was >3 mg L^{-1} in the hypolimnion (>5 mg L^{-1} in the depth 19–46 m; Fig. 3).

During the last week of July in 2010 and 2011, 45 047 juvenile fish belonging to seven species were caught by fry trawl: common bream (*Abramis brama*: Cyprinidae), bleak (*Alburnus alburnus*: Cyprinidae), roach (*Rutilus rutilus*: Cyprinidae), perch, pikeperch (*Sander lucioperca*:

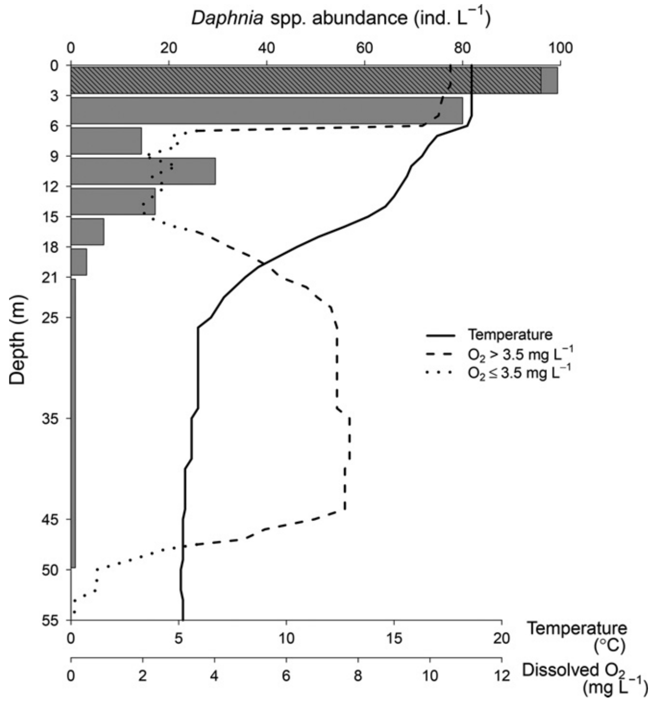

Fig. 3 Abundance of *Daphnia* spp. at different depth layers of the dam section of the Vír Reservoir during the day in 2011. The patterned area shows abundance of zooplankton during the night in the depth layer 0–3 m (other layers were not sampled during night). The average value was used for the depth of 21–50 m. Lines correspond to vertical profiles of dissolved oxygen (dashed/dotted lines) and water temperature (solid lines).

Percidae), ruffe (*Gymnocephalus cernuus*: Percidae) and European catfish (*Silurus glanis*: Siluridae). Percids dominated in excess of 99% of the catch in both years, in all reservoir sections and at all depths (except 0–3 m depth in the upper section in 2011, where cyprinids prevailed; Fig. 2). The most abundant species was perch followed by pikeperch. According to the averaged values from tows, perch composed 98% (12.1 ind. 100 m^{-3}) of daytime and 99% (50.9 ind. 100 m^{-3}) of night-time catches in 2010 and 84% (0.7 ind. 100 m^{-3}) of daytime and 99% (1.32 ind. 100 m^{-3}) of night-time catches in 2011.

According to trawling data, perch dominated in all three reservoir sections and at almost all depths during both day and night (Fig. 2). The highest abundance of perch was observed in the dam and middle sections, while the abundance of perch decreased towards the tributary in both years. Along the vertical profile, the highest concentration of juvenile perch was in the metalimnion, which is the water zone where temperature and oxygen concentration decreased most rapidly (Figs 2 & 4). Apparent during both day and night, the pattern was most striking during the day (Fig. 2). A high abundance of juvenile perch (278 ind. 100 m^{-3}) was found in the 6–9 m depth layer in the middle section of the reservoir in 2010, where the oxygen concentration was only 1.6–2.2 mg L^{-1}. This oxygen concentration corresponds to high hypoxia. In 2011, the highest abundances of juvenile perch also occurred in the hypoxic metalimnion. Based on trawl sampling in both years, juvenile perch were significantly more abundant in the hypoxic pelagic zone (oxygen concentration 1.8–3.5 mg L^{-1}) than in the normoxic pelagic zone (oxygen concentration 5–11 mg L^{-1}; for 2010 at night: $H_{2,17} = 5.08$ $P < 0.03$ and day: $H_{2,17} = 6.34$ $P < 0.01$; for 2011 at night: $H_{2,14} = 4.32$ $P < 0.04$ and day: $H_{2,15} = 6.92$ $P < 0.01$). Based on acoustic measurements in 2010, the highest abundance of small fish occurred at the transition between the epi- and metalimnion, and between the meta- and hypolimnion (Fig. 4a,c). The pelagic zone towards the upper section of the reservoir was more influenced by the tributary, so the interface between these borders was less apparent in sectors 8 and 9 (Fig. 4c), and the hypoxia also gradually disappeared (Fig. 2). In addition, the abundance of juvenile fish in the pelagic zone decreased markedly towards the tributary and vertical zonation was not apparent in the upper section of the reservoir (Figs 2 & 4c).

According to acoustic measurements, juvenile fish occurred at a maximum depth of 30 m during the night compared to 18 m during the day. The total reservoir volume from the surface to a depth of 30 m was 31.59 million m^3 in 2010; from this volume, hypoxic conditions occurred only in 9.81 million m^3 (31%). Nonetheless, *c.* 1.8 million individuals of juvenile fish occurred in this relatively small hypoxic pelagic zone during the day (54% of the juvenile fish observed in the dam and middle sections). During the night, *c.* 3 million individuals occurred in the hypoxic pelagic zone (75% of the juvenile fish observed in the entire reservoir; Table 2).

In 2010, the highest catch by fry trawling during the daytime in the dam section was in the 9–12 m depth layer where the oxygen concentration was the lowest (1.6–2.2 mg L^{-1}) (Fig. 2). In 2011, juvenile perch from the daytime catch were found only at 9–12 and 12–15 m, with similar low oxygen concentrations (2.2–2.5 mg L^{-1}). In contrast, fish larger than 15 cm (identified using hydroacoustics and pelagic gillnets) appeared mainly in the surface zone of the water column associated with high oxygen concentrations and warm water (Figs 4b,d & 5, Table 3). The overall preference for the hypoxic zone by the juvenile perch and for the surface zone with high oxygen concentrations by older fish was clearly apparent. Redundancy analysis of hydroacoustic data revealed statistically significant differences in habitat

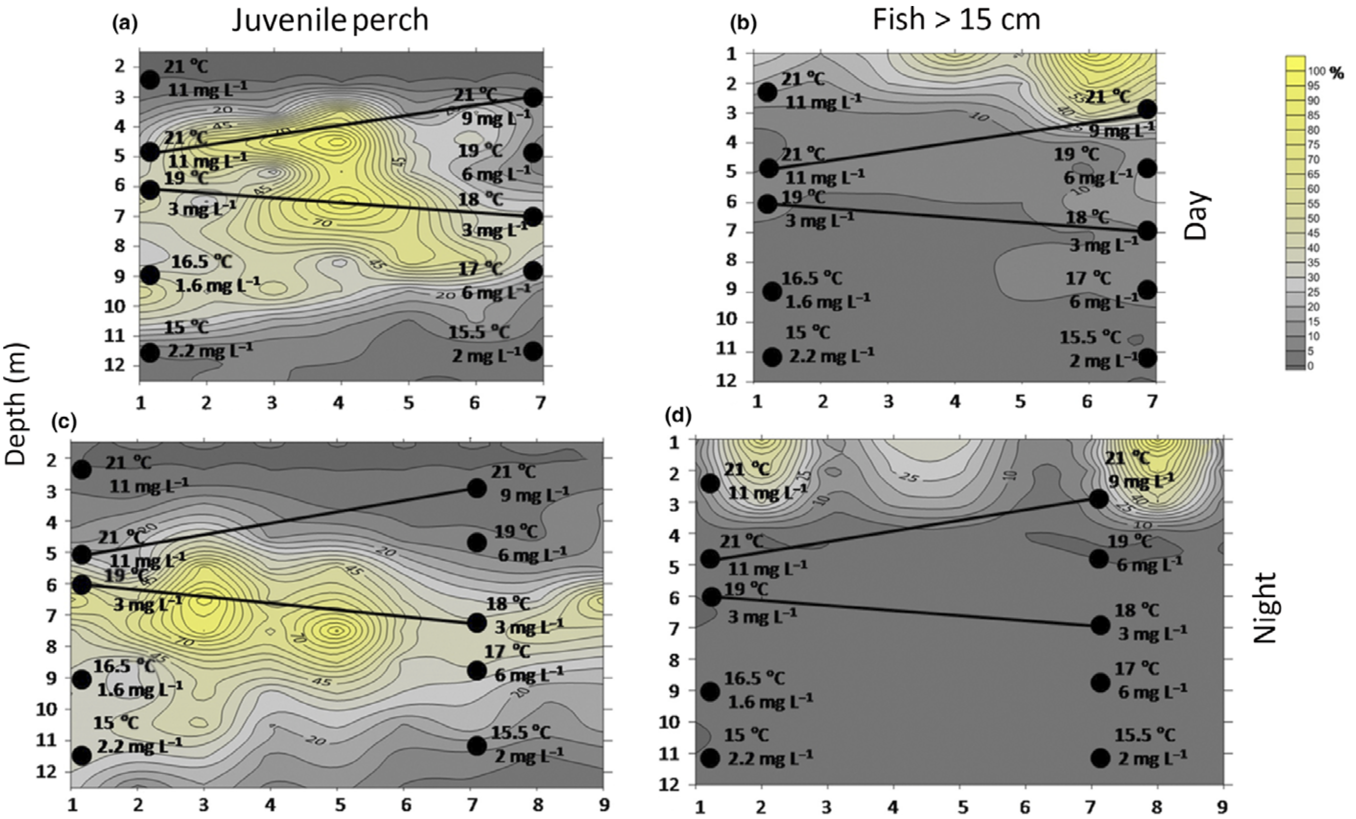

Fig. 4 General model of the distribution of juvenile perch and fish larger than 15 cm during the day and night based on hydroacoustic measurements of the Vír Reservoir in 2010. The numbers along the different isolines correspond to the relative densities at different sectors and depth layers recalculated from the area of highest fish density (given as 100% in each individual panel). Water temperature and dissolved oxygen concentrations are shown as black points and lines show the location of the metalimnion. The numbers along the *x* axis correspond to reservoir sectors shown in Fig. 1.

preferences between the juvenile perch and fish larger than 15 cm during the daytime ($F = 13.3$, $P < 0.001$) as well as the night-time ($F = 30.6$, $P < 0.001$) (Fig. 5). Environmental variables explained 33.6% (daytime) and 47.5% (night-time) of the total variation in the compositional data (juvenile perch and fish larger than 15 cm). Oxygen concentration explained 16.6% of total variability for the daytime ($F = 16.3$, $P < 0.001$) and 46.3% for the night-time ($F = 89.6$, $P < 0.001$). Water temperature explained 15.3% for the daytime ($F = 18.3$, $P < 0.001$) and only 0.4% for the night-time; the latter was not statistically significant ($F = 0.7$, $P = 0.4$). Water depth where fish occurred explained only 1.8% for the daytime and 0.7% for the night-time. Thus, the impact of the depth on fish occurrence and fish segregation was not statistically significant ($F = 2.2$, $P = 0.1$; $F = 0.3$, $P = 0.4$).

The highest density of zooplankton (*Daphnia* spp.) was found typically in epilimnion (depth layers 0–3 and 3–6 m), and the second highest density of zooplankton, during the daytime in 2011, was found in the 9–12 m hypoxic layer (Fig. 3). *Daphnia* represented the most important food source for juvenile perch in 2010 (45%) and 2011 (74%) from all seven categories of food sources. The presence of *Daphnia* in the diet of juveniles increased with depth. The proportion of *Daphnia* in the diet of juvenile perch was highest in the deepest samples of the dam section, peaking in the 9–12 m depth layer (Table 4). In contrast, Bosminidae and *Leptodora kindtii* represented important food sources for juvenile perch from the surface layers of the upper section. The RDA analysis revealed significant differences in the dietary composition of juvenile perch at different depths of the pelagic zone in 2010 ($F = 16.2$, $P < 0.001$) and 2011 ($F = 4.6$, $P < 0.001$) (Fig. 6). Environmental variables explained 50.8% (2010) and 31.3% (2011) of the total variation in species compositional data. The statistically significant variables are shown in Table 5.

In addition, the gut fullness variable of the juvenile perch corresponded to the peak of the vertical distribution of *Daphnia* (9–12 m) within the hypoxic zone. The gut fullness was significantly higher in the depth layer with the lowest oxygen concentrations (regression analysis: 2010, $F_{1.498} = 71.706$, $P < 0.001$; 2011, $F_{1.148} = 16.629$, $P < 0.001$, Table 4).

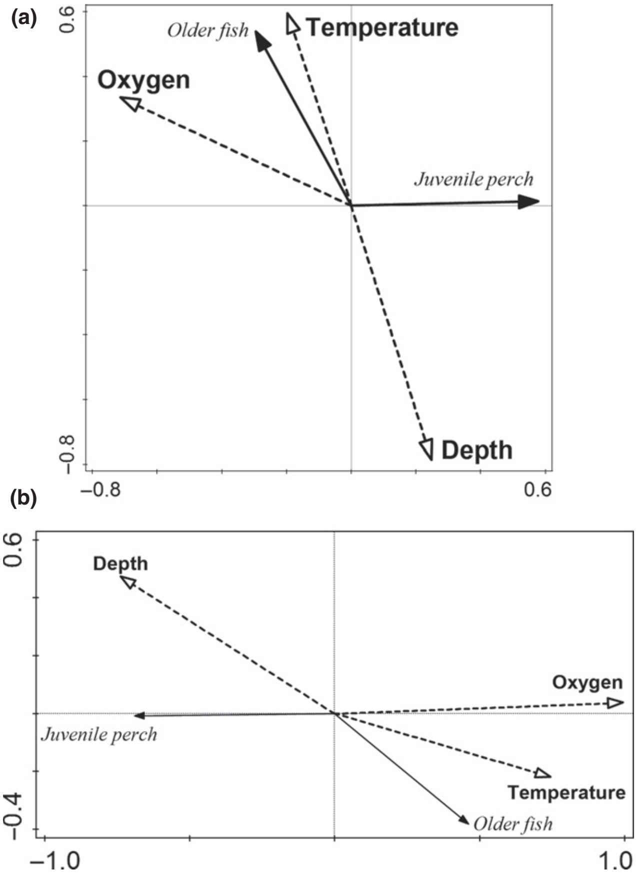

Fig. 5 Redundancy analysis of the distribution of juvenile perch and fish larger than 15 cm (older fish) in the pelagic zone of the Vír Reservoir relative to oxygen concentrations, water temperature and depth in 2010: (a) day, (b) night.

Discussion

The distribution of juvenile perch in deep pelagic zones has been argued to be related to optimal temperature for catching zooplankton (Ward & Robinson, 1974), avoidance of light (Čech *et al.*, 2005, 2007a) and predators (Čech & Kubečka, 2006; Jůza *et al.*, 2009, 2010), reaction to unexpected flood events (Čech *et al.*, 2007b) or even a relation to the apparent marine origin of perciform fish (Holčík, 1998). Hitherto, no study has described the deep pelagic zone as a refuge for small perch (juveniles in general) in terms of hypoxic conditions.

In the Vír Reservoir, juvenile perch were found in relatively high abundances in the hypoxic metalimnion and hypolimnion, especially in the dam and middle reservoir sections. Trawling showed that part of juvenile perch population exhibited a vertical migration. Fish seemed to move towards the surface with decreasing light intensity. However, acoustic measurements implied that a decrease in light resulted in a dispersion of part of the perch population into a wider vertical profile (surprisingly, most fish moved to deeper hypoxic zones). In contrast, juvenile perch during the day were concentrated in the narrow horizontal profile at the normoxic and hypoxic interface. These findings suggest that light intensity is an important mechanism triggering vertical migrations. However, the typical vertical migration of moving to deep water zones with increasing light intensity and moving back to surface layers when the light intensity decreases (Čech *et al.*, 2005) was not observed.

According to Robb & Abrahams (2002), small fish are able to sense that they are not threatened by predators in the hypoxic zones, and therefore can feed efficiently; in experimental conditions small fish remained and frequently fed in hypoxic zones. Our findings are in accordance with this laboratory study: that is, gut fullness of

Table 3 Number of potential predators for the juvenile perch (fish larger than 15 cm) in pelagic gillnets (individuals 1000 m^{-2} of gillnets), adult trawl catches (individuals 100 000 m^{-3} of water sampled) and per night for each year and given section of the Vír Reservoir. In the upper section, only epipelagic gillnets were used due to shallow water. The two numbers in the pelagic gillnets correspond to the two sampled depths 0–4.5 m/ 5–9.5 m.

	2010 (pelagic gillnets)			2011 (pelagic gillnets)			2010 (adult trawl)	
Species	Dam	Middle	Upper	Dam	Middle	Upper	Dam	Middle
Bream	59/2	32/2	356	67/5	69/6	152	216	315
Carp	0/2	0/1	0	0/0	0/0	0	4	20
Asp	10/0	7/0	37	27/4	27/5	52	3	0
Perch	61/11	14/2	255	2/5	3/1	52	8	11
Pikeperch	2/2	3/2	8	0/0	3/3	7	0	3
Pike	0/0	0/0	0	0/0	0/0	0	1	0
European catfish	0/0	0/0	0	0/0	0/0	0	2	4
European eel	0/0	0/0	0	0/0	0/0	0	3	1
Sum	132/17	56/7	656	96/14	102/16	263	237	354

juvenile perch was highest under maximum hypoxia. However, this finding is also likely related to a slower instantaneous gastric evacuation rate at 16°C (depth 9–12 m), which is half the rate observed at 22°C (water surface in 2010) and two-thirds of the rate observed at 19°C (water surface in 2011) (Persson, 1979, 1981). A reduction in the gastric evacuation rate by one-half and one-third corresponds to differences in gut fullness at 9–12 m (41, 55%) and 0–3 m (80, 73%) respectively; consequently, food consumption rate should be similar at both depth layers. The difference in digestion efficiency caused by egestion and excretion at 16 and 22°C equals 1%. Hence, the daily ratio of losses for yellow perch is negligible, that is, equal to 28 and 29% at 16 and 22°C respectively (Kitchell, Stewart & Weininger, 1977).

In both years, *Daphnia* spp. were the main food source of juvenile perch. The highest occurrence of *Daphnia* spp. in the dietary tract of juvenile perch was found in deeper hypoxic zones of the dam section. In addition, zooplankton sampling in 2011 showed that part of the population also utilised the hypoxic zone as a refuge, with zooplankton constituting the second highest abundance after the epilimnion peak. Vanderploeg *et al.* (2009) mentioned that hypoxia provides a refuge for *Daphnia*, where they hide from cyprinid fish which are the largest and most effective zooplanktivores (Vašek & Kubečka, 2004; Jarolím *et al.*, 2010). Although the abundance of zooplankton was higher in the epilimnion than in the hypoxic zones, the second highest peak of *Daphnia* in the hypoxic zone was still sufficient for juvenile perch feeding. The occurrence of juvenile perch in the water column is therefore driven by a sufficient number of zooplankton for food and predator avoidance. Due to the absence of predators, juvenile fish in the hypolimnion can forage on zooplankton more effectively than in the upper layers. According to Roberts *et al.* (2011), yellow perch can still feed efficiently at an oxygen concentration of 2 mg L^{-1}, but weight gain is lower than in oxygen-rich waters. Roberts *et al.* (2011) also emphasised that weight gain is higher at lower temperatures (<20°C).

Together with the lower light intensity, the hypoxic conditions offer refuge to juvenile perch because potential predators cannot survive in such environments for long periods of time (Robb & Abrahams, 2002, 2003). Low oxygen concentration combined with low temperature is not considered a favourable environment for large predatory fish (Jarolím *et al.*, 2010). Adult trawling conducted in the Vír Reservoir concurrently with trawling for juvenile fish revealed that common bream dominated the adult fish stock in the pelagic zone. Bream represented 83% of all individuals and 65% of the fish biomass (Vejřík *et al.*, unpubl. data). Diet analyses showed juvenile perch in the guts of 48% of the common bream analysed, implying an important predatory pressure of bream on the juvenile perch. The juvenile

Table 4 Fullness of the digestive tract of the juvenile perch sampled at the dam section of the Vír Reservoir by fry trawling during the day in 2010 and after dusk in 2011. Mean percentages (±SD) are reported along with the measured dissolved oxygen concentration at different depth layers. ND, no data available.

Depth layer (m)	Fullness (%)		Oxygen (mg L^{-1})	
	2010	2011	2010	2011
0–3	41 ± 25	55 ± 14	11	10.5
3–6	52 ± 26	48 ± 21	8.1	10.2
6–9	64 ± 18	62 ± 16	2.1	4.4
9–12	80 ± 22	73 ± 24	1.9	2.5
12–15	69 ± 27	ND	2.9	2.2

Table 5 Results of redundancy analysis showing the effects of oxygen concentration, depth and reservoir section on the presence of different food sources found in the digestive tract of juvenile perch in the Vír Reservoir. All environmental variables were tested by forward selection. Statistically significant variables are shown in bold.

2010				2011			
Environmental variable	Exp. var. (%)	Pseudo-*F*	*P*	Environmental variable	Exp. var. (%)	Pseudo-*F*	*P*
Upper section	**26.4**	**41.6**	**0.002**	**Depth 0–3 m**	**21.4**	**25.6**	**0.002**
Depth 0–3 m	**7.6**	**13.2**	**0.002**	**Dam section**	**7.1**	**9.2**	**0.004**
Depth 3–6 m	**5.1**	**9.5**	**0.002**	**Depth 6–9 m**	**2.2**	**2.9**	**0.050**
Oxygen	**9.0**	**19.5**	**0.002**	Depth 9–12 m	0.3	0.4	0.806
Depth 12–15 m	**1.7**	**3.8**	**0.016**	Depth 3–6 m	0.3	0.4	0.766
Dam section	0.7	1.6	0.158	Oxygen	0.3	0.4	0.774
Middle section	0.7	1.6	0.146	Upper section	<0.1	<0.1	0.992
Depth 6–9 m	0.3	0.6	0.588				

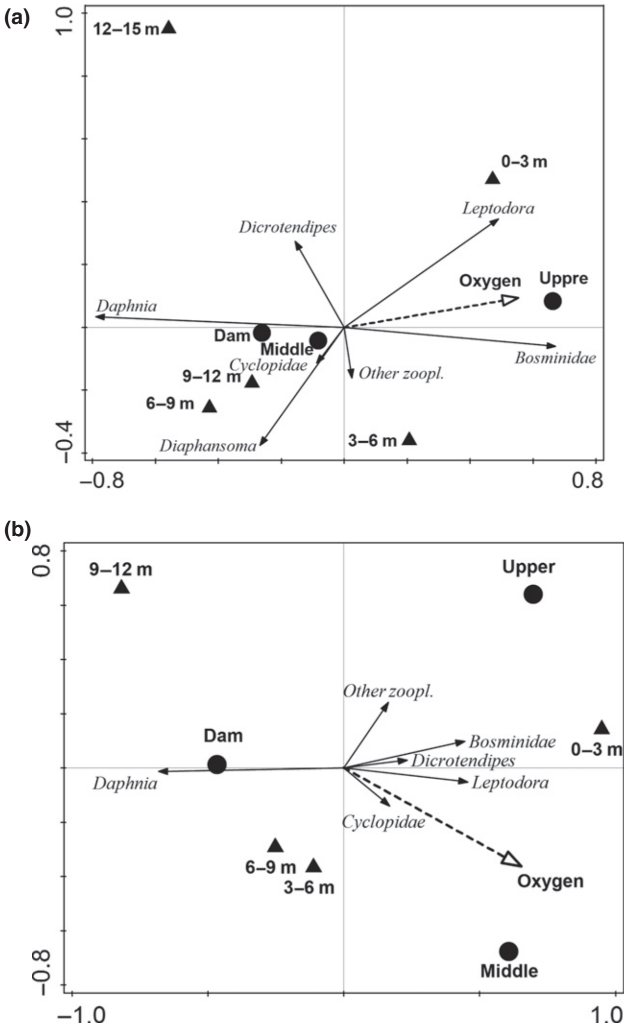

Fig. 6 Redundancy analysis of the diet composition of juvenile perch in the Vír Reservoir. Circles show sections of the reservoir, triangles show depth layers and dashed arrows show an increase in the oxygen concentrations in the water: (a) 2010, (b) 2011.

perch were also observed in the diet of 60% of the carp (*Cyprinus carpio*: Cyprinidae; Vejřík *et al.*, unpubl. data), representing 4% of all individuals and 9% of the fish biomass in the trawl catch. Except for typical zooplanktivorous fish (roach, bleak), the remainder of the fish caught included potential juvenile perch predators such European catfish, pikeperch, European eel (*Anguilla anguilla*: Anguillidae), asp (*Aspius aspius*: Cyprinidae), pike (*Esox lucius*: Esocidae) and perch, which combined represented 6% of all individuals and 25% of the fish biomass (Table 3 and J. Kubečka, M. Říha & T. Jůza, unpubl. data). From these findings, it is clear that predation pressure on juvenile perch in the Vír Reservoir was substantial. Since a uniform pelagic zone offers few refuges from predators, the hypoxic zone is the only possible refuge for small fish. For example, adult perch, one of the main predators of juvenile perch (Brabrant, 1995; Persson, Byström & Wahlström, 2000), avoid oxygen concentrations below 6.7 mg L^{-1} (Alabaster & Robertson, 1961), whereas juvenile perch survive in concentrations of *c.* 1 mg L^{-1} (Gee, Tallman & Smart, 1978; Suthers & Gee, 1986). Therefore, the use of the hypoxic pelagic zone as a refuge by juvenile perch is highly probable. In the Vír Reservoir, a hypoxic zone several metres deep occurred below the oxygenated epilimnion in both years and the oxygen concentration increased again below the hypoxic zone. Nonetheless, the highest abundance of juvenile perch occurred in the hypoxic zone, decreasing in the direction of the light towards the epilimnion, as well as towards the dark, oxygenated hypolimnion (i.e. juvenile perch distribution patterns correlated with increasing hypoxia).

During the day, movement of juvenile perch above the hypoxic refuge is controlled by visual orientation, and they quickly return to the hypoxic refuge when confronted by a potential predator (Jarvalt, Krause & Palm, 2005). At night, visual orientation of perch is limited due to not having a retinal pigment layer (pigment *tapetum lucidum*), which, in contrast, is typical for pikeperch, its predator (Ali, Ryder & Anctil, 1977; Marshall, 1977). The same pigment is typical also for common bream (Kühne & Sewall, 1880), the most important juvenile perch predator in the Vír Reservoir (Vejřík *et al.*, unpubl. data). Visual orientation likely explains why juvenile perch are more concentrated in the hypoxic zone during night than during day. Time in the relative safety of hypoxic refuge is probably dedicated to rest because perch do not feed during the night (Mills, Confer & Kretchmer, 1986; Vašek *et al.*, 2006; Kratochvíl *et al.*, 2008). Although larger fish avoid the hypoxic zones and cannot survive there for extended periods of time (Robb & Abrahams, 2002, 2003), it is not an entirely safe refuge for juvenile perch. Some predators can enter the zone for short periods of time in search of food (Rahel & Nutzman, 1994; Roberts *et al.*, 2009). However, the probability of encountering a predator is much lower than in the upper layers, and the absence of a deep hypoxic zone is probably the main reason why the abundance of juvenile perch was lowest in the upper reservoir section.

In conclusion, our results imply that predator avoidance is main advantage of using the hypoxic pelagic zone as a refuge. Other studies discussing hypoxia, such as Luecke & Teuscher (1994) or Taylor *et al.* (2007), provide evidence of a dietary advantage in hypoxic zones. Our results showed highest gut fullness of juvenile perch under maximum hypoxia, but the values were probably highest due to slower gastric evacuation rates in cold water (Persson, 1979, 1981). Thus, compared to normoxic water with higher temperature (epilimnion) the food consumption rate in the hypoxic pelagic zone was not as high as it may at first appear. For that reason, our results suggest a unique situation where the strong preference of juvenile perch for pelagic hypoxic zones is mainly driven by predation pressure. The presence of sufficient food combined with low predation pressure explains temporary occupation of the hypoxic zone by juvenile perch.

Acknowledgments

We thank Jan Lepš for advice concerning the statistical analyses, three anonymous reviewers and the editor of Freshwater Biology for helpful comments on an earlier version of the manuscript and American journal experts LLC for editing the English. The study was supported by projects No. CZ.1.07/2.3.00/20.0204 (CEKOPOT) of the Ministry of Education, Youth and Sports, 7F14316 of the Norwegian Financial Mechanism 2009–2014 under contract number MSMT-28477/2014; 206/09/P266 and 15-24309S of the Czech Science Foundation, and 159/2013/P of the Grant Agency of University of South Bohemia. D. Ricard was supported by project No. CZ.1.07/2.3.00/30.0032 of the Postdok BIOGLOBE co-financed by the European Social Fund and the state budget of the Czech Republic.

References

Alabaster J.S. & Robertson K.G. (1961) The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of roach (*Rutilus rutilus* (L.)) bream (*Abramis brama* (L)) and perch (*Perca fluviatilis* (L)). *Animal Behaviour*, **9**, 187–192.

Ali M.A., Ryder R.A. & Anctil M. (1977) Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perches (*Perca* spp.) and pikeperches (*Stizostedion* spp.). *Journal of the Fisheries Research Board of Canada*, **34**, 1475–1480.

Appelberg M., Berger H.M., Hesthagen T., Kleiven E., Kurkilahti M., Raitaniemi J. *et al.* (1995) Development and intercalibration of methods in Nordic freshwater fish monitoring. *Water, Air and Soil Pollution*, **85**, 401–406.

Benzie A.H. (2005) Cladocera – genus *Daphnia* including *Daphniopsis*. In: *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World* (Ed. H.J.F. Dumont), pp. 1–376. Vol. 21. Kenobi Productions and Backhuys Publishers, Ghent and Leiden.

Brabrant A. (1995) Intra-cohort cannibalism among larval stages of perch (*Perca fluviatilis*). *Ecology of Freshwater Fish*, **2**, 70–76.

Carpenter S.R., Caraco N.F., Correll D.L., Howarth R.W., Sharpley A.N. & Smith V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications*, **8**, 559–568.

Čech M., Kratochvíl M., Kubečka J., Draštík V. & Matěna J. (2005) Diel vertical migrations of bathypelagic perch fry. *Journal of Fish Biology*, **66**, 685–702.

Čech M. & Kubečka J. (2006) Ontogenetic changes in the bathypelagic distribution of European perch fry *Perca fluviatilis* monitored by hydroacoustic methods. *Biologia Bratislava*, **61**, 211–219.

Čech M., Kubečka J., Frouzová J., Draštík V., Kratochvíl M. & Jarošík J. (2007b) Impact of flood on distribution of bathypelagic perch fry layer along the longitudinal profile of large canyon-shaped reservoir. *Journal of Fish Biology*, **70**, 1109–1119.

Čech M., Kubečka J., Frouzová J., Draštík V., Kratochvíl M., Matěna J. *et al.* (2007a) Distribution of the bathypelagic perch fry layer along the longitudinal profile of two large canyon-shaped reservoirs. *Journal of Fish Biology*, **70**, 141–154.

Chapman L.J., Chapman C.A. & Chandler M. (1996a) Wetland ecotones as refugia for endangered fishes. *Biological Conservation*, **78**, 263–270.

Chapman L.J., Chapman C.A., Ogutu-Ohwayo R., Chandler M., Kaufman L.S. & Keiter A.E. (1996b) Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conservation Biology*, **10**, 554–561.

Diaz R.J. & Rosenberg R. (2008) Spreading dead zones and consequences for marine ecosystems. *Science*, **321**, 926–929.

Einsle U. (1996) Copepoda: Cyclopoida. Genera Cyclops, Megacyclops, Acanthocyclops. In: *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World* (Ed. H.J.F. Dumont), pp. 1–82. Vol. 10. SPB Academic Publishing, The Hague.

Ekau W., Auel H., Pörtner H.-O. & Gilbert D. (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences*, **7**, 1669–1699.

ESRI (2014) ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute.

Flössner D. (2000) *Die Haplopoda und Cladocera Mitteleuropas*. Backhuys Publishers, Leiden.

Foote K.G., Knutsen H., Vestnes G., MacLennan D.N. & Simmonds E.J. (1987) Calibration of acoustic instruments for fish density estimation. *Cooperative Research Report, International Council for the Exploration of the Sea*, **144**, 1–70.

Frouzová J., Kubečka J., Balk H. & Frouz J. (2005) Target strength of some European fish species and its dependence on fish body parameters. *Fisheries Research*, **7**, 86–96.

Gallaugher P. & Farrell A.P. (1998) Hematocrit and blood oxygen-carrying capacity. In: *Fish Physiology* (Eds S.F. Perry & B.L. Tufts), pp. 185–227. Vol. 17. Academic Press, London.

Gee J.H., Tallman R.F. & Smart H.J. (1978) Reactions of some great plains fishes to progressive hypoxia. *Canadian Journal of Zoology*, **56**, 1962–1966.

Holčík J. (1998) Lacustrine fishes and the trophic efficiency of lakes: prelude to the problem. *Italian Journal of Zoology*, **65**, 411–414.

Hughes G.M. (1984) Scaling of respiratory areas in relation to oxygen consumption of vertebrates. *Experientia*, **40**, 519–652.

Jarolím O., Kubečka J., Čech M., Vašek M., Peterka J. & Matěna J. (2010) Sinusoidal swimming in fishes: the role of season, density of large zooplankton, fish length, time of the day, weather condition and solar radiation. *Hydrobiologia*, **654**, 253–265.

Jarvalt A., Krause T. & Palm A. (2005) Diel migration and spatial distribution of fish in a small stratified lake. *Hydrobiologia*, **547**, 197–203.

Jones D.R. (1971) Theoretical analysis of factors which may limit the maximum oxygen uptake of fish: the oxygen cost of the cardiac and branchial pumps. *Journal of Theoretical Biology*, **32**, 341–349.

Jůza T., Čech M., Kubečka J., Vašek M., Peterka J., Kratochvíl M. *et al.* (2010) The influence of the trawl mouth opening size and net colour on catch efficiency during sampling of early stages of perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*) in the bathypelagic layer of a canyon-shaped reservoir. *Fisheries Research*, **105**, 125–133.

Jůza T. & Kubečka J. (2007) The efficiency of three fry trawls for sampling the freshwater pelagic fry community. *Fisheries Research*, **85**, 285–290.

Jůza T., Vašek M., Kubečka J., Sed'a J., Matěna J., Prchalová M. *et al.* (2009) Pelagic underling communities in a canyon-shaped reservoir in late summer. *Journal of Limnology*, **68**, 304–314.

Kitchell J.F., Stewart D.J. & Weininger D. (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens)* and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada*, **34**, 1922–1935.

Klumb R.A., Bunch K.L., Mills E.L., Rudstam L.G., Brown G., Knauf C. *et al.* (2004) Establishment of a metalimnetic oxygen refuge for zooplankton in a productive Lake Ontario embayment. *Ecological Applications*, **14**, 113–131.

Kratochvíl M., Peterka J., Kubečka J., Matěna J., Vašek M., Vaníčková I. *et al.* (2008) Diet of larvae and juvenile perch, *Perca fluviatilis* performing diel vertical migrations in a deep reservoir. *Folia Zoologica*, **57**, 313–323.

Kühne W. & Sewall H. (1880) On the physiology of the retinal epithelium. *Journal of Physiology*, **3**, 88–92.

Larsson P. & Lampert W. (2011) Experimental evidence of a low-oxygen refuge for large zooplankton. *Limnology and Oceanography*, **56**, 1682–1688.

Lass S., Boersma M. & Spaak P. (2000) How do migrating daphnids cope with fish predation risk in the epilimnion under anoxic conditions in the hypolimnion? *Journal of Plankton Research*, **22**, 1411–1418.

Lowe-Jinde L. & Niimi A.J. (1983) Influence of sampling on the interpretation of haematological measurements of rainbow trout, *Salmo gairdneri*. *Canadian Journal of Zoology*, **61**, 396–402.

Ludsin S.A., Kershner M.W., Blocksom K.A., Knight R.L. & Stein R.A. (2001) Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecological Applications*, **11**, 731–746.

Luecke C. & Teuscher D. (1994) *Habitat Selection by Lacustrine Rainbow Trout within Gradients of Temperature, Oxygen, and Food Availability. Theory and Application of Fish Feeding Ecology*. University of South Carolina Press, Columbia.

MacLennan D.N. & Simmonds E.J. (1992) *Fisheries Acoustics*. Chapman & Hall, London.

Marshall T.R. (1977) Morphological, physiological, and ethological differences between walleye (*Stizostedion vitreum vitreum*) and pikeperch (*S. lucioperca*). *Journal of the Fisheries Research Board of Canada*, **34**, 1515–1523.

McCauley E. (1984) The estimation of the abundance and biomass of zooplankton samples. In: *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters* (Eds J.A. Downing & F.H. Rigler), pp. 228–265. Blackwell Publications, Oxford.

Mills E.L., Confer J.L. & Kretchmer D.W. (1986) Zooplankton selection by young yellow perch: the influence of light, prey density and predator size. *Transactions of the American Fisheries Society*, **115**, 716–725.

Muir B.S. (1969) Gill dimensions as a function of fish size. *Journal of the Fisheries Research Board of Canada*, **26**, 165–170.

Persson L. (1979) The effect of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). *Freshwater Biology*, **9**, 99–104.

Persson L. (1981) The effect of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. *Freshwater Biology*, **11**, 131–138.

Persson L., Byström P. & Wahlström E. (2000) Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology*, **81**, 1058–1071.

Rahel F.J. & Nutzman N.W. (1994) Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. *Ecology*, **75**, 1246–1253.

Robb T. & Abrahams M.V. (2003) Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small. *Journal of Fish Biology*, **62**, 1067–1081.

Robb T.L. & Abrahams M.V. (2002) The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. *Behavioral Ecology and Sociobiology*, **52**, 25–30.

Roberts J.J., Brandt S.B., Fanslow D., Ludsin S.A., Pothoven S.A., Savica D. *et al*. (2011) Effects of hypoxia on consumption, growth, and RNA:DNA ratios of young yellow perch. *Transactions of the American Fisheries Society*, **14**, 1574–1586.

Roberts J.J., Grecay P.A., Ludsin S.A., Pothoven S.A., Vanderploeg H.A. & Höök T.O. (2012) Evidence of hypoxic foraging forays by yellow perch (*Perca flavescens*) and potential consequences for prey consumption. *Freshwater Biology*, **57**, 922–937.

Roberts J.J., Höök T.J., Ludsin S.A., Pothoven S.A., Vanderploeg H.A. & Brandt S.B. (2009) Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology*, **381**, 132–142.

Sed'a J., Kolářová K. & Petrusek A. (2007a) *Daphnia galeata* in the deep hypolimnion: spatial differentiation of a "typical epilimnetic" species. *Hydrobiologia*, **594**, 47–57.

Sed'a J., Petrusek A., Macháček J. & Šmilauer P. (2007b) Spatial distribution of the *Daphnia longispina* species complex and other planktonic crustaceans in the heterogeneous environment of canyon-shaped reservoirs. *Journal of Plankton Research*, **29**, 619–628.

Šmilauer P. & Lepš J. (2014) *Multivariate Analysis of Ecological Data Using CANOCO 5*. Cambridge University Press, Cambridge.

Šrámek-Hušek R. (1953) *Copepoda*. Czech Academy of Science Publishing, Prague.

Šrámek-Hušek R., Straškraba M. & Brtek J. (1962) *Phylopoda*. Czech Academy of Science Publishing, Prague.

Stanley D.R. & Wilson C.A. (2004) Effect of hypoxia on the distribution of fishes associated with a petroleum platform off coastal Louisiana. *North American Journal of Fisheries Management*, **24**, 662–671.

Suthers I.M. & Gee J.H. (1986) Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1562–1570.

Taylor J.C., Rand P.S. & Jenkins J. (2007) Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Marine Biology*, **152**, 939–957.

Ueda H. & Reid J.W. (2003) Copepoda – genera Mesocyclops and Thermocyclops. In: *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World* (Ed. H.J.F. Dumont), pp. 1–316. Vol. 20. Backhuys Publishers, Leiden.

Vanderploeg H.A., Ludsin S.A., Ruberg S.A., Hook T.O., Pothoven S.A., Brandt S.B. *et al*. (2009) Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology*, **381**, 92–107.

Vašek M. & Kubečka J. (2004) *In situ* diel patterns of zooplankton consumption by subadult/adult roach *Rutilus rutilus*, bream *Abramis brama*, and bleak *Alburnus alburnus*. *Folia Zoologica*, **53**, 203–2147.

Vašek M., Kubečka J., Josef Matěna J. & Sed'a J. (2006) Distribution and diet of 0+ fish within a canyon-shaped European reservoir in late summer. *International Review of Hydrobiology*, **91**, 178–194.

Ward F.J. & Robinson G.G.C. (1974) A review of research on the limnology of West Blue Lake, Manitoba. *Journal of the Fisheries Research Board of Canada*, **31**, 977–1005.

Weider L.J. & Lampert W. (1985) Differential response of *Daphnia* genotypes to oxygen stress: respiration rates, hemoglobin content and low-oxygen tolerance. *Oecologica*, **65**, 487–491.

West G.B., Brown J.H. & Enquist B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–126.

Yamamoto K. (1991) Relationship of respiration to body weight in the carp *Cyprinus carpio* under resting and normoxic conditions. *Comparative Biochemistry and Physiology*, **100**, 113–116.

Yamamoto K. (1992) Relationship of respiration to body weight in the tilapia *Oreochromis niloticus* under resting and normoxic conditions. *Comparative Biochemistry and Physiology*, **103**, 81–83.

Yamanaka H., Kohmatsu Y. & Yuma M. (2007) Difference in the hypoxia tolerance of the round crucian carp and largemouth bass: implications for physiological refugia in the macrophyte zone. *Ichthyological Research*, **54**, 308–312.

Zanuy S. & Carrillo M. (1985) Annual cycles of growth, feeding rate, gross conversion efficiency and hematocrit levels of sea bass (*Dicentrarchus labrax* L.) adapted to different osmotic media. *Aquaculture*, **44**, 11–25.

(Manuscript accepted 18 February 2016)

Paper V

Thirty-year-old paradigm about unpalatable perch egg strands disclaimed by the freshwater top-predator, the European catfish (*Silurus glanis*)

PLOS ONE

RESEARCH ARTICLE

Thirty-Year-Old Paradigm about Unpalatable Perch Egg Strands Disclaimed by the Freshwater Top-Predator, the European Catfish (*Silurus glanis*)

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OPEN ACCESS

Citation: Vejřík L, Vejříková I, Kočvara L, Sajdlová Z, Hoang The SC, Šmejkal M, et al. (2017) Thirty-Year-Old Paradigm about Unpalatable Perch Egg Strands Disclaimed by the Freshwater Top-Predator, the European Catfish (*Silurus glanis*). PLoS ONE 12(1): e0169000. doi:10.1371/journal.pone.0169000

Editor: Vyacheslav Yurchenko, University of Ostrava, CZECH REPUBLIC

Received: October 25, 2016

Accepted: December 11, 2016

Published: January 6, 2017

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: The study was supported by projects No. CZ.1.07/2.3.00/20.0204 (CEKOPOT) of the Ministry of Education, Youth and Sports, No. 7F14316 of the Norwegian Financial Mechanism 2009–2014 under contract number MSMT-28477/2014, No. 206/09/P266 of the Czech Science Foundation, No. 677039 (CLIMEFISH) of the European Union's

Abstract

So far, perch egg strands have been considered unpalatable biological material. However, we repeatedly found egg strands of European perch (*Perca fluviatilis*) in the diet of European catfish (*Silurus glanis*) caught by longlines in Milada and Most Lakes, Czech Republic. The finding proves that perch egg strands compose a standard food source for this large freshwater predatory fish. It extends the present knowledge on catfish foraging plasticity, showing it as an even more opportunistic feeder. Utilization of perch egg strands broadens the catfish diet niche width and represents an advantage against other fish predators. Comparison of datasets from extensive gillnet and SCUBA diver sampling campaigns gave the evidence that at least in localities where food sources are limited, multilevel predation by catfish may have an important impact on the perch population.

Introduction

A study published 31 years ago by Newsome and Tompkins [1] described perch (*Perca* spp.) egg strands as repellent matter for predators. Observation and testing of six fish and four invertebrate species proved that perch egg strands are an undesirable food source for them. One year later, Diamond and Wakefield [2] published a topical study referring to the utilization of perch egg strands by three species of caddisfly larvae (Trichoptera) and two species of flatworms (Tricladida). The authors pointed out that these represent only a small fraction of aquatic invertebrates and predation pressure exerted on perch is irrelevant. The paradigm of perch egg strands as unpalatable biological matter has since been widely accepted by researchers all over the world [3–9].

European catfish (*Silurus glanis*), one of the world biggest freshwater fish, is a typical opportunist with a wide diet niche. It has successfully spread worldwide accompanied by human

Horizon 2020 research and innovation programme, and No. 04-151/2016/P of the Grant Agency of University of South Bohemia.

Competing Interests: The authors have declared that no competing interests exist.

activity [10–14]. Recent studies demonstrated that European catfish uses atypical food sources including sources not originating from freshwater but marine or terrestrial ecosystems [15,16].

Although the European catfish is a top predator, only a few studies regarding its diet have been carried out, and most of them are recent (for review see [12]). The main reason is the poor capture success by standard ichthyological methods [17]. In the present study, we prove that perch (*Perca fluviatilis*) egg strands are a part of the European catfish diet. Further, we discuss the potential impact of European catfish on perch populations as a result of multilevel predation.

Materials and Methods

Study site

The study was conducted in two water bodies created after aquatic restorations of mining pits, Milada and Most Lakes, Czech Republic. The oligo- to mesotrophic Milada Lake has an area of 250 ha, volume of 36×10^6 m^3 and maximum depth of 25 m (Fig 1). Aquatic restoration lasted from 2001 to 2011. Northern pike (*Esox lucius*) was introduced in 2005 (789 individuals, mean weight 0.3 kg) and European catfish in 2007 (316 individuals, mean weight 1.2 kg), both for biomanipulation purposes. The oligotrophic Most Lake has an area of 310 ha, volume of 70×10^6 m^3 and maximum depth of 75 m (Fig 1). Aquatic restoration lasted from 2008 to 2014. Northern pike (2332 individuals, mean weight 1.1 kg) and European catfish (694 individuals, mean weight 3.7 kg) were both introduced in 2011, 2012 and 2013. In both lakes, all catfish individuals were individually tagged with a passive integrated transponder tag (PIT-tag, Oregon RFID, full-duplex, length 12 mm, diameter 2.15 mm, weight 0.11 g, 11784/11785 compatible).

Fish sampling and stomach content analysis

European catfish and northern pike from both lakes were caught by longlines in early May 2014 and 2015 during a 4-day-and-night-long campaign (see Fig 2 for illustrative description). Animal treatment (including method of longlines and stomach content analysis) was performed in accordance with the guidelines from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01679) and with permission of Palivový kombinát Ústí, státní podnik, owner of the study sites. The work was approved by the Ethics Committee of the Czech Academy of Sciences. The field study did not involve endangered or protected species. The main line was 60 m long with three main buoys situated at both ends and in the middle of the line. Anchoring ropes, 3.5–7 m long, with weights (32 kg each) fixing the main line in place were tied to the buoys. Auxiliary buoys were situated every 5 m between the main buoys with a hanging 2.5 m long snood made of two parts i) 2-m long fishing-line with maximum load of 50 kg and ii) more durable 0.5 m long fishing-line with maximum load of 100 kg with a swivel between the two parts to preventing twisting. There was also a 150 g sinker keeping the snood at the appropriate depth. At the end of the snood, there was a catfish rig composed of a single hook with bait (total length of the bait: L_T = 180–300 mm) and a fishing treble. The predator (catfish or pike) was hooked by the fishing treble hanging under the baited hook while it tried to catch and tear down the bait. Altogether 30 individual bait fish on 3 longlines were used each day of sampling. To cover the shore area of the lake evenly, the lines were moved each day to a new place and they were checked three times per day (before dusk, soon after midnight, and shortly after dawn). Most of the catfish were caught during the night, most of the pike during the day. All individuals were measured, weighed and non-invasive stomach content analyses were provided. In the case of catfish, stomach content was extracted by hand through the opened mouth and gullet [18]. In the case of pike, water was pumped through a small tube into the pike´s stomach and the content was washed out through a larger tube into a

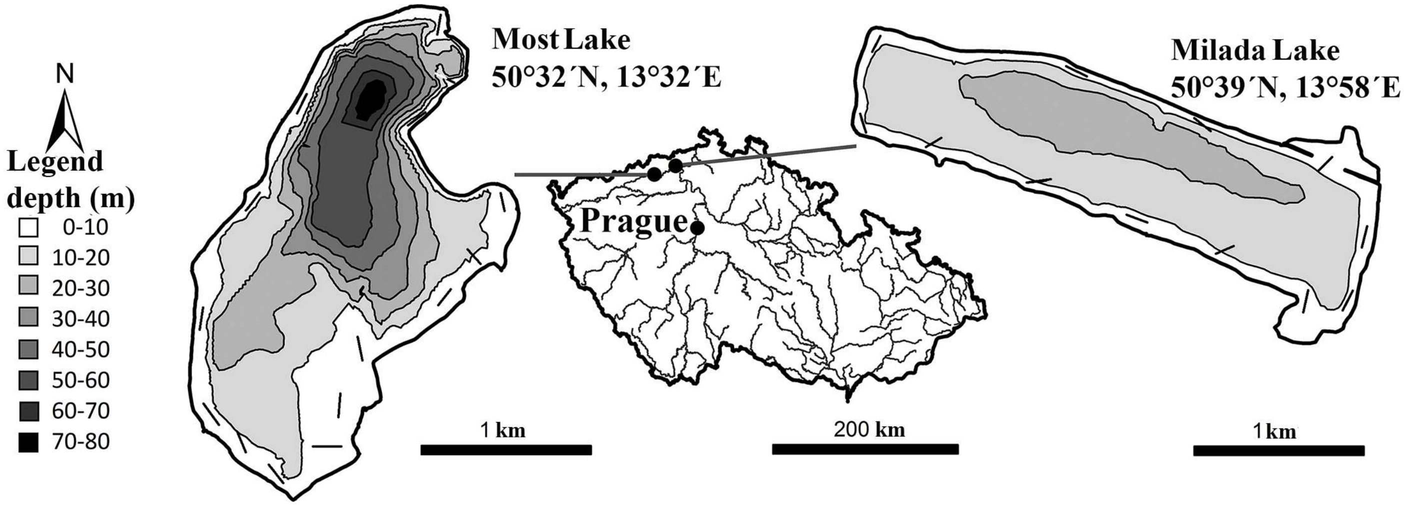

Fig 1. Map showing the location and relevant depths of the two study sites, Milada and Most Lakes, Czech Republic. Localities sampled by longlines are shown by lines along the lake shores.

doi:10.1371/journal.pone.0169000.g001

jar [19]. The fish were released back into the lake as soon as possible. The stomach contents were consequently identified, or fixed by 70% ethanol in case of highly digested matter requiring precise laboratory identification using diagnostic elements including fish bones [20,21].

To obtain quantitative assessment of perch egg strands, SCUBA divers monitored their occurrence, numbers and sizes at transects from the shore to a depth of ~20 m in April and May in 2015 (for details of the methodology and results from previous years see [9, 22–25]).

Sizes of female perch that had contributed to the spawning were estimated from the width of individual egg strands, using the equation of Dubois et al. [26]. Perch abundance was estimated by multi-mesh gillnets (see [24] for detailed description). The gillnets were set overnight (September; installed 2 h before sunset, lifted 2 h after sunrise) at depths of 0–3, 3–6, 6–9 and 9–12 m in benthic and 0–5 and 5–10 m (or 0–6 and 6–12 m in 2014, respectively) in pelagic habitats at three to four localities. Altogether, 224 benthic and 74 pelagic gillnets were set, representing a total exposed area of 25,860 m^2. Only 6% and 2% of fish community was annually caught by gillnets in Milada and Most Lakes, respectively. In case of perch population, it was 9% and 2% in Milada and Most Lakes, respectively (for more details see to supplementary materials).

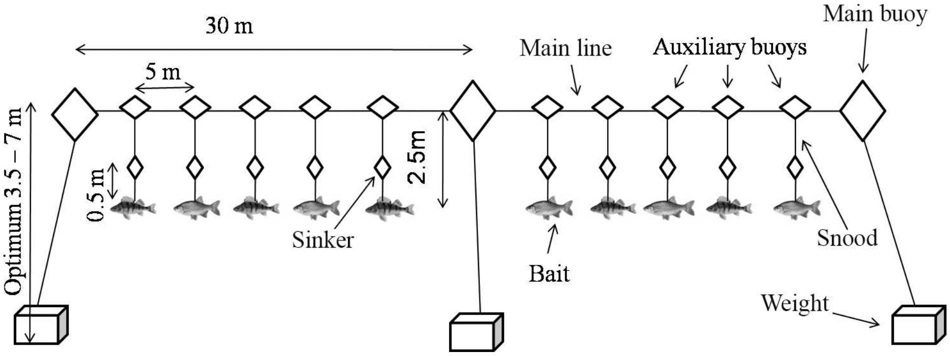

Fig 2. The scheme of longlines, fishing method used for catfish sampling in Milada and Most Lakes.

doi:10.1371/journal.pone.0169000.g002

Abiotic factors

Water temperature measurements were taken between 12:00 and 14:00 during the sampling campaign in both years (2014 and 2015) and lakes. Measurements were made at 1 m depth intervals using a calibrated YSI 556 MPS probe (YSI Incorporated—Yellow Springs, Ohio, USA). Temperature of epilimnion was used for purpose of this study.

Statistical analysis

To evaluate whether the trend in decreasing numbers of spawned egg strands was caused by decreasing size of the perch spawning stock, only perch $\geq$ 230 mm L_T were used in the analysis. This size limit was set for two main reasons: 1) The SCUBA diving results from 2007 and 2009 have shown that in Milada Lake 97% and 92% of perch egg strands were spawned by females $\geq$ 230 mm L_T [9, 23]. 2) Based on gillnet catches, almost 90% of perch $\geq$ 230 mm L_T were females [24]. Regression analysis was used for determining the relationship between CPUE (catch per unit effort) of perch $\geq$230 mm L_T caught by 1,000 m^2 of gillnets in September of year X-1 and the CPUE of egg strands found by SCUBA divers (egg strands per 10 hours of diving) during spawning season in following spring, *i.e.* April/May of year X. The CPUE of perch caught by gillnets was calculated as the mean of catches of perch individuals $\geq$230 mm L_T over all depth layers of benthic and pelagic habitats. This comparison is not biased by the growing season because female perch of 230 mm L_T caught in September of year X-1 will be of approximately the same size in April/May of year X (for more details see [24]). The statistical test was performed in the R environment for statistical computing (version 3.2.2) [27]. A non-parametric Kruskal–Wallis test (Statistica 12; Stat-Soft Inc., Tulsa, OK) was used to test for differences between sizes of catfish with perch egg strands and catfish with other food items in the stomachs.

Results

In total, 128 individuals of the European catfish (including three recaptures) were caught in Milada and Most Lakes during spring sampling in 2014 and 2015 (L_T range 710–1580 mm, weight range 0.8–23.5 kg). Altogether, 56 food items in the stomachs of 37 individuals were found. Perch egg strands were recorded in ten different catfish (verified by PIT-tags; one egg strand per catfish; Table 1). One of them had perch egg strand and juvenile perch in the stomach. Otherwise, only perch egg strands were found. In contrast, no perch egg strands were found in pike (41 individuals, L_T 690–1190 mm, weight 3.6–14.2 kg).Perch egg strands were not detected in stomachs of catfish in Milada Lake, in 2014, but in 2015. Excluding Milada Lake 2014, perch egg strands composed 13–71% of identified diet items (by numbers; Table 1). Catfish with perch egg strands in the stomachs were significantly smaller than catfish with other food items in the stomachs in both lakes ($F_{1,28} = 5.6$, $p < 0.05$; Table 1). All perch egg strands extracted from catfish stomachs included a jelly coat. The width of egg strands from catfish stomachs in Most Lake was 63 ± 8 mm (mean ± SD) in both years, corresponding with L_T of perch female 278 ± 20 mm. The width of egg strands from catfish stomachs in Milada Lake in 2015 was 50 and 55 mm, corresponding with L_T of perch female 242 and 256 mm.

In Most Lake 2015, SCUBA divers found 3 perch egg strands of width >40 mm, corresponding with L_T of perch female >230 mm, during three dives in three consecutive weeks (total duration 3.5 h). In Milada Lake 2015, 23 perch egg strands were found during six dives in three consecutive weeks (total duration 9 h). The width of 11 of them was 30–40 mm, corresponding with L_T of perch female 180–213 mm, and 12 of them were wider than 40 mm, corresponding with L_T of perch female >230 mm.

Table 1. Total number of catfish, number of catfish with egg strands, with other food items and with empty stomach caught by longlines in Milada and Most Lakes in spring 2014 and 2015. Values in lines show number of catfish, size of catfish (mean L_T ±SD, in mm) and number of given stomach content (some individuals had more than one food items in the stomach). In Milada 2015, one individual is included in two categories (with egg strands, with other food items) because an egg strand and also a small perch were found in the stomach.

Lake		Most		Milada	
Year		2014	2015	2014	2015
Date of sampling		6.–9. 5.	6.–7. 5.	12.–15. 5.	5.–7. 5.
Water temp. ˚C		12. 1	12. 4	16. 3	12. 2
Number of catfish	Total	56 (850±161)	29 (877 ±122)	26 (1125±168)	17 (1153±215)
	With egg strands	3 (803±32), 3	5 (825±38), 5	0	2 (1070±113), 2
	With other food items	11 (915±102), 19 [‡]	2 (898±96), 2 [*]	10 (1226±81), 17 [&]	5 (1152±152), 8 [#]
	With empty stomach	42 (836±175)	22 (887±134)	16 (1065±179)	11 (1196±261)

[‡] 8× rudd (*Scardinius erythrophthalmus*), 4× ruffe (*Gymnocephalus cernua*), 3× tench (*Tinca tinca*), 1× perch, 2× bird (Aves), 1× frog (Anura).

[*] 2× roach (*Rutilus rutilus*).

[&] 9× rudd, 3× perch, 2× asp (*Aspius aspius*), 1× tench, 2× bird.

[#] 7× perch, 1× rudd.

doi:10.1371/journal.pone.0169000.t001

According to gillnet sampling, an increase in perch abundance ($L_T \geq 230$ mm) in Milada Lake was observed only between the years 2006 and 2007. A decrease in perch abundance has been observed since 2007, the year when catfish were stocked. A similar trend has been observed by SCUBA divers during perch egg strand monitoring. A strong relationship was found between the CPUE of perch $\geq$230 mm L_T caught by gillnets and the CPUE of perch egg strands found by SCUBA divers during the following springs (regression analysis; $F_{1,2} = 179.2$, $p < 0.001$; y = 4.27x-25.51, $R^2 = 0.98$; Fig 3). The relationship was not observed between the perch abundance in 2006 and the number of perch egg strands in 2007, *i.e.* the period before catfish mass stocking in Milada Lake. At that time, one larger perch individual caught into the gillnets in late summer corresponded with three times more perch egg strands deposited next spring compared to following years (Fig 3; for complete dataset see S1 Data).

Discussion

It is clear that perch egg strands were eaten after they were spawned because the occurrence of jelly coat indicates their deposition in water [1]. No fish remains were found along with perch egg strands in the stomachs, indicating that egg strands were consumed intentionally, not with female perch preyed on before spawning or during the spawning event. Only in one exception, we found a well-preserved perch (150 mm L_T) along with a perch egg strand, but the strand width of 55 mm corresponds with perch female of 256 mm L_T [26] implying no relation. Catfish apparently eat perch egg strands directly from the flooded vegetation, which are frequently found in post-mining lakes and are commonly used by perch as spawning substrate [9, 22,24]. In one case, a small part of the spawning substrate (branch of a tree) was also found in the egg cluster extracted from the catfish stomach.

Perch egg strands were present in catfish stomachs in the case of Most Lake 2014 and 2015 and also Milada Lake 2015. Catfish most likely utilized perch egg strands also in Milada Lake in 2014, but water temperature of 16.3˚C during longline sampling was already much higher than the optimal temperature for perch spawning, *i.e.* 12˚C [28, 29, 24] and, most probably, the perch had probably already hatched. Unfortunately, direct monitoring of perch egg strands was not carried out in Milada Lake in 2014. Population of adult perch in Most Lake is three times higher in comparison to Milada Lake (28.4 vs. 8.6 ind. $\geq$230 mm L_T per 1,000 m^2 of gillnets; [30,31]). Nevertheless the catfish population is also more abundant in Most Lake (1.86

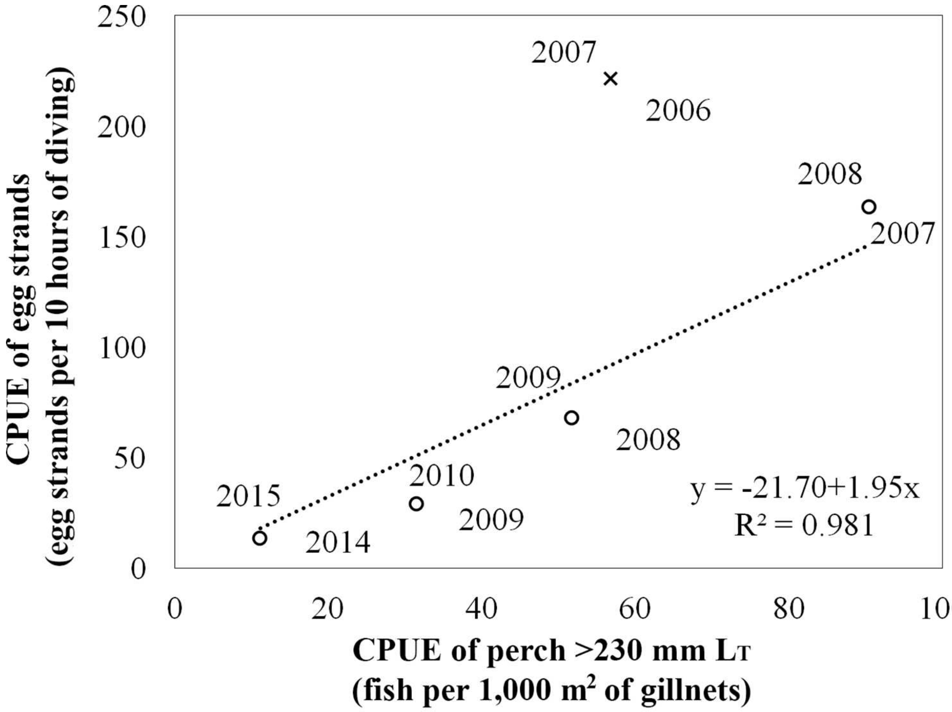

Fig 3. The relationship between the CPUE of perch ≥230 mm L_T caught by gillnets during late summer in Milada Lake (years 2006–2009, 2014) and the CPUE of perch egg strands found by SCUBA divers during the following spring (years 2007–2010, 2015). Regression analysis was provided for all years of monitoring (marked by empty circles), excluding the year marked by a cross (*i.e.* CPUE of perch ≥230 mm L_T caught by gillnets in 2006, and CPUE of perch egg strands found by SCUBA divers in 2007). The cross corresponds with the period before catfish mass stocking in Milada Lake, *i.e.* before impact of catfish on perch population.

doi:10.1371/journal.pone.0169000.g003

ind. ha^{-1}, 7.65 kg ha^{-1}, mean L_T 850 mm) than in Milada Lake (0.72 ind. ha^{-1}, 5.94 kg ha^{-1} mean L_T 1030 mm; Vejřík et al., in prep.). The catfish population represents 24.4% and 39.3% of the total fish biomass in Milada and Most Lakes, respectively. In Milada Lake, the populations of the top predator (only) is close to the average biomass of all predators (including e.g. perch ≥15 cm standard length) calculated for other aquatic ecosystems of a similar size in the Czech Republic [32], in Most Lake the biomass of the top predator almost doubled this value.

The low number of perch egg strands found in Most Lake in 2015 (3 pieces, *i.e.* 8.6 pcs. per 10 hours of diving) was probably influenced by high predation pressure by the smaller catfish. It is supported by the fact that catfish with perch egg strands in the stomachs were significantly smaller (mean 867 mm L_T) than catfish with other food items in the stomachs (1067 mm L_T). Smaller individuals are gape limited and their prey capture efficiency is lower, therefore readily available food sources such as egg strands are preferred. In Most Lake in 2015, catfish presence in perch spawning areas was also confirmed by SCUBA divers, where nine catfish were observed (per 3.5 h of diving) giving the ratio of three catfish to one perch egg strand.

Perch reproduction in Milada Lake has been intensively monitored for some years [9,25], previous years have shown an apparent decrease in the abundance of adult perch and a related decrease of perch egg strands since predators, catfish and pike, were stocked [24]. An increase in perch abundance was observed only between the years 2006 and 2007. Since 2007, the year of catfish mass stocking, a continuous decrease in the abundance of adult perch and subsequent decrease in abundance of perch egg strands has been observed. Čech et al. [24], monitoring the continuous decrease in abundance of adult perch and perch egg strands, hypothesized that the predation pressure exists on a single-level, *i.e.* catfish eat spawning perch. According to [33,12], perch is a common part of the catfish diet. Nevertheless, the new finding showing predation on perch egg strands, which were considered to be unpalatable [1,2], throws new light on the predator-prey interaction between catfish and perch.

Since perch (both *P. fluviatilis* and *P. flavescens*) exhibit a reproductive style unique among teleosts (single ovary is enclosed in a membrane forming an ovisac), the yearly effort of a perch female committed to reproduction is comprised of one item (egg strand) with only one defence–unpalatability [1]. In contrast to pike, catfish seem to be one of a few and presently the only known predators able to digest this easily available food source. The substantial impact on perch reproductive material induced by catfish predation is apparent from the triple decrease in abundance of perch egg strands per adult perch caught after catfish mass stocking in Milada and Most Lakes. From an evolutionary perspective, such behaviour, where catfish utilize the whole reproductive potential of a single perch female, represents a serious bottleneck for gene flow within the perch population. Thus coexistence with catfish presents a serious threat for perch on more than one level.

Catfish utilize egg strands even though they are nutritionally poor due to high water content after expanding in the aquatic environment [1,34]. The advantage is probably the short search and handling time, profitable mainly in cold water during spring time. Therefore, the impact on perch in some localities must be significant as perch egg strands are easily available and may be utilized in high quantity to cover the nutritional needs of catfish. In practice, a significant impact on the perch population is apparent in Milada Lake (Fig 3). A similar trend is also predicted to occur in Most Lake within the following few years.

Considering the overlapping indigenous areas of perch and catfish [35] to the present stage of knowledge the catfish occurrence does not seem to be fatal for perch in these areas. Nevertheless, catfish have been spread to new localities in south-west Europe and south Kazakhstan which may favour this thermophilic species [12]. Any catfish occurrence in a locality with perch has a potential to shrink the gene pool [36] and reduce fitness of at least some perch individual. Evidence of perch egg strands in catfish diet (thus far regarded as unpalatable) demonstrates their generalist behaviour as a top predator of freshwater ecosystems. It shows the extremely wide dietary niche of catfish likewise the study dealing with beaching behaviour of catfish, an impressive method of catching pigeon on beaches [16]. Our finding from Most and Milada Lakes broadens the knowledge about European catfish, its dietary plasticity and impact on lower trophical levels. In addition, we may assume that the spread of catfish to new localities caused by man and by global warming [12, 14] will favour this species at the expense of many other species.

Supporting Information

S1 Data.
(XLSX)

Acknowledgments

We thank two anonymous reviewers and the editors of PLoS ONE for helpful comments on an earlier version of the manuscript. We thank Ingrid Steenbergen for editing the English, all FishEcU members for their help during gillnet sampling, Josef Beneš for help with catfish sampling and Petr Blabolil for graphics processing.

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Supervision: MČ.

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Writing – review & editing: MČ JP.

References

1. Newsome GE, Tompkins J. Yellow perch egg masses deter predators. Can J Zoolog 1985; 63: 2882–2884.
2. Diamond M, Wakefield PM. The consumption of eggs of the perch, *Perca fluviatilis* L., by macroinvertebrates in the field. Freshwater Biol 1986; 16: 373–376.
3. Newsome GE, Aalto SK. An egg-mass census method for tracking fluctuations in yellow perch (*Perca flavescens*) populations. Can J Fish Aquat Sci 1987; 44: 1221–1232.
4. Zeh M, Ritter E, Ribi G. Spawning and egg development of *Perca fluviatilis* in Lake Zürich. Aquat Sci 1989; 51: 101–107.
5. Aalto SK, Newsome GE. Additional evidence supporting demic behaviour of a yellow perch (*Perca flavescens*) population. Can J Fish Aquat Sci 1990; 47: 1959–1962.
6. Gunthorpe L, Cameron AM. Widespread but variable toxicity in scleractinian corals. Toxicon 1990; 28: 1199–1219. PMID: 1979891
7. Smith C, Douglas A, Jurajda P. Oviposition site selection and embryo mortality in perch. J Fish Biol 2001; 58: 880–882.
8. Nunn AD, Harvey JP, Britton JR, Frear PA, Cowx IG. Fish, climate and the Gulf Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in lowland rivers. Freshwater Biol 2007; 52: 1576–1586.
9. Čech M, Peterka J, Říha M, Jůza T, Kubečka J. Distribution of egg strands of perch (*Perca fluviatilis* L.) with respect to depth and spawning substrate. Hydrobiologia 2009; 630: 105–114.
10. Van Neer W, Ervynck A. Archeologie en vis. Herlevend verleden 1, Instituut voor het Archeologisch Patrimonium, Zellik 1993; 96 pp.
11. Carol J, Zamora L, García-Berthou E. Preliminary telemetry data on the movement patterns and habitat use of European catfish (*Silurus glanis*) in a reservoir of the River Ebro, Spain. Ecol Freshw Fish 2007; 16: 450–456.
12. Copp HG, Britton JR, Cucherousset J, García-Berthou E, Kirk R, Peeler E, et al. Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. Fish Fish 2009; 10: 252–282.
13. Elvira B, Almodóvar A. Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. J Fish Biol 2001; 59: 323–331.
14. Cunico AM, Vitule JRS. First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). BioInvasions Rec 2014; 3: 117–122.
15. Syväranta J, Cucherousset J, Kopp D, Crivelli A, Céréghino R, Santoul F. Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. Aquat Biol 2010; 8: 137–144.
16. Cucherousset J, Boulêtreau S, Azémar F, Compin A, Guillaume M. "Freshwater Killer Whales": beaching behavior of an alien fish to hunt land birds. PLoS ONE 2012; 7: e50840. doi: 10.1371/journal.pone.0050840 PMID: 23227213

17. Alp A, Kara C, Buyukcapar HM. Reproductive biology in a native European catfish, *Silurus glanis* L., 1758, population in Menzelet Reservoir. Turk J Vet Anim Sci 2003; 28: 613–622.
18. Hyslop EJ. Stomach contents analysis—a review of methods and their application. J Fish Biol 1980; 4: 411–429.
19. Seaburg KG. A stomach sampler for live fish. Prog Fish-Cult 1957; 19: 137–139.
20. Čech M, Čech P, Kubečka J, Prchalová M, Draštík V. Size selectivity in summer and winter diets of great cormorant (*Phalacrocorax carbo*): Does it reflect season-dependent difference in foraging efficiency? Waterbirds 2008; 31: 438–447.
21. Čech M, Vejřík L. Winter diet of great cormorant (*Phalacrocorax carbo*) on the River Vltava: estimate of size and species composition and potential for fish stock losses. Folia Zool 2011; 60: 129–142.
22. Čech M, Peterka J, Říha M, Draštík V, Kratochvíl M, Kubečka J. Deep spawning of perch (*Perca fluviatilis*, L.) in the newly created Chabařovice Lake, Czech Republic. Hydrobiologia 2010; 649: 375–378.
23. Čech M, Peterka J, Říha M, Muška M, Hejzlar J, Kubečka J. Location and timing of the deposition of egg strands by perch (*Perca fluviatilis* L.): the roles of lake hydrology, spawning substrate and female size. Knowl Manag Aquat Ec 2011; 403/08: 1–12.
24. Čech M, Vejřík L, Peterka J, Říha M, Muška M, Jůza T, et al. The use of artificial spawning substrates in order to understand the factors influencing the spawning site selection, depth of egg strands deposition and hatching time of perch (*Perca fluviatilis* L.). J Limnol 2012a; 71: 170–179.
25. Čech M, Peterka J, Říha M, Vejřík L, Jůza T, Kratochvíl M, et al. Extremely shallow spawning of perch (*Perca fluviatilis* L.): the roles of sheltered bays, dense semi-terrestrial vegetation and low visibility in deeper water. Knowl Manag Aquat Ec 2012b; 406: 1–12.
26. Dubois JP, Gillet C, Bonnet S, Chevalier-Weber Y. Correlation between the size of mature female perch (*Perca fluviatilis* L.) and the width of their egg strands in Lake Geneva. Ann Zool Fenn 1996; 33: 417–420.
27. R Development Core Team R. A language and environment for statistical computing 2015.
28. Gillet C, Dubois JP. A survey of the spawning of perch (*Perca fluviatilis*), pike (*Esox lucius*), and roach (*Rutilus rutilus*), using artificial spawning substrate in lakes. Hydrobiologia 1995; 300–301: 409–414.
29. Gillet C, Dubois JP. Effect of water temperature and size of females on the timing of spawning of perch *Perca fluviatilis* L. in Lake Geneva from 1984 to 2003. J Fish Biol 2007; 70: 1001–1014.
30. Peterka J. Complex fish stock assessment of Most Lake in year 2014. Report of the Biology Centre, Academy of Sciences of the Czech Republic, Institute of Hydrobiology 2015a; 22 pp (in Czech).
31. Peterka J. Complex fish stock assessment of Milada Lake in year 2014. Report of the Biology Centre, Academy of Sciences of the Czech Republic, Institute of Hydrobiology 2015b; 22 pp (in Czech).
32. Vašek M, Prchalová M, Peterka J, Ketelaars HAM, Wagenvoort AJ, Čech M, et al. The utility of predatory fish in biomanipulation of deep reservoirs. Ecol Eng 2013; 52: 104–111.
33. Adámek Z, Fašiać K, Siddiqui MA. Prey selectivity in wels (*Silurus glanis*) and African catfish (*Clarias gariepinus*). Fisheries 1999; 57: 47–60.
34. Guma'a S.A. The effects of temperature on the development and mortality of eggs of perch, *Perca fluviatilis*. Freshwater Biol.1978; 8: 221–227.
35. Kottelat M, Freyhof J. Handbook of European freshwater fishes. Publications Kottelat, Cornol and Freyhof, Berlin 2007; 646 pp.
36. Krueger CC, May B. Ecological and genetic effects of salmonid introductions in North America. Can J Fish Aquat Sci 1991; 48: 66–77.

Paper VI

Area of catfish occurrence and risks connected with introductions to new localities

Chapter

AREAS OF CATFISH OCCURRENCE AND RISKS CONNECTED WITH INTRODUCTIONS TO NEW LOCALITIES

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ABSTRACT

The family of silurid fishes (Siluridae) contains approximately 100 species with a presence in Eurasia. Although the family Siluridae occurs across much of Europe and Asia, its diversity hotspot is located in Asia. Four species of catfish are closely related to European catfish: i) Acheloos catfish (*Silurus Aristotelis*), ii) Amur catfish (*Silurus asotus*),

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iii) Kunming catfish (*Silurus mento*), and iv) Soldatov's catfish (*Silurus soldatovi*).

European catfish (*Silurus glanis*) originally comes from countries in Central and Eastern Europe, and catchment areas of Asian rivers with estuaries in the Black and Caspian Seas. European catfish is now invasive in Southern and Western Europe. Further, humans have introduced this large catfish species to other countries. Information about the impact of catfish in these new localities is generally lacking. Aquatic ecosystems in these localities are complex and rich in fish species, therefore we may expect a lower negative impact of an invasive species here in comparison with localities such as the Iberian Peninsula in Europe. However, the European catfish is a large species with only a few competitors, and so the impact is likely to be apparent in any locality. Moreover, there is the additional threat of hybridization between the invasive European catfish and closely related native species.

Catfish (Order Siluriformes) are a diverse clade with more than 3,000 species (Eschmeyer et al. 2004). The number of undocumented species is estimated to be 1,750 (Sabaj et al. 2004). For instance, 332 new species were described between the years 2000 and 2006 (Sullivan et al. 2006). The order Siluriformes contains ca. 28 families occurring in both freshwater and marine ecosystems all over the world, except for polar regions (Sullivan et al. 2006).

Siluridae, the family of silurid fishes, consists of ca. 100 species occurring in Eurasia. However, the hotspot for catfish diversity is located in Southeast Asia and diversity decreases in temperate East Asia, the Indian subcontinent, Southwest Asia, and Europe. (Weber and de Beaufort 1913; Roberts 1982; Bornbush 1995). Silurid fishes have not been recorded in Central and North Asia (Figure 1). Distributional patterns among silurid subgroups range from broad sympatry to allopatry. At least nine species are endemic to one or a few close localities, such as *Pterocryptis furnessi* (Fowler), or *Hemisilurus mekongensis* (Bornbusch 1991; Bornbusch and Lundberg 1989).

The family Siluridae contains nine genera: *Belodontichthys, Hemisilurus, Ceratoglanis, Kryptopterus, Ompok, Silurichthys, Pterocryptis, Wallago, Silurus* (Bornbush 1995). The common feature of the Siluridae family is that all species are predators. Other features are very diverse, for instance, length ranges from 3 to 300 cm. The biggest species belong to the genus *Wallago* and *Silurus* (Haig 1950; Watrous and Wheeler 1981; Howes and Fumihito 1991; Boulêtreau and Santoul 2016).

Four species from the genus *Silurus* are closely related to European catfish (*Silurus glanis*): i) Acheloos catfish (*Silurus Aristotelis*) originally occurring in the Acheloos drainage and introduced to Lakes Pamvotis and Volvi, all three areas located in Greece, ii) Amur catfish (*Silurus asotus*) with presence in Japan, the Korean Peninsula, Taiwan, China, and Russia, iii) Kunming catfish (*Silurus mento*) endemic to Dian Chi Lake, Yunnan in China, and iv) Soldatov’s catfish (*Silurus soldatovi*) occurring in the Amur River basin in Asia (Bornbush 1995; FishBase 2018).

The European catfish is a Eurasian species, but it originated in Asia and subsequently spread to the West. Catfish reached the European rivers Danube, Dnieper and Volga via the Caspian, Black and Aral Seas. European catfish is not particularly saline tolerant, but the crossing was possible due to relatively low salinity levels (up to 15‰) in coastal areas. Their native distribution reaches from Germany to Poland and Southern Sweden in the North and Southern Turkey and Northern Iran in the South. It extends to the Baltic States, Russia and the Aral Sea of Kazakhstan and Uzbekistan (Figure 2; Copp et al. 2009).

Its native distribution maintains the same area, however, its non-native area is expanding (Copp et al. 2009; Cucherousset et al. 2017). Aquaculture and angling are the main reasons for the spread of European catfish throughout Europe (Copp et al. 2005) and nowadays angling prevails (Cucherousset et al. 2017). European catfish has currently spread to Belgium, France, The Netherlands, The United Kingdom, Spain, Portugal, Italy, The Baltic Sea, Macedonia and The Peloponnese. The species has established self-sustained populations, especially in major river basins. More details about the presence of European catfish in Europe may be found in Kottelat, M. and Freyhof, J. (2007), Copp et al. (2009) and Cucherousset et al. (2017).

European catfish plays the key role of an apex predator in all European non-native localities. Its size exceeds sizes of native predators and so it presents a marked impact on the native fauna (Cucherousset et al. 2017;

Vejřík et al. 2017). Catfish may dramatically affect localities such as Iberia and other countries in Southern Europe where high endemism of small-bodied fish species is combined with the absence of native piscivorous fish (Copp et al. 2009). Outside Europe, European catfish in non-native localities has spread in Africa, Asia and also to South America (Figure 1). In Africa, introduction historically took place in North Africa, particularly Algeria and Tunisia. In Algeria, it was introduced in 1985 to the Djorf Torba Dam for the purpose of fisheries but the introduction was probably unsuccessful (FAO 2018). In contrast, introduction in Tunisia in 1990 for the purpose of aquaculture and fisheries was successful and reproduction of European catfish is already natural. Introduction first took place in Sidi Salem dam and continued in northern Tunisia. Catfish form 10% of total fish production in local dams (Boughedir 200; Mili et al. 2015; FAO 2018).

In South America, European catfish was first recorded in August 2006 in the State of Santa Catarina, Southern Brazil. In March 2010, the Laboratory of Ecology, Ichthyology and Fisheries (LEPI) of the Federal University of Paraná received a dead individual European catfish from a small pond next to the Piquiri River, in the State of Paraná. These two records are from remote localities. Therefore, a real threat of areal expansion in South America exists. Timing and reasons for of the illegal introduction of catfish to Brazil have not been clear thus far (Cunico and Vitule 2014).

In Asia, particularly in Kazakhstan and China, European catfish appeared due to aquaculture. In Kazakhstan, catfish occurs in three rivers (Ili, Syr Darya and Amurdarja) and Balkhash Lake. Approximately 800 and 150 tons of catfish are caught annually in Balkhash Lake and Ili River, respectively. Introduction probably took place between 1957 and 1958 from some region of former USSR, but the exact locality is unknown (Petr and Mitrofanov 1998; Kustareva and Naseka 2015; Graham et al. 2017). In China, European catfish occurs in the Yilii River-basin in Xinjiang Uygur Autonomous Region, and in north-west China close to Mongolia and

Kazakhstan. The species has a high growth rate, resistance to primitive transport and tolerance to inhospitable places such as concrete ponds (Ren 2012; Adakebaike *at al.* 2015), so we can expect the continuance of expansion in these localities. Another record from China came from Xinghu Lake in Guangdong, close to Guangzhou. The lake is connected to the wide basin of the Pearl River (length: 2,400 km, area 453,700 km^2). Further, catfish probably occurs in Thailand and thus also in the Mekong River basin but these records have not been scientifically proved. Angling is expected to be the reason for the introduction of catfish and other large-bodied fish species from all over the world (check the web- http://www.palmtreelagoon.co.uk/wels_catfish_gallery.html).

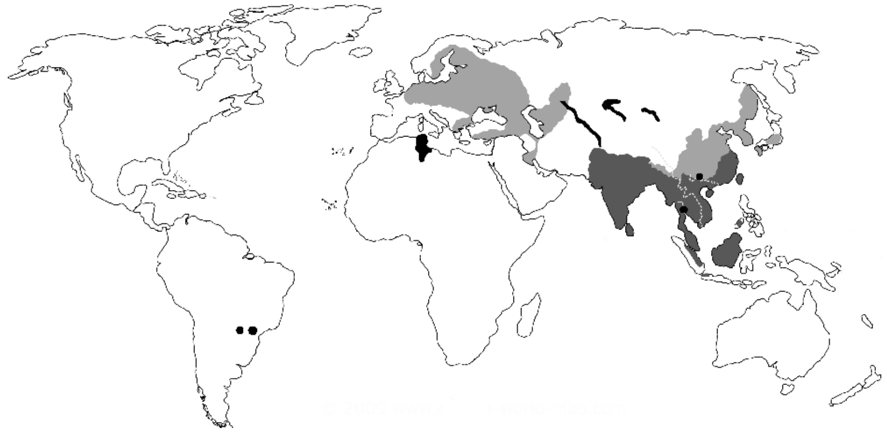

Figure 1. Area of occurrence of the family Siluridae. Light grey color shows the native area of the clade including genus *Silurus* with a minimum of 5 species. Dark grey shows the native area of the clade that contains the remaining genera: *Hito*, *Belodontichthys*, *Hemisilurus*, *Ceratoglanis*, *Ktyptopferus* and *Ompok* (Bornbush 1995). Black shows the non-native occurrence of European catfish (*Silurus glanis*), except Europe. In Africa, it occurs in Tunisia mainly in dam reservoirs (Boughedir 2006). In South America, there are two localities in Brazil (Cunico and Vitule 2014). In Central Asia, it occurs in a wide area in Kazakhstan and China (Petr and Mitrofanov 1998; Kustareva and Naseka 2015; Graham et al. 2017). In South-East Asia, there were two confirmed areas of occurrence in Thailand and China (black dots; Chen et al. 2010). Dashed lines show large rivers in South-East Asia, Mekong River and Pearl River, where we can soon expect confirmation of the occurrence of European catfish.

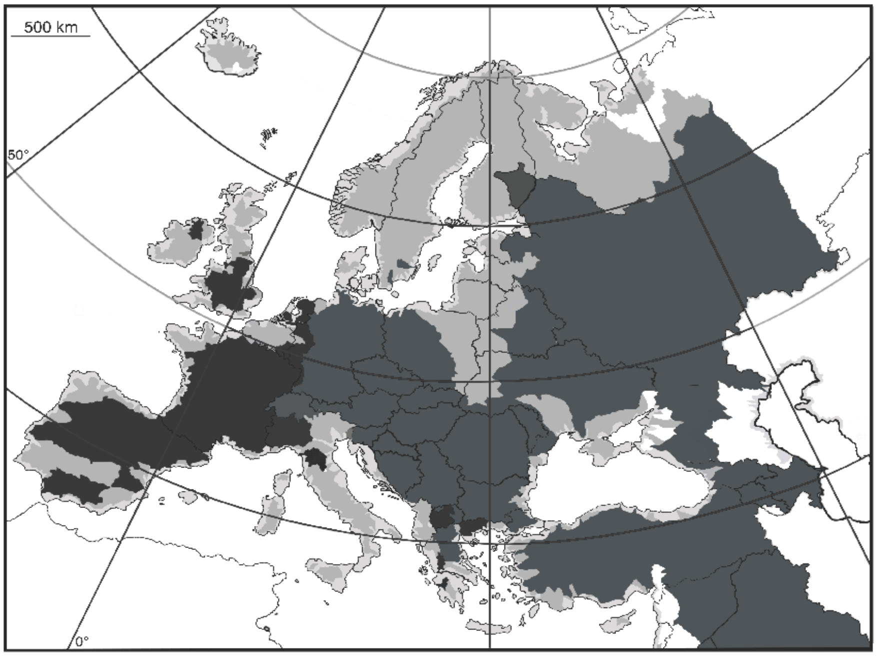

Figure 2. Native (dark grey) and introduced (black) area of occurrence of European catfish (*Silurus glanis*) in Eurasian watersheds with an area >1,000 km^2 according to Cucherousset et al. (2017). Light grey shows watersheds with no official evidence of introduction.

Expansion of catfish to new localities poses several ecological threats, such as predation of native fish species, alteration of the food web, importation of diseases and theoretical hybridization with native species (Copp et al. 2009). Paschos et al. (2004) indicated that European catfish is able to hybridize with its congener Acheloos catfish (*Silurus aristotelis*), originally from Greece. Laboratory studies proved that there is no significant variation in the survival, growth and morphology of European catfish and its hybrid with Acheloos catfish. Whereas pure Acheloos catfish exhibit low survival and variable morphology (Paschos et al. 2004), the hybrid had equally good survival and virtually identical morphology to European catfish. It is not known whether the two species hybridize naturally, but it is likely given that both species have the same type of reproductive strategy, i.e., nest-guarding (Maehata 2007). Behavior and other aspects of the hybrid under natural conditions are also unknown (Coop et al. 2009). Hybridization of European catfish with native species in Asia is also very probable, particularly with the closely related Amur catfish (*Silurus asotus*), Kunming catfish (*Silurus mento*) and Soldatov's catfish (*Silurus soldatovi*). Moreover, these three species have also been transported to diverse non-native habitats within China, which increases the chance of an encounter (Ma et al. 2003).

Considerable attention has been devoted to the spread of European catfish across Europe in the last decades (Copp et al. 2009; Cucherousset et al. 2017). However, information dealing with the occurrence and impact of catfish in Southeast and East Asia is missing. A similar problem with practically no information about the actual area of occurrence is related to South America (Cunico and Vitule 2014). The extremely rich biodiversity of these regions may theoretically present a barrier to the ecological invasion of European catfish (Kennedy et al. 2002). The most affected area facing the spread and invasion of European catfish are not in Europe, but areas in Asia and South America that represent mega-diverse regions of the world.

REFERENCES

Adakebaike, K., Zhang, R., Yushanjiang, Y. and Guo, Y. (2015). Experimental study of capturing and short distance transportation with in situ temporary rising of *Silurus glanis* Linnaeus in Yili River. Xinjiang. *Agriculture Science* 52: 961–968.

Boulêtreau, S. and Santoul, F. (2016). The end of the mythical giant catfish. *Ecosphere* 7: e01606.

Bornbusch, A. H. (1991). Redescription and reclassification of the silurid catfish *Apodoglanis furnessi* Fowler (Siluriformes: Siluridae), with diagnoses of three intrafamilial silurid subgroups. *Copeia* 7997: 1070–1084.

Bornbusch, A. H. and Lundberg, J. G. (1989). A new species of Hemisilum (Siluriformes, Siluridae) from the Mekong River, with comments on its relationships and historical biogeography. *Copeia* 7989: 434–444.

Bornbusch, A. H. (1995). Phylogenetic relationships within the Eurasian catfish family Siluridae (Pisces: Siluriformes), with comments on generic validities and biogeography. *Zoological Journal of the Linnean Society* 115: 1–46.

Boughedir, W. (2006). Etude de l'ecobiologie du Silure (*Silurus glanis*, L. 1978) dans la retenue du barrage de Sidi Dalem. Tunis, *Institut National Agronomique de Tunisie*: 81 p.

Copp, H. G., Britton, R., Cucherousset J., García-Berthou, E., Kirk, R., Beeler, E. and Skaténas, S. (2009). Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries* 10: 252–282.

Clarke, S. (2005). CCG Guide to UK Catfish Waters. Charterlith, Hampshire, England, 160 pp.

Cucherousset, J., Horký, P., Slavík, O., Ovidio, M., Arlinghaus, R., Boulêtreau, S., Britton, R., García-Berthou, E. and Santoul, F. (2017). Ecology, behaviour and management of the European Catfish. *Reviews in Fish Biology and Fisheries*, https://doi.org/10.1007/s11160-017-9507-9.

Cunico, A. and Vitule, J. R. S. (2014). First records of the European catfish, *Silurus glanis* Linnaeus, 1758 in the Americas (Brazil). *Bioinvasions Records* 3:117–122.

Chen, S., andWei, Y. (1995). The initial study of Siluriforms fish species in China. *Chinese Journal of Zoology* 30: 10–16.

Chen, X. N., Guo, Y. J. and Wu, G. H. (2010). Fish fauna and characteristic of Xinghu Lake in Guangdong. *Journal of Hydroecology* 3: 29–33.

Eschmeyer, W. N., Ferraris, C. J., Jr., Hoang, M. D. and Long, D. J. (2004). The Catalog of Fishes, ON-LINE, Species of Fishes.

FAO (2014). FAO Database of Introduced Aquatic Species (DIAS). Available at: http://www.fao.org/fishery/introsp/search/en (accessed 1st December 2017).

FishBase (2018). Available at: http://www.fishbase.org/search.php (accessed 19th April 2018).

Graham, N. A., Pueppke, G. S. and Uderbayev, T. (2017). The Current Status and Future of Central Asia's Fish and Fisheries: Confronting a Wicked Problem. *Water* 9: 701; doi:10.3390/w9090701.

Haig, J. (1950). Studies on the classification of the catfishes of the Oriental and Palaearctic family Siluridae. *Records of the Indian Museum* 48: 59–116.

Howes, G. J. and Furnihito, A. (1991). Cranial anatomy and phylogeny of the South-East Asian catfish genus *Belodontichthys. Bulletin of the British Museum (Natural History), Zoology* 57: 133–160.

Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M. H., Tilman D. and Reich P. (2002). Biodiversity as a barrier to ecological invasion. *Nature* 417: 636–638.

Kottelat, M. and Freyhof, J. (2007). Handbook of European Freshwater Fishes. Kottelat, Cornol and Freyhof, Berlin.

Kustareva, L. A. and Naseka, A. M. (2015). Fish diversity in Kyrgyzstan: Species composition, fisheries and management problems. *Aquatic Ecosystem Health and Management* 18: 149–159.

Ma, X., Bangxi, X., Yindong, W. and Mingxue, W. (2003). Intentionally introduced and transferred fishes in China's inland waters. *Asian Fisheries Science* 16: 279–290.

Maehata, M. (2007). Reproductive ecology of the Far Eastern catfish, *Silurus asotus* (Siluridae), with a comparison to its two congeners in Lake Biwa. *Environmental Biology of Fishes* 78: 136–146.

Mili, S., Ennouri, R., Laouar, H. and Missaoui, H. (2015). Fisheries in the Tunisian dams: diagnosis of the current situation and development opportunities. *First Regional Symposium on Sustainable Small-Scale Fisheries in the Mediterranean and Black Sea*, 95–106.

Paschos, I., Nathanailides, C., Perdikaris, C. and Tsoumani, M. (2004). Comparison of morphology, growth and survival between *Silurus* *glanis*, *S. aristotelis* and their hybrid during larval and juvenile stages. *Aquaculture Research* 35: 97–99.

Petr, T. and Mitrofanov, V. P. (1998). The impact on fish stocks of river regulation in Central Asia and Kazakhstan. Lakes and Reservoirs: *Research and Management* 3: 143–164.

Ren, B. (2012). Biological study of Silurus glanis Linnaeus in Yili River. *Chinese Journal of Fishery* 25: 51–55.

Roberts, T. R. (1982). Systematics and geographical distribution of the Asian silurid catfish genus Wallago, with a key to the species. *Copeia* 7982: 890–894.

Sabaj, M. H., Page, L. M., Lundberg, J. G., Ferraris, C. J., Jr., Armbruster, J. W., Friel, J. P. and Morris, P. J. (2004). All Catfish Species Inventory Website. Internet address: <http://clade.acnatsci.org/allcat Wsh>.

Sullivan, J. P., Lundberg, J. G. and Hardman, M. (2006). A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using rag1 and rag2 nuclear gene sequences. *Molecular Phylogenetics and Evolution* 41: 636–662.

Vejřík, L., Vejříková, I., Blabolil, P., Eloranta, A. P., Kočvara, L., Peterka, J., Sajdlová, Z., Chung S. H. T., Šmejkal, M., Kiljunen, M. and Čech, M. (2017). European catfish *(Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability. *Scientific Reports* 7: 15970.

Weber, M. and De Beaufort, L. F. (1913). The Fishes of the Indo-Australian Archipelago. V. 2. Leiden: Brill.

Watrous, L. E. and Wheeler, Q. D. (1981). The out-group comparison method of character analysis. *Systematic Zoology* 30: 1–11.

Paper VII

Methods for capturing catfish and potential regulation of catfish population

Chapter

METHODS FOR CAPTURING CATFISH AND THE POTENTIAL REGULATION OF THE CATFISH POPULATION

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ABSTRACT

European catfish is a fish species that is difficult to capture by standard ichthyologic methods (gillnets, trawls, purse and beach seines, etc.). The poor capture success by nets is due to the large cylindrical body shape, slimy scale-less skin, distinct ability of reverse swimming and unconventional ecology and behavior. Electrofishing is commonly used method but it is not so efficient due to low reach and avoidance reaction

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of a fish. Speer fishing is an efficient and occasionally used method, however, high water visibility is needed and the individual is killed, which is not always desirable. Angling with a supporting buoy and fish bait seems to be the most efficient method. Moreover, angling is a very efficient technique when, besides the bait, also mechanical catfish lure is used. However, it is a time consuming method as far as more catfish individuals are needed. Therefore, a method of long-lines is an ideal fishing technique with high efficiency, low financial and time requirements and low number of people needed for installation and handling. The method simulates angling with a supporting buoy that is commonly used by sport fishermen. The fish are caught alive and only low mortality is connected with the method of long-lines in comparison to other methods.

The European catfish is a powerful fish species that reaches large body sizes. These features complicate capturing of the fish and so obtaining data necessary for scientific studies. Except for moments when chasing prey, catfish spend most of their time in hardly accessible habitats such as places with submerged trees, tree roots, macrophytes or in old flooded ruins. All these obstacles disable capturing catfish by standard ichthyologic methods. This is probably the reason why catfish have not often been studied in the past (Carol 2007). The first information about catfish came from fishermen's catches that were only random and sporadic (Lusk et al. 1992). However, this is not a good method for obtaining a sufficient number of catches for scientific purposes.

Multimesh gillnets are frequently used passive fishing gear. The most commonly used benthic and pelagic multimesh gillnets encompassing twelve mesh sizes according to the EU norm (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm; CEN 2015) are fully insufficient because the largest mesh size of 55 mm is still too small in comparison with mean catfish diameter (Šmejkal et al. 2015). However, large-mesh gillnets that consist of mesh sizes 70, 90, 110 and 135 mm (knottoknot,10m panels) seem to be insufficient too (Šmejkal et al. 2015). The poor capture success by nets is due to the catfish's large cylindrical body shape, slimy scale-less skin, distinct ability of reverse swimming and unconventional ecology and behavior (Slavík 2013; Vejřík et al. submitted). In addition, most fish captured by gillnets die and this is not desirable. Despite the low level of efficiency and high level of mortality, the gillnet method is still used for capturing catfish. For instance, Doğan Bora and Gül (2004) captured 162 individual catfish within one year (Hirfanli Dam Lake, Turkey). In contrast, Carol (2007) with high effort caught only one catfish using gillnets (Spain, Catalonia, various reservoirs).

In terms of active fishing gear, large seine nets and purse seine nets seem to be applicable. A large seine net (length 800 m, 16 mm mesh size in the cod end, sampling area 5 ha per haul) was used 15–20 times per year during three-year-long monitoring of Feldberger Haussee Lake in Germany (Wysujack and Mehner 2005). A purse seine net was used by Carol (2007) in Catalan reservoirs. In these water bodies, 97 individual catfish were captured by the purse seine in October and November 2005. The great advantage is the minimum of sacrificed fish in comparison to gillnets. However, it is a non-selective method which is an apparent disadvantage in so far as the sampling is focused only on predatory fish that make up a small part of the catch (i.e., the by-catch is usually enormous). In addition, it is demanding in terms of man-power and time.

Electrofishing appears to be a more efficient method for capturing catfish (Carol 2007). Daněk et al. (2014) and Guilleault et al. (2015) also considered electrofishing to be the most efficient. Slavík and Horký (2012) used this method to capture catfish in rivers in the Czech Republic. Thus, electrofishing is generally rated as the most used method. It is sufficient in the shallow littoral zone with obstacles, and when not many individuals are needed. However, it has several disadvantages. It is not efficient in large and deep (>1.5 m) water bodies such as canyon-shaped reservoirs, deep lakes or gravel pits due to the short reach of the electric current (Zalewski and Cowx 1989). In addition, large fish individuals are exposed to the risk of injury (fatal, many times; Goffaux et al. 2005).

Recently, cooperation with local recreational or commercial fishermen has been reinitialized (Alp et al. 2003; Syväranta et al. 2010). The most common method used by fishermen is angling with a supporting buoy. The necessary equipment is a fishing rod, troll and a hook where the fish bait is fixed (Boulêtreau et al. 2016). Angling is a very efficient technique when, besides the bait, a mechanical catfish lure is also used. This angling method is known as ‘clonking’ (Copp et al. 2007). The lure is usually a piece of wood producing repetitive smacking sound when pulled out of the water, which enormously increases fish curiosity and aggression. Movements of catfish are then registered by echo sounder. However, the method has some disadvantages. It is time consuming especially when many catfish individuals are needed. Further, the sound made by the lure is not attractive to catfish in shallow water, and the more often the lure is used the less efficient it is (habituation effect; Vágner 2010). Moreover, after an apparent boom in the last decades, ‘clonking’ is starting to be prohibited again at many localities (Czech Fishing Union, unpubl. data).

Another applicable method is spear fishing carried out by divers. It is an efficient and occasionally used method, however, high water visibility is needed and the individual is killed, which is not always desirable. When only fish tissue is needed, a spear gun equipped with a stainless steel biopsy tip can be used. This method is very friendly to fish and is useful for collecting samples for analyses such as stable isotope analysis (Cucherousset et al. 2012). However, classic somatic measurements, like fish length and weight, are lacking.

The most efficient method for capturing catfish is the long-line method that is illustrated in Figure 1. The main line is 60 m long with three main buoys situated at the ends and in the middle of the line. Anchoring ropes, 3.5–7 m long, with weights (32 kg each) are tied to the buoys and fix the main line in the right place. Every five meters between the main buoys, auxiliary buoys are placed with a hanging 2.5 m long snood made of two parts i) 2-m long fishing-line with maximum load of 50 kg and ii) more durable 0.5 m long fishing-line with maximum load of 100 kg. A swivel is placed between these two parts to prevent twisting and a 150 g sinker is hung on the snood to keep it at the appropriate depth. At the end of the snood, there is a multi hooks system with one single hook and one treble with bait (total length of the bait: L_T = 180–300 mm). When catfish try to tear down the bait, it is hooked by the fishing treble hanging under the baited hook (Vejřík et al. 2017a; Vejřík et al. 2017b; Vejřík et al. submitted). The parameters for long-lines such as length of the main line, length of snood, number of snoods or size of bait can be individually adjusted where necessary. The efficiency is very high. With the given parameters used in two dam reservoirs in the Czech Republic, the efficiency was between 0.4 to 5.5 individuals per day per 10 baited hooks depending on the season and locality (Vejřík et al. submitted).

The method of using long-lines is an ideal fishing technique with high efficiency, low financial and time requirements and low number of people needed for installation and handling. The method simulates angling with a supporting buoy that is commonly used by sport fishermen. The fish individuals are caught alive and only low mortality (<5%) is connected with this method in comparison to other methods. Reduction of a catfish population to harmless levels may be efficiently achieved by using long-lines in localities where catfish is an unwanted or invasive species. (Vejřík et al. submitted). The high selectivity of the method is a great advantage because mainly adult catfish and sometimes large pikes (*Esox lucius*; L_T> 70 cm) are caught. The only disadvantage is that only piscivorous catfish are likely to be caught. Individuals that specialize on alternative food sources, for instance semiaquatic prey such as waterfowl, can theoretically be underestimated. However, Vejřík et al. (2017a) caught individuals that frequently had waterfowls or mammals (particularly water voles) in their stomachs. Also individuals that utilized an atypical diet such as perch (*Perca fluviatilis*) egg strands were caught (Vejřík et al. 2017b). These results imply that catfish populations are not made up of strictly specialized individuals but they have short-term specialization on easily available food sources (Vejřík et al. 2017a). When such an individual encounters easily available fish bait, it is expected to readily attack the fish hooked on long-lines. All the described features of long-lines pose this method as the ideal method for capturing catfish to obtain a sufficient number of catches for scientific purposes or for the regulation of a catfish population.

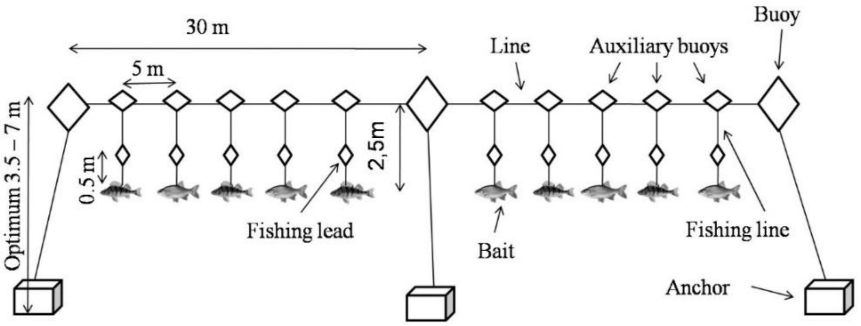

Figure 1. Scheme of longlines, the fishing method used for catfish sampling according to Vejřík et al. (2017a; 2017b).

REFERENCE

Alp, A., Kara, C. and Buyukcapar, H. M. (2003). Reproductive Biology in a Native European Catfish, *Silurus glanis* L., 1758, Population in Menzelet Reservoir. *Turkish Journal of Veterinary and Animal Science* 28: 613–622.

Boulêtreau, S., Verdeyroux, P., Lorthiois, E., Azémar, F., Compin, A. and Santoul, F. (2016). Do You Eat or Not? Predation Behaviour of European Catfish (*Silurus glanis*) Toward Live Bait on a Hook. *The Open Fish Science Journal* 9: 8–14.

Carol, J. (2007). *Ecology of invasive (Silurus glanis) in Catalan reservoirs.* Ph.D. Thesis. Universitat de Girona, Spain.

CEN (2015). Water Quality _ Sampling of fish with multimesh gillnets. European Committee for Standardization, EN 14757, Brussels, Belgium.

Copp, G.H., Moffatt, L. and Wesley, K. J. (2007). Is European catfish *Silurus glanis* really becoming more abundant in the River Thames? *Aquatic Invasions* 2: 113–116.

Cucherousset, J., Boulêtreau, S., Azémar, F., Compin, A. and Guillaume, M. (2012). “Freshwater Killer Whales”: beaching behavior of an alien fish to hunt land birds. *Plos One* 7: e50840.

Daněk, T., L. Kalous, M. Petrtýl and P. Horký. (2014). Move or die: change in European catfish (*Silurus glanis L.*) behaviour caused by oxygen deficiency. *Knowledge and Managament of Aquatic Ecosystem* 414: 1–11.

Doğan Bora, N. and Gül., A. (2004). Feeding Biology of *Silurus glanis* (L., 1758) Living in Hirfanli Dam Lake. *Turkish Journal of Veteriary and Animal Science* 28: 471–479.

Goffaux, D., Grenouillet, G. and Kestemont, P. (2005). Electrofishing versus gillnet sampling for the assessment of fish assemblages in large rivers. *Archiv für Hydrobiologie* 162: 73–90.

Guilleault, N., Delmotte, E., Boulêtreau, S., Lauzeral, C., Poulet, N. and Santoul, F. (2015). Does the non-native European catfish *Silurus glanis* threaten French river fish populations? *Freshwater Biology* 60: 922–928.

Lusk, S., Baruš, V. and Vostradovský, J. (1992). *Ryby v našich vodách* [Fishes in natural waters]. Academia, Praha, CZ, 248 pp.

Slavík, O. and Horký, P. (2012). Diel dualism in the energy consumption of the European catfish *Silurus glanis*. *Journal of Fish Biology* 81: 2223–2234.

Slavík, O. (2013). Behaviour of European catfish in natural conditions and aquaculture (Habilitation Thesis), Czech University of Life Sciences, Prague, CZ.

Šmejkal, M., Ricard, D., Prchalová, M., Říha, M., Muška, M., Blabolil, P., Čech, M., Vašek, M., Jůza, T., Herreras, A.M., Encina, L., Peterka, J. and Kubečka, J. (2015). Biomass and abundance biases in European standard gillnet sampling. *Plos One* 10: e0122437.

Syväranta, J., Cucherousset, J., Kopp, D., Crivelli, A., Cereghin, R. and Santoul, F. (2010). Dietary breadth and trofic position of introduced European catfish *Silurus glanis* on the river Tarn (Garonne River basin), southwest France. *Aquatic Biology* 8: 137–144.

Vágner, J. (2010). Můj přítel sumec [My friend, catfish], 1st ed., Fraus, Prague, CZ, 362 pp.

Vejřík, L., Vejříková, I., Blabolil, B., Eloranta, A.P., Kočvara, L., Peterka. J., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Kiljunen, M. and Čech,

M. (2017a). European catfish *(Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability. *Scientific Reports* 7:15970.

Vejřík, L., Vejříková, I., Kočvara, L., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Peterka, J. and Čech, M. (2017b). Thirty- Year-Old Paradigm about Unpalatable Perch Egg Strands Disclaimed by the Freshwater Top- Predator, the European Catfish (*Silurus glanis*). *PLoS ONE* 12: e0169000.

Vejřík, L., Vejříková, I, Kočvara, L, Blabolil, P., Peterka, J., Sajdlová, Z., Jůza, T., Šmejkal, M., Bartoň. D., Kubečka, J. and Čech, M. (submitted). *The pros and cons of the freshwater apex predator,* European catfish *Silurus glanis,* and angling as a powerful mechanism for its reduction.

Wysujack, K. and Mehner, T. (2005). Can feeding of European catfish prevent cyprinids from reaching a size refuge? *Ecology of Freshwater Fish* 14: 87–95.

Zalewski, M. and Cowx, I.G. (1989). Factors affecting the efficiency of electrofishing. In: I.G. Cowx and P. Lamarque (eds) Fishing with Electricity – *Application in Freshwater Fisheries Management.* Blackwell, Oxford, UK, 89–110.

Paper VIII

Catfish as a potential key species for biomanipulation purposes

Chapter

CATFISH AS A POTENTIAL KEY SPECIES FOR BIOMANIPULATION PURPOSES

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ABSTRACT

The European catfish is able to produce abundant populations thanks to its longevity, social tolerance and low level of cannibalism. Thus its significant impact on aquatic ecosystems is unquestionable. Catfish, similar to other apex predators, influence all trophic levels of the food web. However, the impact is not equally distributed. Species with

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nocturnal activity are more affected by predation of catfish than those with diurnal activity. Further, predators at lower trophic levels (mesopredators) are more sensitive to predation of catfish than omnivorous species. The catfish population can dispose of up to 26% of the total fish biomass. Therefore, it plays an important role in the biomanipulation of many freshwater systems. Even with natural annual recruitment, a decrease in total fish biomass is distinctive over time. Catfish can easily adapt to new food sources and some individuals reveal a short-term specialization on currently available, commonly seasonal, food sources, e.g., semiaquatic prey like amphibians, waterfowl, or mammals. Similarly, terrestrial prey such as pigeons, and marine prey have been described in the catfish diet. These adaptations enable catfish to maintain the population at high abundances.

Predatory fish play a key role in aquatic ecosystems. They control the abundance of fish at lower trophic levels from the top down, indirectly affecting water quality in the ecosystem. This is known as the top-down effect, reduction of zooplanktivorous fish induces an increase in zooplankton, which in turn reduces phytoplankton that mostly cause turbidity (Hrbáček et al. 1961; Brooks and Dodson 1965). Thus, predatory fish seem to be ideal mediators for biomanipulation. A high abundance of predatory fish should increase water transparency in an ecosystem (Hrbáček et al. 1961). Nevertheless, until now it has not been clear which fish species would be ideal for biomanipulation purposes. Typical features of fish that may cause natural limitations are: body size, gape limitation, low efficiency of capturing fish, high level of cannibalism or diet specializations (Wysuljack et al. 2001; Wysujack and Mehner 2005). Therefore, the most efficient biomanipulation would be ensured by a key species and by one or more companion species that coexist together. This multiple predator effect provides high stability and well-balanced biodiversity in an ecosystem (Wasserman et al. 2016; Vejřík et al. 2017a).

Catfish in comparison with other European fish species have many special features. First of all, their longevity, catfish commonly live for 20 years (Orlova 1989; Rossi et al. 1991; Sedlár 1987; Tandon and Oliva1977). The maximum recorded age was 26 years for a catfish observed in the Danube Delta (Bruyenko 1971), but maximum age is expected to be even higher. The second favorable feature is a fast growth rate, really large sizes can be reached. The growth rate depends mainly on the sufficiency of food and water temperature (Copp et al. 2009). However, mean sizes are 20 and 35 cm in the first and second year, respectively. Sexual maturity is reached at around the third or fourth year when size reaches 40–70 cm. After reaching sexual maturity, the growth rate slows down and a size of 100 cm is attained at around 7 to 9 years. Further, sizes of 150 cm are attained at around 11–15 years and 200 cm at the age of 19 and more (Tandon and Oliva1977; Rossi et al. 1991; Copp et al. 2009). Recently, individuals exceeding a size of 270 cm and mass of 130 kg were recorded (Boulêtreau and Santoul 2016). Thanks to extreme body sizes, catfish have very large mouths and so gape size is overwhelming in comparison to other European predatory fish (Wysujack and Mehner 2005; Cucherousset et al. 2017). In addition, large sizes ensure protection against consumption by other predators. Therefore, these features enable catfish to utilize large prey and so to affect food webs to a large extent (Cucherousset et al. 2017). Other special features are related to behavior. First of all, catfish can live in abundant populations (Vejřík et al. 2017a). Catfish seem to have complex social behavior that includes massive aggregations (Boulêtreau et al. 2011), nest-guarding (Maehata 2007) and low levels of cannibalism (Vejřík et al. 2017a). Further, catfish take advantage of successful ecological strategies such as large egg sizes and high fecundity (Cucherousset et al. 2017). Additionally, the catfish is a species with low requirements for water quality (David 2006). All these features, related either to body structure or to behavior, pose catfish as an ideal fish species for biomanipulation purposes.

Wysujack and Mehner (2005) claimed that catfish is not an efficient biomanipulation species, particularly due to its preferences for relatively small prey. However, their study was based on the diet of catfish of small sizes (mostly smaller than 80 cm). This is probably the reason why Vejřík et al. (2017a) presented opposite results evidencing that catfish has a clear impact on the entire fish community, including frequent consumption of large prey. The sizes of prey reached up to 50% of catfish sizes. The diet spectrum of catfish is wide, thus catfish affect the entire fish community.

However, predation pressure is distributed among many species and thus the pressure on a particular species is moderate (Syväranta et al. 2010). Therefore, catfish are able to regulate practically the entire fish community thanks to their size (Boulêtreau and Santoul 2016) and their extreme width of diet niche (Syväranta et al. 2010; Vejřík et al. 2017a).

A high biomanipulation effect may be achieved with an abundant population of catfish (Vejřík et al., 2017a) and may be noticeably increased by the multiple predation effect, when other predators, such as pike (*Esox lucius*) and perch (*Perca fluviatilis*), are present (Wasserman et al. 2016; Vejřík et al. 2017a). However, a certain amount of predation pressure of catfish against these smaller predatory fish must be taken into consideration (Carol 2007; Vejřík et al. 2017a).

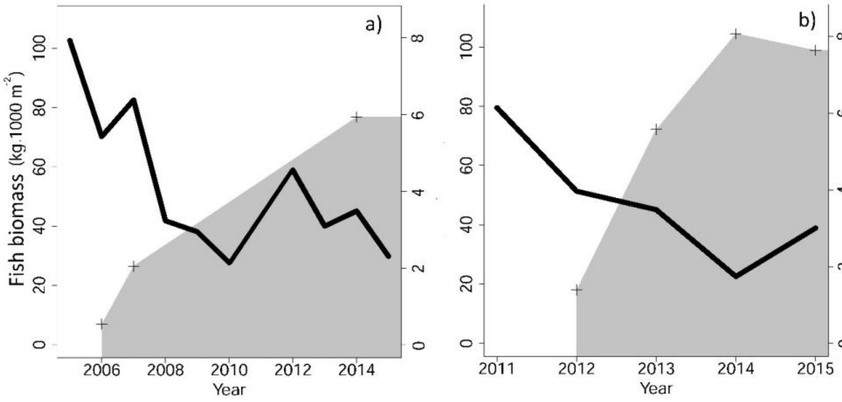

Figure 1. Biomass in gillnet catches (fish older than 0 +; kg per 1,000 m^2 of gillnets) in (a) Milada and (b) Most Lakes according to Vejřík et al. (2017a). Beginning of grey area shows the first relevant presence of catfish in the lakes (2006 and 2012 for Milada and Most, respectively) and subsequently represents the estimated biomass of the catfish population (kg ha^{-1}). Catfish were stocked in the autumn of previous years (2005and 2011 for Milada and Most, respectively), in both cases well after individual gillnet sampling campaigns. This is the reason why illustrations of catfish presence begin one year later when the potential impact of catfish on populations of fish is reflected for the first time in gillnet catches. Catfish biomasses for the years 2006–2007 in Milada and 2012–2014 in Most are based on the cumulative amount of stocked fish. Biomasses for the years 2014–2015 and 2015 in Milada and Most, respectively, are calculated from recaptures.

Guillerault et al. (2015) stated that introduction of catfish to France affected only low numbers of freshwater fish communities. Specifically, they observed a decrease in fish species richness, evenness and diversity by 1.4, 1.4 and 5.8% after the establishment of European catfish in 112 French studied sites, respectively. The reason is probably the highly generalist feeding strategy of catfish and the fact that its predation pressure was distributed among all species present. Vejřík et al. (2017a) also observed many different prey species in the catfish diet but there was a significant preference for species with nocturnal activity such as rudd (*Scardinius erythrophthalmus*) or tench (*Tinca tinca*). Nevertheless, the predation pressure of catfish still reduces the fish community with lower variations in species diversity than predation pressure of other predatory fish. Thanks to its generalist feeding strategy, catfish is an ideal species to use for biomanipulation purposes in overstocked fish communities, where the effect of biomanipulation is most apparent, such as in the oligotrophic Most Lake, Czech Republic. After stocking an abundant population of catfish (7.65 kg ha^{-1}; Vejřík et al. 2017b), abundances of other fish species decreased significantly (Vejřík et al. 2017a). Monitoring of these stocked catfish revealed very slow growth rates indicating that the stocked population is more abundant than a theoretically naturally occurring population in the lake (exceeding carrying capacity). Nevertheless, mortality of catfish is very low because starving catfish start to utilize alternative food sources, particularly semiaquatic prey such as migrating waterfowl (remarkable bypass of inner lake carrying capacity; Vejřík et al. submitted.). A similar behavior, the utilization of birds by catfish, was observed in France (Cucherousset et al. 2012) and in Spain (Carol 2007). These adaptations are apparently impossible for other piscivorous fish such as pike or pikeperch (*Sander lucioperca*; Wysuljack et al. 2001; Argillier et al. 2012).

The optimal biomass of catfish stocked for biomanipulation purposes is dependent mainly on the specific conditions of each locality. The level of isolation of the locality is important because good manipulation cannot be achieved in localities with massive immigration and emigration of fish. Probably the most important factor is the trophic structure of the locality.

The effects of biomanipulation on localities in the Czech Republic are apparent with the following sizes of catfish population: 6 kg of adult catfish per hectare had a marked impact on mesotrophic Milada Lake, 8 kg per hectare seemed to be sufficient in the eutrophic Žlutice Reservoir, and 7.65 kg of catfish per hectare in oligotrophic Most Lake had too strong a biomanipulation effect when 8–26% of fish biomass was supposed to have been eaten annually by catfish. In the long-term, total fish biomass decreased on average by 50% after the stocking of catfish (Fig. 1), however, other predatory fish species also contribute to the biomanipulation effect (Vejřík et al. 2017a, Vejřík et al. 2017b; Vejřík et al. submitted).

REFERENCES

Boulêtreau, S., Cucherousset, J., Villéger, S., Masson, R. and Santoul, F. (2011). Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. *Plos One* 6: e25732.

Boulêtreau, S. and Santoul, F. (2016). The end of the mythical giant catfish. *Ecosphere* **7**: e01606.

Brooks, J. L. and Dodson, S. I. (1965). Predation, body size, and composition of plankton. *Science* **150**: 28–35.

Bruyenko, V.P. (1971). Age and seasonal variation in the feeding of *Silurus glanis* in the lower reaches of the Danube. *Zoologicheskij zhurnal* **50**: 1214–1219 [In Russian].

Carol, J. (2007). *Ecology of an Invasive Fish (Silurus glanis) in Catalan Reservoirs*. PhD Thesis, Universitat de Girona, Girona, 120 pp.

Copp, G.H., Britton, J.R., Cucherousset, J., García-Berthou, E., Kirk, R., Peeler and E., Stakenas S. (2009). Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries* **10**: 252–282.

Argillier, C., Barral, M. and Irz, P. (2012). Growth and diet of the pikeperch *Sander lucioperca* (L.) in two French reservoirs *Archives of Polish. Fisheries* **11**: 99–114.

Cucherousset, J., Boulêtreau, S., Azémar, F., Compin, A. and Guillaume, M. (2012). "Freshwater Killer Whales": beaching behaviour of an alien fish to hunt land birds. *Plos One* **7**: e50840.

Cucherousset, J., Horký, P., Slavík, O., Ovidio, M., Arlinghaus, R., Bouletreau, S. Britton, R., Berthou, E.G. and Santoul, F. (2017). Ecology, behaviour and management of the European Catfish. *Reviews in Fish Biology and Fisheries*, https://doi.org/10.1007/s11160-017-9507-9.

David, J.A. (2006). Water quality and accelerated winter growth of European catfish using an enclosed recirculating system. *Water and Environmental Journal* **20**: 233–239.

Guillerault, N., Delmotte, S., Boulêtreau, S., Lauzeral, C., Poulet, N. and Santoul, F. (2015). Does the non-native European catfish *Silurus glanis* threaten French river fish populations? *Freshwater Biology* **60**: 922–928.

Hrbáček, J., Dvořáková, M., Kořínek, V. and Procházková, L. (1961). Demonstration of the effect of the fish stock on the species compo composition of zooplankton and the intensity of metabolism of the whole plankton assemblage. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **14**: 192–195.

Maehata, M. (2007). Reproductive ecology of the Far Eastern catfish, *Silurus asotus* (Siluridae), with a comparison to its two congeners in Lake Biwa. *Environmental Biology of Fishes* **78**: 136–146.

Orlova, E.L. (1989). Peculiarities of growth and maturation of the catfish, *Silurus glanis,* in the Volga Delta under regulated flow conditions. *Journal of Ichthyology* **28**: 35–45.

Rossi, R., Trisolini, R., Rizzo, M.G., Dezfuli, B.S., Franzoi, P. and Grandi, G. (1991) Biologia ed ecologia di una specie alloctona, il siluro (*Silurus glanis* L.)(Osteichthyes, Siluridae), nella parte terminale del fiume Po. [Biology and ecology of an allochthonous species, catfish

(*Silurus glanis* L.) (Osteichthyes, Siluridae), in the terminal part of the river Po.] *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **132**: 69–87 (only in Italian).

Sedlár, J. (1987). Age and growth of the European catfish from the Hungarian section of the Tisza River. *Fischer und Teichwirt* **38**: 286–288.

Syväranta, J., Cucherousset, J., Kopp, D., Crivelli, A., Céréghino, R. and Santoul, F. (2010). Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. *Aquatic Biology* **8**: 137–144.

Tandon, K.K. and Oliva, O. (1977). The growth of the sheatfish, *Silurus glanis* in Czechoslovakia. *Věstník Československé společnosti zoologické* **41**: 271–282.

Vejřík, L., Vejříková, I., Blabolil, B., Eloranta, A.P., Kočvara, L., Peterka. J., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Kiljunen, M. and Čech, M. (2017a). European catfish *(Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability. *Scientific Reports* **7**: 15970.

Vejřík, L., Vejříková, I., Kočvara, L., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Peterka, J. and Čech, M. (2017b). Thirty- Year-Old Paradigm about Unpalatable Perch Egg Strands Disclaimed by the Freshwater Top- Predator, the European Catfish (*Silurus glanis*). *Plos One* **12**: e0169000.

Vejřík, L., Vejříková, I., Kočvara, L., Blabolil, P., Peterka, J., Sajdlová, Z., Jůza, T., Šmejkal, M., Bartoň, D., Kubečka, J. and Čech, M. (submitted). *The pros and cons of the freshwater apex predator, European catfish Silurus glanis, and angling as a powerful mechanism for its reduction.*

Wasserman, J.R., Alexander, M.E., Dalu, T., Ellender, B.L., Kaiser, H. and Weyl, O.L. (2016). Using functional responses to quantify interaction effects among predators. *Functional Ecology* **30**: 1988–1998.

Wysujack, K., Laude, U., Anwand, K. and Mehner, T. (2001). Stocking, population development and food composition of pike *Esox lucius* in the biomanipulated Feldberger Haussee (Germany) — Implications for fisheries management *Limnologica - Ecology and Management of Inland Waters* **31**: 45–51.

Wysujack, K. and Mehner, T. (2005). Can feeding of European catfish prevent cyprinids from reaching a size refuge? *Ecology of Freshwater Fish* **14**: 87–95.

List of co-authored research papers not included in this Ph.D. Thesis

Blabolil, P., Duras, J., Jůza, T., Kočvara, L., Matěna, J., Muška, M., Říha, M., **Vejřík, L.**, Holubová, M., Peterka, J. (2018) Assessment of burbot *Lota lota* (L. 1758) population sustainability in central European reservoirs. *Journal of Fish Biology,* DOI:10.1111/jfb.13610

Blabolil, P., Čech, M., Jůza, T., Kočvara, L., Matěna, J., Říha, M., **Vejřík, L.**, Peterka, J. (2018) Condition and feeding behaviour of subadult burbot (*Lota lota*) in riverine and lacustrine environments. *Biologia* **73**: 83-91. DOI: 10.2478/s11756-018-0008-7.

Jůza, T., Blabolil, P., Baran, R., Draštík, V., Holubová, M., Kočvara, L., Muška, M., Říha, M., Sajdlová, Z., Šmejkal, M., Tušer, M., Vašek, M., **Vejřík, L.,** Vejříková, I., Wagenvoort, A.J., Žák, J., Ketelaars, H.A.M. (2018) Comparison of two passive methods for sampling invasive round goby (*Neogobius melanostomus*) populations at different depths in artificial lakes. *Fisheries Research*.

Jůza, T., Blabolil, P.,Baran, R., Bartoň D., Čech, M., Draštík V., Frouzová J., Holubová, M., Kočvara, L., Kubečka, J., Muška, M., Prchalová M., Řıíha, M., Sajdlová, Z., Šmejkal, M., Tušer, M., Vašek, M.,**Vejřík, L.**,Vejříková I., Žák, J., Peterka, J. (2017) Collapse of the native ruffe (*Gymnocephalus cernua*) population in the Biesbosch lakes (the Netherlands) owingto round goby (*Neogobius melanostomus*) invasion. *Biological Invasions*. https://doi.org/10.1007/s10530-017-1644-5.

Šmejkal, M., Ricard, D., Sajdlová, Z., Čech, M., **Vejřík, L.**, Blabolil, P., Vejříková, I., Prchalová, M., Vašek, M., Souza, A.T., Brönmark, C., Peterka, J. (2018) Can species-specific prey responses to chemical cues explain prey susceptibility to predation? *Ecology and Evolution*. DOI: 10.1002/ece3.4000.

Žák, J., Jůza, T., Blabolil, P., Baran, R., Bartoň, D., Draštík, V., Frouzová, J., Holubová, M., Laars, H.K., Kočvara, L., Kubečka, J., Mrkvička, T., Muška, M., Říha, M., Sajdlová, Z., Šmejkal, M., Tušer, M., Vašek, M., **Vejřík, L.**, Vejříková, I. (*online first*) Invasive Round Goby (*Neogobius melanostomus*) has sex dependent locomotor activity and is under-represented in catches from passive gear compared to seine catches. *Journal of Fish Biology*. DOI: 10.1111/jfb.13646.

Eloranta, A.P., Vejříková, I., Čech, M., **Vejřík, L.**, Holubová, M., Šmejkal, M., Frouzová, J., Kiljunen, M., Jones, R.I., Peterka, J. (2017) Some like it deep: Intraspecific niche segregation in ruffe (*Gymnocephalus cernua*) *Freshwater Biology* (62), DOI: 10.1111/fwb.12953.

Baran, R., Jůza, T., Tušer, M., Balk, H., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Jayasinghe, A.D., Koliada, I., Mrkvička, T., Muška, M., Ricard, D., Sajdlová, Z., **Vejřík, L**., Kubečka, J. (2017) A novel upward-looking hydroacoustic method for improving pelagic fish surveys. *Scientific Reports* (7), DOI: 10.1038/s41598-017-04953-6.

Blabolil, P., Říha, M., Ricard, D., Peterka, J., Prchalová, M., Vašek, M., Čech, M., Frouzová, J., Jůza, T., Muška, M., Tušer, M., Draštík, V., Sajdlová, Z., Šmejkal, M., **Vejřík, L**., Matěna, J., Boukal, D.S., Ritterbusch, D., Kubečka, J. (2017) A simple fish-based approach to assess the ecological quality of freshwater reservoirs in Central Europe. *Knowledge and Management of Aquatic Ecosystems* (418), 52, 12p.

Šmejkal, M., Ricard, D., **Vejřík, L.**, Mrkvička, T., Vebrová, L. , Baran, R., Blabolil, P., Sajdlová, Z. , Vejříková, I., Prchalová, M. , Kubečka, J. (2017) Seasonal and daily protandry in a cyprinid fish. *Scientific Reports* (7), DOI: 10.1038/s41598-017-04827-x.

Šmejkal, M., Baran, R., Blabolil, P., **Vejřík, L**., Prchalová, M., Bartoň, D., Mrkvička, T., Kubečka, J. (2017) Early life-history predátor-prey reversal in two cyprinid fishes. *Scientific Reports* (7), DOI: 10.1038/s41598-017-07339-w.

Blabolil, P., Boukal, D.S., Ricard, D., Kubečka, J., Říha, M., Vašek, M., Prchalová, M., Čech, M., Frouzová, J., Jůza, T., Muška, M., Tušer, M., Draštík, V., Šmejkal, M., **Vejřík, L**., Peterka, J. (2017) Optimal gillnet sampling design for the estimation of fish community indicators in heterogeneous freshwater ecosystems. *Ecological Indicators* (77), 368–376.

Vašek, M., **Vejřík, L**., Vejříková, I., Šmejkal, M., Baran, R., Muška, M., Kubečka, J., Peterka, J. (2017). Development of non-lethal monitoring of stable isotopes in asp (*Leuciscus aspius*): a comparison of muscle, fin and scale tissues. *Hydrobiologia* (785), 327–335.

Vejříková, I., Eloranta, A.P., **Vejřík, L**., Šmejkal, M., Čech, M., Sajdlová, Z., Holubová, M., Frouzová, J., Kiljunen, M., Peterka, J. (2017) Macrophytes shape individual trophic niche variation among generalist fishes. *PLoS ONE* (12), e0177114.

Vejříková, I., **Vejřík, L**., Syväranta, J., Kiljunen, M., Čech, M., Vašek, M., Sajdlová, Z., Chung, S.H.T., Šmejkal, M., Blabolil, P., Frouzová, J., Peterka, J. (2016) Distribution of herbivorous fish is frozen by low temperature. *Scientific Reports* (6), DOI: 10.1038/srep39600.

Vašek, M., Prchalová, M., Říha, M., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Jůza, T., Kratochvíl, M., Muška, M., Peterka, J., Sajdlová, Z., Šmejkal, M., Tušer, M., **Vejřík, L**., Znachor, P., Mrkvička, T., Seďa, J., Kubečka, J. (2016) Fish community response to the longitudinal environmental gradient in Czech deep-valley reservoirs: Implications for ecological monitoring and management. *Ecological Indicators* (63)**,** 219–230. DOI: 10.1016/j.ecolind.2015.11.061.

Jůza, T., Ricard, D., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Muška, M., Peterka, J., Prchalová, M., Říha, M., Sajdlová, Z., Šmejkal, M., Tušer, M., Vašek, M., **Vejřík, L**., Kubečka, J. (2015) Species-specific gradients of juvenile fish density and size in pelagic areas of temperate reservoirs. *Hydrobiologia* (762), 169–181. DOI: 10.1007/s10750-015-2346-6.

Čech, M., Peterka, J., Říha, M., **Vejřík, L**., Jůza, T., Kratochvíl, M., Draštík, V., Muška, M., Znachor, P., Kubečka, J. (2012) Extremely shallow spawning of perch (Perca fluviatilis L.): the roles of sheltered bays, dense semi-terrestrial vegetation and low visibility in deeper water. *Knowledge and Management of Aquatic Ecosystems* (406), 09p1–09p12.

Čech, M., **Vejřík, L**., Peterka, J., Říha, M., Muška, M., Jůza, T., Draštík, V., Kratochvíl, M., Kubečka, J. (2012) The use of artificial spawning substrates in order to understand the factors influencing the spawning site selection, depth of egg strands deposition and hatching time of perch (*Perca fluviatilis* L.). *Journal of Limnology* (71), 170–179.

Čech, M., **Vejřík, L**. (2011) Winter diet of great cormorant (*Phalacrocorax carbo*) on the River Vltava: estimate of size and species composition and potential for fish stock losses. *Folia Zoologica* (60), 129–142.

In Czech

Vejřík, L., Vejříková, I. (2017) Australský svět ježur a ptakopysků. *Příroda* (9–10) 46–50.

Vejřík, L., Vejříková, I. (2017) Mizející podmořské pralesy. *Rybářství* (5) 94–95**.**

Vejřík, L., Matějíčková, I., Peterka, J., Jůza T. (2016) Makrofyta: nemilovaná, ale užitečná. *Rybářství* (3) 38–43**.**

Vejřík, L., Vejříková, I. (2016) Kliďas od protinožců. *Příroda* (9–10) 20–24.

Vejřík, L., Matějíčková, I. (2015) Mramor v horských peřejích. *Příroda* (7–8) 54–59.

Vejřík, L., Matějíčková, I. (2014) Hojící se jizvy severozápadu Čech. *Moje země* (4) 44–47.

Vejřík, L., Matějíčková, I. (2014) Stane se písmeno M synonymem českého potápění? *Buddy potápění* (4) 24–28.

Vejřík, L., Matějíčková, I. (2013) Historie, současnost a nejistá budoucnost nově vznikajících jezer na našem území – Úvod a jezero Barbora. *Rybářství* (1) 44–47.

Vejřík, L., Peterka, J. (2013) Historie, současnost a nejistá budoucnost nově vznikajících jezer na našem území – Jezero Milada. *Rybářství* (2) 40–43.

Vejřík, L. (2013) Historie, současnost a nejistá budoucnost nově vznikajících jezer na našem území – Jezero Most. *Rybářství* (3) 56–59.

Vejřík, L. (2013) Historie, současnost a nejistá budoucnost nově vznikajících jezer na našem území – Jezera Medard a Michal. *Rybářství* (4) 56–58.

Vejřík, L., Matějíčková, I. (2013) Historie, současnost a nejistá budoucnost nově vznikajících jezer na našem území – Dokončení Limnologie, morfologie a chemicko-fyzikální vlastnosti vod hydrických rekultivací důlních jam. *Rybářství* (5) 56–59.

Vejřík, L. (2013) Proč opomíjená treska tmavá. *Rybářství* (2) 80–82.

Vejřík, L. (2011) Pilkerování není jen prosté tlučení nástrahou o dno. *Rybářství* 8.

Vejřík, L., Čech, M. (2010) Jak je to s potravními zvyklostmi kormoránů v Evropě? *Rybářství* (3) 36–39.

Vejřík, L., Pikrt, M. (2010) Lov tresek v chalupových mělčinách. *Rybářství* 10.

Vejřík, L., Rusňák, Š., Andreska, J. (2009) Potrava kormoránů v Praze aneb od spekulací k faktům. *Rybářství* (3) 52–55.

Chapters in books

Peterka, J., Adámek, Z., Blabolil, P., Bouše, E., Čech, M., Draštík, V., Frouzová, J., Havel, L., Hohausová, E., Jankovský, M., Jarolím, O., Jurajda, P., Jůza, T., Kočvara, L., Kratochvíl, M., Kubečka, J., Muška, M., Prchalová, M., Richta, J., Říha, M., Sajdlová, Z., Soukalová, K., Tušer, M., Uhlířová, A., Uhlíř, F., Vašek, M., **Vejřík, L**., Veselý, L., Vlasák, P. (2012) Ryby nádrže Milada (Fish in the Milada Lake). 92–111. In: Šutera *et al.* (eds.) Příroda nádrže Milada – území po zatopení lomu Chabařovice. Lesnická práce, s.r.o., Kostelec n. Č. L., 207 pp.

Conferences

Oral presentations

Vejřík, L. (2017) Řízení sladkovodních ekosystémů Evropy vrcholovým predátorem, sumcem velkým (*Silurus glanis*), a řízení vrcholového predátora člověkem. 23.–24. 11. 2017, Kostelecké inspirování, Kostelec n. Č. L.

Vejřík, L., Čech, M., Peterka, J. (2017) Ichtyologický výzkum jezera Most a doporučení pro budoucí management – Předpokládaný vliv sportovního rybolovu na rybí obsádku jezera Most: příklad sumce velkého. 15. 11. 2017, Krajský úřad Most.

Vejřík, L., Čech, M., Peterka, J. (2016) Ichtyologický výzkum jezera Milada a doporučení pro budoucí management – Předpokládaný vliv sportovního rybolovu na rybí obsádku jezera Milada: příklad sumce velkého. 22. 11. 2016, Krajský úřad Ústí nad Labem.

Posters

Vejřík, L., Matějíčková, I., Jůza, T., Frouzová, J., Seďa, J., Blabolil, P., Ricard, D., Vašek, M., Kubečka, J., Říha, M., Čech, M. (2016) Small fish use the hypoxic pelagic zone as a refuge from predators. Poster presentation, *Conference Species on the Move*, Hobart, Tasmania.

Vejřík, L., Čech, M., Matějíčková, I., Frouzová, J., Jůza, T., Kubečka, J. (2014) Hypoxic pelagial as a refuge for small fish in freshwater ecosystem. Poster presentation, *Conference Ecology of Fish in Lakes and Reservoirs*, 8–11 September 2014, České Budějovice, Czech Republic. 1st place in Student poster competition.

Matějíčková, I., Peterka, J., Syväranta, J., **Vejřík, L**., Kočvara, L. (2014) Strong effect of macrophytes on fish trophic relationships, example of cyprinids in post-mining lakes (Czech Republic). Ecology of Fish in Lakes and Reservoirs, 8–11 September 2014, České Budějovice, Czech Republic.

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2010–2013 Master degree in Zoology, Faculty of Science, USB (Mgr.)

2010–2012 Master degree in Fisheries, Faculty of Fisheries and Protection of Waters, USB (Ing.)

2006–2010 Bachelor degree in Biology, specialisation: Zoology, Faculty of Science, USB

Working experience

Since 2018 Institute of Hydrobiology, Biology Centre CAS, member of project Biomanipulation as a tool for improving water quality of dam reservoirs, No. CZ.02.1.01/0.0/0.0/16_025/0007417.

Since 2017 Institute of Hydrobiology, Biology Centre CAS, member of project Soil and Water (SoWa) Research Infrastructure funded by MEYS CZ grant LM2015075, programme Projects of Large Infrastructure for Research, Development, and Innovations.

2014–2017 Institute of Hydrobiology, Biology Centre CAS, member of project MacFish supported by Norwegian Financial Mechanism (7F4316). Job description: Quantitative and qualitative surveys of the fish stock of post-mining lakes, analysis of fish fry, fish gut content analyses, fish sex determination, and publication.

Since 2014 Fishery manager in local organization Loket, regional board Plzeň

2013–2014 Institute of Hydrobiology, member of project CEKOPOT (CZ.1.07/2.3.00/20.0204)

2012–2014 Representative of fishery manager in local organization Loket, regional board Plzeň

2011 Member of ichthyologial research of Brabantse Biebosch Reservoir, Netherland

2008 –2013 Part time job in Institute of Hydrobiology, Biology Centre CAS

Teaching and supervision experience

Supervisor of Jindra, T. (2015) Modelování vlivu sportovního rybolovu na populaci sumce velkého na nově vznikajících jezerech po těžbě hnědého uhlí v Podkrušnohoří. Středoškolská odborná činnost (SOČ), Gymnázium, Česká 6, České Budějovice,

Supervisor of Chung, S.H.T. (in prep) Vliv sumce velkého (*Silurus glanis*) na ichtyocenózu oligotrofních jezer podle analýz obsahu žaludků a stabilních isotopů neinvazivními metodami. Bakalářská práce, Jihočeská univerzita v Českých Budějovicích.

Lectures at Faculty of Science at the University of South Bohemia in České Budějovice: Ecology of Aquatic Vertebrates, Practicum in Vertebrate Zoology,

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Biology of predatory fishes in dam reservoirs and lakes

Printed in the Czech Republic by
Edition of 20 copies

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